Anatomical notes and discussion of the first described aetosaur *Stagonolepis robertsoni* (Archosauria: Suchia) from the Upper Triassic of Europe, and the use of plesiomorphies in aetosaur biochronology (#25967)

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Anatomical notes and discussion of the first described aetosaur *Stagonolepis robertsoni* (Archosauria: Suchia) from the Upper Triassic of Europe, and the use of plesiomorphies in aetosaur biochronology

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Stagonolepis robertsoni was the first named aetosaurian from the Late Triassic of Scotland. Known mostly from a series of natural molds from two localities, the osteology of this taxon has been difficult to interpret. Detailed work on this material in the late 1950s resulted in a monograph that set the standard for the understanding of aetosaurians, making *Stagonolepis robertsoni* the best known aetosaurian; however, little has been done with this material since. Reanalysis of this material shows that the despite the limitations of the material, the early 1960s reconstruction work depicts the preserved characteristics faithfully, especially in the skull. The first cervical rib is extremely anteroposteriorly elongate as in *Alligator*, a character not previously recognized in aetosaurians. Diapophyseal and zygapophyseal vertebral laminae are present in the cervical and trunk vertebrae. The ilium is autapomorphic with distinct pre- and post-processes of the iliac blade. The osteoderms differ from North and South American material that has been ascribed to the genus and those assignments are based on plesiomorphies within Aetosauria, such as a radial ornamentation and a posteriorly located and medially offset dorsal eminence. Biostratigraphic correlations using taxonomic conclusions based on plesiomorphic characters should not be used. The holotype specimen of *S. robertsoni* is currently diagnostic in part because ventral osteoderms are not known for many aetosaurian taxa and the surface ornamentation of randomly distributed, closely packed oblong pits found in *S. robertsoni* is unique for Aetosauria.

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ABSTRACT

Stagonolepis robertsoni was the first named aetosaurian from the Late Triassic of Scotland. Known mostly from a series of natural molds from two localities, the osteology of this taxon has been difficult to interpret. Detailed work on this material in the late 1950s resulted in a monograph that set the standard for the understanding of aetosaurians, making *Stagonolepis robertsoni* the best known aetosaurian; however, little has been done with this material since. Reanalysis of this material shows that the despite the limitations of the material, the early 1960s reconstruction work depicts the preserved characteristics faithfully, especially in the skull. The first cervical rib is extremely anteroposteriorly elongate as in *Alligator*, a character not previously recognized in aetosaurians. Diapophyseal and zygapophyseal vertebral laminae are present in the cervical and trunk vertebrae. The ilium is autapomorphic with distinct pre- and post-processes of the iliac blade. The osteoderms differ from North and South American material that has been ascribed to the genus and those assignments are based on plesiomorphies within Aetosauria, such as a radial ornamentation and a posteriorly located and medially offset dorsal eminence. Biostratigraphic correlations using taxonomic conclusions based on plesiomorphic characters should not be used. The holotype specimen of *S. robertsoni* is currently diagnostic in part because ventral osteoderms are not known for many aetosaurian taxa and the surface ornamentation of randomly distributed, closely packed oblong pits found in *S. robertsoni* is unique for Aetosauria.

INTRODUCTION

Aetosaurs are exclusively Late Triassic quadrupedal, heavily armored pseudosuchians known globally with the exception of some parts of Gondwana: South Africa, Antarctica, and Australia. The most recent overview of this clade is by Desojo et al. (2013). The first described aetosaurian fossil was christened *Stagonolepis robertsoni* for a series of ventral osteoderms. Because the unit they were discovered in was thought to be the Devonian 'Old Red Sandstone', these osteoderms were considered to represent a large ganoid fish (Agassiz 1844). Subsequent discoveries (detailed in Walker 1961) demonstrated that these remains belonged instead to a stem pseudosuchian, and that the rocks they were found in were instead more likely Triassic in age (Huxley 1859, 1869; 1875; 1877). The original materials worked on by Louis Agassiz and T.H. Huxley, as well as additional discoveries made in the 1920s and 1930s, were the subject of an extensive monograph (Walker 1961). This work was influential because it finally solidified that aetosaurians were a globally distributed Late Triassic group distinct from phytosaurs.

Although since that time the only material described for *Stagonolepis robertsoni* is a braincase (MCZD 2-4; Gower & Walker 2002), *S. robertsoni* is still considered to be the 'model' aetosaurian (Desojo et al. 2013) and the taxon is featured prominently in phylogenetic analyses (e.g., Parrish 1994; Heckert, Hunt, & Lucas 1996; Heckert & Lucas 1999; Parker 2007; Parker 2016a). However, since 1961 the taxon has never been adequately re-evaluated in terms of the great strides that have been made in our understanding of aetosaurian morphology and systematics, particularly the recognition that armor surface ornament, width-length ratios, and lateral osteoderm morphology are diagnostic to clades, and in some cases, to species (Long & Ballew 1985; Long & Murry 1995; Heckert & Lucas 2000; Parker 2007; Martz & Small 2006). Other named taxa (e.g., *Calyptosuchus wellesi*, *Aetosauroides scagliai*) have been assigned to the genus *Stagonolepis* based on similarity of the dorsal paramedian osteoderm ornamentation (e.g.,

Long and Murry, 1995; Heckert & Lucas 2002); however, these assignments have been questioned by other workers (e.g., Desojo & Ezcurra 2011; Parker 2018).

The purpose of this paper is the reanalyze referred material of *Stagonolepis robertsoni* present at the Natural History Museum, London and evaluate it in recent context based on our current understanding of aetosaurian anatomy. The material is not completely redescribed here as the original descriptions by Walker (1961) and Gower & Walker (2002) are still quite adequate, instead we focus on characteristics whose taxonomic significance was not fully recognized by Walker given the understanding of aetosaurians at the time of his monograph. These newly recognized characteristics are useful for examining the phylogenetic relationships of *S. robertsoni* and other aetosaurians.

MATERIALS

The materials of *Stagonolepis robertsoni* at the Natural History Museum, London that were available to Huxley (1859, 1875, 1877) consist only of a couple of now chipped casts of a left femur (NHMUK R581) and a paramedian osteoderm and phalange (NHMUK R582). The rest of the material are in other institutions such as the Geological Survey Museum, London and the Elgin Museum in Scotland (Walker 1961; Walker undated and unpublished notes at the NHMUK). More prominent materials consist almost entirely of large blocks of a highly indurated sandstone that preserve natural molds of the various bones. Painted casts of these were created in 1885 and presented to the museum by the Reverend George Gordon. These specimens allow study of portions of the bones in two dimensions, and were available for study by Charles Camp in 1935 (Camp unpublished notes at the UCMP, 1935) and Alick Walker in the 1950s (Walker 1961). Walker (1961) also created a series of PVC casts (e.g., NHMUK 4787) from the

original sandstone molds that preserved more detail and allowed for 3D visualization of the bones. These PVC casts are still in the NHMUK collections although many have deteriorated.

For this study the following blocks/specimens were examined and photographed: MCZD2 (5 parts), partial skull and articulated cervical osteoderms; NHMUK R581, cast of left femur; NHMUK R582, cast of paramedian osteoderm and phalange; NHMUK R4784a, cast of slab with basioccipital and associated articulated series of cervical and trunk vertebrae, including the cervical ribs, scapulocoracoid, partial humerus; NHMUK R4785a, cast of slab with osteoderms and ribs; NHMUK R4786a, cast of slab with anterior caudal centra and ribs in articulation, distal end of left tibia; NHMUK R4787; Sandstone block containing natural mold of much of a skull plus associated PVC cast; NHMUK R4787a, cast of specimen showing the lower portion of the left side of a good skull, especially the mandible; NHMUK R4789a, cast of slab with ribs, osteoderms, right ilium, partial maxilla; NHMUK R4790a, cast of slab with osteoderms, right ilium, ischium; NHMUK R4797a, cast with lower limb bones and appendicular osteoderms; NHMUK R4799, sandstone block with impression of an anterior cervical vertebra; NHMUK R8586, cast of EM38R, left side of internal surface of snout (figured by Huxley, 1877); NHMUK R27404, cast of the holotype specimen that consists of a segment of the articulated ventral carapace; NHMUK R36392, sandstone slab with osteoderms, including six articulated left lateral osteoderms; NHMUK R36394; sandstone slab with impressions of articulated ventral osteoderms;

An attempt was made to use the CT scanner at the NHMUK to scan the negative space in block NHMUK R4787 to get a three-dimensional view of the skull, but unfortunately that scanner could not penetrate the hard sandstone matrix of the block.

SYSTEMATIC PALEONTOLOGY

Archosauria Cope 1869 sensu Gauthier & Padian 1985

Pseudosuchia Zittel 1887-1890 sensu Gauthier & Padian 1985

Aetosauria Marsh 1884 sensu Parker 2007

Desmatosuchia sensu Parker 2016a

Stagonolepidinae sensu Heckert & Lucas 2000

***Stagonolepis* Agassiz 1844**

***Stagonolepis robertsoni* Agassiz 1844**

(Figs. 1-7, 9, 11)

1844 *Stagonolepis robertsoni*: Agassiz, p. 139, pl. XXXI, figs. xiii, xiv

1859 *Stagonolepis robertsoni*: Huxley, p. 440, pl. XIV, figs. 1-3

1877 *Stagonolepis robertsoni*: Huxley, p. 1, pl. I-X.

1902 *Staganolepis* [sic] *robertsoni*: Huene, p. 54, figs. 62-67, 72, 73.

1908 *Stagonolepis robertsoni*: Huene, p. 392, figs. 347-348.

1936 *Stagonolepis robertsoni*: Huene, p. 207, fig. 3.

1942 *Stagonolepis robertsoni*: Huene, p. 223, figs. 45-49.

1961 *Stagonolepis robertsoni*: Walker, p. 103, figs. 2-23, 24b, 25b, pl. 9-12.

1976 *Stagonolepis robertsoni*: Krebs, p. 40, figs. 3, 4, 9, 10d, 12, 15, 16, 17c-e, 19d-e, 20d-e, 26b, 27.

1978 *Staganolepis* [sic]: Bonaparte, p. 300, figs. 137b, 138.

1986 *Stagonolepis*: Parrish, p. 8, fig. 6, 14c3.

1988 *Stagonolepis*: Carroll, p. 273, figs. 13.15, 13.16.

1988 *Stagonolepis*: Fraser, p. 132, fig. 5b.

1991 *Stagonolepis*: Sereno, p. 11, fig. 10, 27f.

1996 *Stagonolepis*: Lucas & Heckert, p. 57, fig. 4.

2000 *Stagonolepis robertsoni*: Heckert & Lucas, 2000, p. 1552, figs. 4c, e.

2001 *Stagonolepis robertsoni*: Lucas & Heckert, p. 719, figs. 2, 3.

2002 *Stagonolepis robertsoni*: Gower & Walker, p. 7, figs. 1-4, 6.

2010 *Stagonolepis robertsoni*: Sulej, p. 878, figs. 8a, 9f.

2011 *Stagonolepis robertsoni*: Desojo & Ezcurra, p. 599, figs. 3d-f, 7b.

2013 *Stagonolepis robertsoni*: Desojo et al., p. 207, figs. 3e-f, 4g, 5a-h, 6a-f, 7c-f.

2016a *Stagonolepis robertsoni*: Parker, p. 32, figs. 1, app. B, fig. 11j.

Holotype – ELGNM 27R, impression of a segment of the ventral carapace (Agassiz 1844). NHMUK R27404 is a negative cast of this specimen.

Referred Material – see Materials for a list of NMHUK specimens.

Occurrence – Lossiemouth Sandstone Formation, Morayshire, Scotland, U.K (Walker 1961).

Age – Late Triassic, Late Carnian to Early Norian (Benton & Walker 2010).

Diagnosis – *Stagonolepis robertsoni* is diagnosed by the following autapomorphies: ventral osteoderms rectangular with randomly arranged, oblong pits*; first cervical vertebrae with elongate cervical ribs that extend back to the position of the 4th cervical vertebra*; trunk paramedian osteoderms lack ornament along the posterior edge in the region of the dorsal eminence*; posterior process of iliac blade forms an acute angled tip and the anterior process of the iliac blade is anteroposteriorly short, dorsoventrally thin, and ventrally hooked*; pubis with two obturator foraminae* (convergent in *Scutarx deltatylus*).

Stagonolepis robertsoni can also be distinguished by the following combination of character states: premaxilla with four, possibly five teeth as in "*Stagonolepis*" *olenkae* and *Paratypothorax andressorum* (differs from the three in *Stenomyti huangae* and the absence of premaxillary teeth in *Desmatosuchus smalli*); premaxillary tip expanded laterally as in "*Stagonolepis*" *olenkae*, *Desmatosuchus smalli, and Neoaetosauroides engaeus* (absent in *Aetosaurus ferratus*, *Stenomyti huangae*; *Paratypothorax andressorum*); distinct ridge on lateral side of maxilla beneath antorbital fossa as in *Paratypothorax andressorum* and *Stenomyti huangae* (this ridge is absent in *Desmatosuchus smalli*, *Longosuchus meadei*, *Neoaetosauroides engaeus*, and "*Stagonolepis*" *olenkae*); long axis of the jugal anterodorsally inclined as in *Desmatosuchus spurensis* and *Longosuchus meadei* (the ventral margin of the jugal is level in *Aetosaurus ferratus*, *Paratypothorax andressorum*, and *Stenomyti huangae*); teeth thecodont with a swollen base and non-recurved tip as in *Desmatosuchus smalli* (differs from *Aetosauroides scagliai* and *Aetosaurus ferratus*); parabasisphenoid elongate, with anteroposteriorly separated basal tubera and basipterygoid processes as in *Neoaetosauroides engaeus*, *Aetosaurus ferratus, and Desmatosuchus smalli* (differs from *Scutarx deltatylus*; *Paratypothorax andressorum, Tecovasuchus chatterjeei,* and *Desmatosuchus spurensis*); mandible "slipper-shaped" with ventrolateral portion of splenial visible in lateral view beneath the ventral margin of the dentary as all aetosaurs except for *Aetosauroides scagliai and Typothorax coccinarum*; posterior cervical vertebrae with ventral keel (as in *Aetosauroides scagliai, Calyptosuchus wellesi, Sierritasuchus macalpini,* and *Scutarx deltatylus* (keels absent in *Longosuchus meadei* and *Desmatosuchus spurensis*; trunk paramedian osteoderms with a length/width ratio of about 2.5:1 as in *Desmatosuchus spurensis*, *Longosuchus meadei*, and *Aetobarbakinoides brasiliensis* (differs from the much wider paramedians of *Typothorax*

coccinarum and *Paratypothorax andressorum*); raised anterior bar on osteoderms as in all non-desmatosuchin aetosaurs; anteromedial and anterolateral projections of the anterior bar present on the trunk osteoderms as in all non-desmatosuchin aetosaurs; anterolateral projection of the anterior bar not elongate as in "*Stagonolepis*" *olenkae*, *Aetosaurus ferratus*, and *Typothorax coccinarum* (differs from *Adamanasuchus eisenhardtae* and *Scutarx deltatylus*); dorsal eminence of trunk paramedian osteoderms situated on the posterior osteoderm margin and offset medially (as in most aetosaurs except *Desmatosuchus* and *Paratypothorax andressorum*); dorsal surface ornament of the paramedian and lateral osteoderms anastomosing (interconnected series of radiating ridges surrounding subrounded and subrectangular pits); lateral osteoderms are nearly equant with distinct lateral and dorsal flanges as in all non-desmatosuchin aetosaurs; lateral osteoderms lack pronounced horns or spines as in most aetosaurs outside of Typothoracisinae and Desmatosuchini.

DESCRIPTION

Skull

Block NHMUK R4787a is a cast of the lower portion of a skull in semi-articulation including much of the lower jaw, quadrate, portions of the palate and maxilla, and the premaxilla (Figure 1A). These elements represent the left side of the skull, so the cast provides an internal (medial) view. The semi-articulated condition allows for the determination of the skull length, which from the retroarticular process to the tip of the premaxilla is about 240 mm. The dentigerous elements show the presence of at least eight dentary, four maxillary, and four premaxillary teeth. Alick Walker's PVC cast of this specimen shows even more details (Figure 1B) including the upper portions of the skull and the braincase, especially the parabasisphenoid. Thus block NHMUK R4787 is the natural mold of a nearly complete skull of *Stagonolepis robertsoni* (Walker 1961).

Details of this specimen include: 1) a possible 5th premaxillary tooth crown, or alternatively the tip of the right premaxilla in articulation with the left; 2) a portion of the right squamosal and impressions of the skull roof, 3) the left quadrate in articulation with the left articular, and 4) impressions of the braincase, especially the basisphenoid including the left and right basitubera and basipterygoid processes, and the cultriform process is also preserved.

A cast of the right maxilla from NHMUK R4787 (Figure 2) shows that overall the element is more slender than that of "*Stagonolepis*" *olenkae* (Sulej 2010) with at least six alveoli, but the anterior portion is covered. A very distinct transverse ridge is present on the lateral surface along the anterior and ventral borders of the antorbital fossa, making the fossa extremely pronounced; this ridge also occurs in *Stenomyti huangae* (Small and Martz, 2013) and *Paratypothorax andressorum* (Schoch and Desojo, 2016), but is not present in "*Stagonolepis*" *olenkae* (Sulej 2010), *Desmatosuchus* (Case, 1922; Small, 2002), *Longosuchus* (Parrish, 1994), or *Neoaetesauroides* (Desojo and Báez, 2007). The medial side of the maxillary body is marked by an elongate medial shelf that articulates with the palatal bones (Walker 1961). The articulations with the lacrimal and jugal are each complex, with regions of overlap between the two bones; this is also the case at least in *Longosuchus meadei* (J. Martz, unpublished notes), but this region is rarely found sufficiently disarticulated in aetosaurs to establish the relationships between these elements. Finally, a pneumatic accessory cavity is present on the medial size of the ascending process as described for *Desmatosuchus smalli* (Small 2002).

NHMUK R8586 is a cast of ELGNM 38R (Figure 3), which was figured by Huxley (1877) and features the left side of the internal portion of the snout, including the premaxilla, maxilla, and nasals. The premaxilla measures 63 mm in length, bears four teeth with an edentulous anterior portion typical for aetosaurians; four or more teeth also occur in *Aetosaurus*

ferratus (Schoch, 2007) "*Stagonolepis*" *olenkae* (Sulej, 2010), and *Paratypothorax andressorum* (Schoch and Desojo, 2016), whereas *Stenomyti huangae* only possesses three (Small and Martz, 2013), and *Desmatosuchus* lacks any (Small, 2002). The maxilla bears six teeth as preserved, but it is missing the posterior portion. The external naris is 22 mm at its deepest point and 72 mm in length, but missing the posteriormost section. The nasal has a pronounced ridge on the medial edge, which at a position just dorsal to the 3rd premaxillary tooth migrates ventrally to the ventral margin of the nasal where it contacts the premaxilla. The anterior tip of the premaxilla bears a prominent ridge that divides the element into a flat surface that slopes into the external naris, and a second triangular area that slopes anteroventrally (Figure 3). This ridge is the anterior expansion and also occurs in other aetosaurians such as *Desmatosuchus smalli* (Small 2002), *Neoaetosauroides engaeus* (PVL 4363), and differs from aetosaurians such as *Aetosaurus ferratus* (Schoch 2007); *Aetosauroides scagliai* (PVL 2073), and *Typothorax coccinarum* (YPM 58121). The premaxilla bears a small dorsal protuberance above the first tooth position that extends dorsally into the external naris, which also occurs in "*Stagonolepis*" *olenkae* (Sulej 2010) and *Desmatosuchus smalli* (Small 2002); however, in "*S*". *olenkae* it is dorsal to the second tooth position (Antczak 2016) and *D. smalli* has an edentulous premaxilla (Small 2002). There is only a slight swelling in this position in *Stenomyti huangae* (Small and Martz, 2013).

The best-preserved skull material is MCZD 2, which consists of seven small blocks that fit together to present much of the skull and the anterior section of the neck (Walker 1961:figs. 26-29; Gower & Walker 2002:fig. 1). The material consists of well-preserved bone and is not a natural mold as is most of the *S. robertsoni* material. This specimen has previously been described in great detail so this will not be duplicated here (Walker 1961; Gower & Walker 2002). However, notable is that the basitubera and basipterygoid processes are widely separated

anteroposteriorly from each other so that the parabasisphenoid is elongate supporting what can be observed in NHMUK R4787. *Neoaetosauroides engaeus* (PVL 5698; Desojo & Báez 2007), *Aetosaurus ferratus* (Schoch 2007) and the basal taxon *Aetosauroides scagliai* (PVSJ 326) also have an elongate parabasisphenoid so that is the plesiomorphic state within Aetosauria. This differs significantly from the condition in "*S*". *olenkae*, where the basitubera and basipterygoid processes nearly contact (Sulej, 2010: figs. 1d, f) and thus the parabasisphenoid is anteroposteriorly short. In *Scutarx deltatylus* (Parker, 2016b: fig. 7) and *Desmatosuchus spurensis* (UMMP 7476) the parabasisphenoid is also anteroposteriorly short; whereas the condition in *Calyptosuchus wellesi* is unknown (Parker 2018).

Cervical vertebrae and ribs

In block NHMUK R4784a, which is a cast created from a natural mold and represents the postcranial skeleton of the skull NHMUK R4787 (Walker 1961), the occipital condyle and left paroccipital process of the skull are present (Figure 4A). If the cervical count is nine (as in *Desmatosuchus spurensis*), the four anterior cervicals are missing (including the axis and atlas); however, cervical ribs are present for three of these positions. Very striking are two very elongate posteriorly projecting cervical ribs underlying the ventral surfaces of the two more posteriorly positioned ribs (Figure 4A). The elongate ribs (left and right sides) originate where the axis/atlas would be located and are very similar to the greatly elongate cervical ribs found in *Alligator* (Reese 1915). As exposed these ribs measure 85mm in length (the ends are covered), more than three times the lengths of the other exposed cervical ribs. The elongate ribs were not noted by Walker (1961) and have not previously been described for any aetosaur. The axis/atlas and third cervical are present in MCZD 2, but unfortunately are very poorly preserved; however, this block also preserves a very elongate first cervical rib.

The first well-preserved cervical vertebra in NHMUK R4784a is the 8th (Walker 1961), which is visible in right lateral view and preserves details of the centrum and much of the neural arch and transverse process (Figure 4B). A disarticulated cervical rib is present across the centrum and probably does not belong to this vertebra. The centrum measures 25 mm in length and the ventral surface is strongly keeled. Keels occur on the ventral surface of the cervical vertebrae in *Aetosauroides* (Desojo and Ezcurra, 2011) and *Scutarx* (Parker 2016) while the ventral surface of the cervicals lacks keels in *Longosuchus* (Long and Murry, 1995) and *Desmatosuchus* (Case, 1922; Parker, 2018). The condition may be variable in *Typothorax*; ventral keels are absent in the cervicals of the small specimen described by Martz (2002) but present in at least some larger specimens (Heckert et al., 2010), suggesting there may be allometric or ontogenetic variability. The parapophysis in the 8th cervical of NHMUK R4784a is low on the anterior rim of the centrum, but not completely at the base. The transverse process projects laterally and slightly ventrally, is 25 mm long, and bears a flaring sub-rectangular head in lateral view. A distinct posterior centrodiapophyseal lamina (Wilson 1999) stretches from the base of the transverse process to the posterior portion of the neurocentral suture. This is the "T-beam" structure described by Case (1922) for the posterior cervical and dorsal vertebrae of *Desmatosuchus spurensis* and described as present in *Stagonolepis robertsoni* (Walker, 1961) and *Typothorax* (Martz, 2002) and also occurs in *Paratypothorax* (Martz et al., 2013, fig. 9D). The right prezygapophysis is present but not enough is present to tell if a hyposphene was present. The neural spine is present, but missing the apex.

The next three vertebrae are preserved in articulation (Figure 4B). The parapophysis on the 9th cervical is still situated on the centrum, but slightly higher than its position in the preceding vertebra. The centrum is more elongate as well measuring 31 mm. Pre- and

postzygadiapophyseal laminae (Wilson 1999) are visible on the 9th and 10th presacrals (Figure 4B). The 10th presacral is transitional between the cervical and dorsal series as previously described for *Desmatosuchus spurensis* (Case 1922; Parker 2008). The centrum is more elongate than the previous vertebra with a length of 36mm. However, there is still a slight ventral keel as in the other cervicals, and although the parapophysis has migrated upwards onto the base of the neural arch, it is not located on the arch itself as in the dorsal vertebrae. The neurocentral suture appears to be open.

The 11th presacral is the first true dorsal vertebra as the parapophysis would now situated on the posteroventral surface of the transverse process, unfortunately this can't be seen clearly as it is broken away (Walker 1961:fig. 7i). The centrum has a length of 39 mm and is unkeeled. The 12th presacral is present, but covered by broken ribs. The cervical and trunk vertebrae of *S. robertsoni* lack oval depressions on the lateral sides just below the neurocentral sutures as in *Aetosauroides scagliai* (Desojo & Ezcurra 2011).

Caudal Vertebrae

NHMUK R4799b is a PVC cast of an isolated anterior caudal vertebra providing more details of the neural arch and spine (Walker 1961: figs. 10c-e). The broad transverse processes (left equals 79 mm) do not extend ventral to the base of the centrum; the postzygapophyses are oriented at 45 degrees above horizontal. The centrum is blocky, with equant width and height of about 40 mm, but the entire vertebral height is 112 mm, with the neural spine contributing 40 mm to this measurement. Spinopostzygapophyseal laminae (Wilson 1999) are present, as is the expanded neural spine table.

Osteoderms

Numerous osteoderms of *Stagonolepis robertsoni* are preserved as natural molds; however, often they only produce partial casts. Walker (1961) discussed the osteoderms in what we now consider superficial terms, therefore we redescribe one each of the best preserved dorsal paramedian and lateral osteoderms. The dorsal trunk paramedian osteoderm (NHMUK 4790a; Figure 5A) is from the left side and has a surface patterning of what we call anastomosing, an interlaced network of high ridges surrounding circular and elongate pits closer to the posterior plate margin, and elongate, but irregular grooves on the anterior portion of the osteoderm. This is similar to the pattern in *Aetosaurus ferratus*, *Aetosauroides scagliai*, *Neoaetosauroides engaeus*, "*Stagonolepis*" *olenkae*, and *Paratypothorax andressorum* in that the ornamentation is non-radial posteromedially, but elongate and radial anteriorly along the full length of the anterior bar. However, in *S. robertsoni*, the ornamentation on the posterolateral region of the paramedians is distinctly non-radial and faint to absent along the entire posterior margin, whereas in the other taxa the paramedians possess very elongate grooves in the posterolateral portion of the paramedian osteoderm that are nearly parallel to the posterior margin.

This anastomosing ornamentation in *S. robertsoni* radiates from an elongate, but narrow, raised dorsal eminence that contacts the posterior osteoderm margin as in most non-desmatosuchine taxa that possess an eminence; in desmatosuchines, the eminence often contacts the posterior margin (Parker, 2018; Parker and Martz, 2010). This eminence is rounded rather than distinctly pyramidal as in *Typothorax* (Martz, 2002) and *Longosuchus* (Parker and Martz, 2010), and offset slightly medial to the center of the osteoderm as in nearly all aetosaur trunk paramedians. The anterior portion of the osteoderm bears a raised, transverse, smooth strip of bone called the anterior bar (Long & Ballew 1985) that bears anterolateral projection and anteromedial projections as in most non-desmatosuchine aetosaurs. The anterior bar maintains an

even width across the lateral portion of the osteoderm, but thins significantly medially before expanding again at the anteromedial projection. We term this distinct medial thinning, 'scalloping' (Parker, 2016b). This feature occurs in several other aetosaurians including *Aetosauroides scagliai* (PVL 2073); *Calyptosuchus wellesi* (UCMP 126844; Parker 2018), *Scutarx deltatylus* (Parker 2016b), and *Paratypothorax andressorum* (SMNS 5721; unpublished data). The medial edge is straight and the lateral edge slightly sinuous in dorsal view. In posterior view the osteoderm is moderately flexed.

The lateral trunk osteoderm (NHMUK 4789a; Figure 5B) is from the right side based on the presence of a distinct beveling of the anteromedial corner of the anterior bar, which represents an articulation surface for the anterolateral process of the adjacent paramedian osteoderm. The bar is thin but stretches across the entire anterior margin of the osteoderm. The osteoderm is trapezoidal in dorsolateral view and a ridge-like dorsal eminence that contacts the posterior margin divides the osteoderm into distinct dorsal and lateral flanges. The dorsal flange is roughly trapezoidal in dorsal view, whereas the lateral flange is slightly larger and sub-rectangular in dorsolateral view. The surface ornamentation is anastomosing and very faint in the posterior portion of the osteoderm, as seen in the paramedian. The osteoderm is slightly flexed ventrally and the angle between the two flanges is obtuse. In dorsolateral view the lateral margin is gently rounded. The medial margin is angled posteromedially, corresponding with the shape of the adjacent paramedian osteoderm.

The ventral osteoderms (NHMUK R27404 [negative cast of holotype ELGNM 27R]; NHMUK R4789a; Figure 6A, B) are rectangular in dimension, bear an anterior bar, and possess an ornamentation of randomly arranged oblong pits, the 'drops' which Agassiz (1844) used to formulate the genus name. These differ from what is seen in *Calyptosuchus wellesi* (UCMP

27225; Parker 2018), *Aetosauroides scagliai* (MCP13-a-b-PV; Desojo & Ezcurra 2013), and *Typothorax coccinarum* (Martz, 2002; Heckert et al. 2010). These taxa also have rectangular ventral osteoderms, but the ornamentation arrangement is more radial and consists of very elongate furrows and ridges, even in *Typothorax*, where paramedian osteoderm ornamentation is distinctly pitted. *Coahomasuchus kahleorum* (Heckert & Lucas 1999) and *Aetosaurus ferratus* (Schoch 2007) preserve more equant, overlapping ventral osteoderms; but the surface ornament on these specimens is poorly preserved and difficult to comprehend. Where they are preserved; however, they appear to consist of finer pits, less densely packed, but nonetheless have a strong radial distribution as in *Coahomasuchus chathamensis* (Heckert, Fraser & Schneider 2017) and the previous taxa. The ventral osteoderms of *S. robertsoni* also differ from *Stenomyti huangae* where the osteoderms are subrounded rather than square and broadly separated rather than overlapping (Small & Martz 2013).

Ilium

Described in detail by Walker (1961) the ilium of *Stagonolepis robertsoni* is autapomorphic. The shapes and sizes of the processes of the iliac blade are particularly diagnostic for aetosaurian taxa. *S. robertsoni* possesses an elongate postacetabular blade that ends in an acute angled end in medial view (Figure 7). Most other aetosaurians have a squared-off end of the postacetabular blade such as *Aetosauroides scagliai* (PVSJ 326; PVL 2073), *Calyptosuchus wellesi* (UCMP 32422), *Longosuchus meadei* (TMM 31185-40) and *Neoaetosauroides engaeus* (PVL 3525). *Typothorax coccinarum* (UMCP 35255) has a postacetabular blade that has a squared off end and is very short, barely extending past the posterior edge of the ischiadic peduncle.

397 The preacetabular blade of *S. robertsoni* differs from almost all aetosaurians in that it is
398 very short (does not extend to the anterior margin of the public peduncle, very narrow, and
399 ventrally hooked (Figure 7). Most aetosaurians have preacetabular blades that extend anteriorly
400 to the edge of the pubic peduncle, and a thick and triangular in lateral view, such as
401 *Aetosauroides scagliai* (PVL 2073), *Desmatosuchus spurensis* (UMMP 7476), and
402 *Calyptosuchus wellesi* (UCMP 32422). *Neoaetosauroides engaeus* (PVL 3525) and *Typothorax*
403 *coccinarum* (UCMP 35255) both have thin preacetabular blades and the element in *T.*
404 *coccinarum* is very strongly hooked ventrally; however, in both taxa the postacetabular blades
405 are much more elongate than in *S. robertsoni*, even extending past the anterior margin of the
406 public peduncle.
407 Two ilia similar to that of S. robertsoni are TMM-31100-1 and UMMP 7322. TMM-
408 31100-1, assigned to *Lucasuchus hunti* by Long & Murry (1995) has the elongate and acute
409 angled tip of the postacetabular blade, as well as a narrower and slightly ventrally hooked
410 preacetabular blade; however, the preacetabular blade is more anteroposteriorly elongate than
411 that of *S. robertsoni* extending to the margin of the pubic peduncle. UMMP 7322, referred to
412 *Desmatosuchus spurensi*s by Long & Murry (1995) also has an acutely angled postacetabular
413 blade end and a relatively narrow and slightly ventrally hooked preacetabular blade, but again
414 the preacetabular blade is more elongate, in this case extending slightly anterior to the anterior
415 margin of the public peduncle.
416 Overall the ilium most resembles that of *Aetosaurus ferratus* (Schoch, 2007) with a
417 short, narrow and ventrally hooked preacetabular blade, but the posterior acetabular blade end is
418 not as acutely angled in medial view.
419 *Pubis*

An odd characteristic of the pubis of *Stagonolepis robertsoni* is the presence of two large pubic foramina, the uppermost which represents the obturator foramen (Walker 1961). This was unique until the discovery of the same feature in the pubis of *Scutarx deltatylus* (Parker 2016b). The pubis is poorly known in many aetosaurs; however, *Desmatosuchus spurensis* (MNA V9300) has only a single opening.

PHYLOGENY

The most inclusive recent phylogenetic analysis of the Aetosauria is that of Parker (2016a). That study is the only analysis to include both species of *Stagonolepis* (*S. robertsoni*; "*S*". *olenkae*), and tests the relationships of other species that have historically been considered to belong to *Stagonolepis* (*Calyptosuchus wellesi*; *Aetosauroides scagliai*) (Heckert & Lucas 1999, 2000, 2002). That analysis analyzed relationships between 26 in-group taxa utilizing 83 characters (Parker 2016a). *Stagonolepis robertsoni* is recovered in a clade (Stagonolepidinae with *Polesinesuchus aurelioi*) within Desmatosuchia and as the sister taxon to Desmatosuchinae (Figure 8). "*Stagonolepis*" *olenkae* and *Calyptosuchus wellesi* are recovered within Desmatosuchinae, whereas *Aetosauroides scagliai* is recovered outside of Stagonolepididae as in other recent studies (Desojo et al. 2012; Heckert et al. 2015).

Stagonolepis sensu Sulej (2010) is found to be paraphyletic, with *S. robertsoni* and *Polesinosuchus* forming a sister clade to "*S*". *olenkae* and all other desmatosuchines. The previous published differences between *S. robertsoni* and "*S*". *olenkae* all appear to be in the cranium (Sulej 2010; Antczak 2016; Parker 2016a); however, many sections of the published description of the skull of "*S*". *olenkae* (Sulej 2010) are nearly verbatim to those published by Walker (1961) for *S. robertsoni*, so it is difficult to determine what material is actually being described in the Sulej paper.

Antczak (2016) used newly referred material from the Krasiejów quarry to hypothesize that that the two taxa may be conspecific, with some of the cranial differences between *S. robertsoni* and "*S*". *olenkae* representing individual variation. Further support for this hypothesis was cited by Antczak (2016) as coming from the postcranial analysis of "*S*". *olenkae* by Lucas, Spielmann & Hunt (2007) who also argued that "*S*". *olenkae* was a synonym of *S. robertsoni*. However, this synonymy is based on plesiomorphies and not a detailed determination of apomorphies in the material. Moreover, the findings of Antczak (2016) suggest that the skull roof (ZPAL AbIII/466/17) proposed by Sulej (2010) may not serve adequately as a holotype for *S. olenkae*, making comparisons between the two taxa problematic

Comparison of the paramedian osteoderms of the two taxa demonstrate that although both have similar width/length ratios, and anterior bars, and radial patterning, the patterning is quite distinct with that of "*S*". *olenkae* consisting of more closely packed elongate ridges and grooves (Figure 9). Nonetheless, this comparison is based on a single published osteoderm of "*S*". *olenkae* (Lucas, Spielmann & Hunt 2007:fig. 4a) and more osteoderm material is needed to further support any proposed differences. Thus, a full description of the postcrania and osteoderms of "*S*". *olenkae* is required to further examine potential differences between these two species.

Another recent phylogenetic analysis (Figure 10; Hoffman, Heckert & Zanno 2018) of the Aetosauria that also builds on progressive analyses from Heckert & Lucas (1999), Parker (2007), Desojo, Ezcurra & Kischlat (2012), Heckert et al (2015), and Schoch & Desojo (2016), but does not include all currently known taxa (e.g., "*Stagonolepis*" *olenkae*) also recovers *S. robertsoni* in Stagonolepidinae as the sister taxon to Desmatosuchinae (=Desmatosuchini of Parker 2016a). Interestingly with the exclusion of "*S*". *olenkae* from the analysis, the sister taxon

467 to *S. robertsoni* is *Calyptosuchus* (*Stagonolepis*) *wellesi*. Thus presently there is strong
468 agreement between the phylogenetic position of *S. robertsoni* in these studies as more closely
469 related to Desmatosuchinae than to Typothoracinae (Figures 7, 9; Parker 2016a; Hoffman,
470 Heckert & Zanno 2018).

471 **DISCUSSION**

472 The first formal diagnosis of *S. robertsoni* (Heckert & Lucas 2000:1556) was based on
473 plesiomorphies that do not even comprise a unique combination of characters within Aetosauria
474 and was intended to only diagnose the genus. This conservative assessment of the taxon has
475 allowed other specimens (e.g., *Aetosauroides scagliai*, *Calyptosuchus wellesi*) from other areas
476 (North and South America) to be easily assigned to the genus, mainly for the purpose of building
477 a global terrestrial vertebrate biostratigraphy for the Upper Triassic (e.g., Lucas & Heckert 1996;
478 Heckert & Lucas 1999, 2000, 2002; Lucas, Spielmann, & Hunt 2007; Lucas 2017). However,
479 detailed comparison demonstrates that these taxa all bear unique combinations of characters that
480 allow them to be differentiated (e.g., Desojo & Ezcurra 2011; Parker 2018). Assignment of
481 specimens to genera can be subjective and based upon the taxonomic philosophy of the
482 researcher. We have argued elsewhere (Parker 2018) that utilizing monotypic genera in
483 aetosaurian work can aid in removing some of the ambiguity regarding use of these taxa in
484 broader scale studies where genera are often used as a proxy for species. Diagnoses should be
485 apomorphy based, at the species level, or provide unique combinations of characters. Thus it is
486 important that holotype specimens be reexamined utilizing discrete apomorphies in a
487 phylogenetic context (Nesbitt, Irmis & Parker 2007; Irmis et al. 2007; Nesbitt & Stocker 2008).

488 This is especially true when taxa are being utilized for intercontinental biostratigraphic
489 correlations (Irmis et al. 2010). For another example of how taxa may be lumped based on

plesiomorphies for biostratigraphic convenience, a recent discussion on global biostratigraphy for the Late Triassic proposes a new hypothesis that *Neoaetosauroides engaeus* is a junior subjective synonym of *Aetosaurus ferratus* (Lucas 2017). Support is given based on the width/length ratios and ornamentation patterns of the paramedian osteoderms (both symplesiomorphies for Aetosauria based on their presence in the non-stagonolepidid *Aetosauroides scagliai*) as well as an interpretation of similar sutural patterns of the skull based on published figures (Lucas 2017:369). However, this interpretation ignores several key characters such as the presence of a laterally expanded premaxillary tip in *Neoaetosauroides engaeus* (Desojo & Báez 2007), which is apomorphic for Aetosauria (Parker 2016a; Hoffman, Heckert & Zanno 2018) and absent in *Aetosaurus ferratus* (Schoch 2007) as well as *Aetosauroides scagliai*, which polarizes the character distribution. Among other character differences with *A. ferratus*, *N. engaeus*, also lacks a well-developed antorbital fossa. Thus, synonomy between the two taxa is based on overall general similarity and symplesiomorphy rather than discrete synapomorphies, and currently unsupported. The practice of using plesiomorphic characters to assign specimens and to synonymize taxa has long been out of favor in vertebrate paleontology and should no longer be acceptable (e.g., Sereno 1990; Padian, Lindberg & Polly 1994; see further discussion in Nesbitt & Stocker 2008). Data that utilize this approach should be strongly suspect and not used for broader scale studies until the synapomorphy distributions among included taxa are fully evaluated and supported.

Status of the holotype of *Stagonolepis robertsoni* Agassiz, 1844

The holotype of *Stagonolepis robertsoni* is the impression of a fragment of the ventral carapace of a single specimen (ELGNM 27R) that shows several partial rows and columns of imbricated predominantly rectangular osteoderms (Figure 11; Huxley 1877:pl.1, fig. 1). These

osteoderms have an anterior bar and a surface pattern of numerous drop shaped pits radiating from the osteoderm center; hence the name *Stagonolepis*, which means "drop scale". Since the initial descriptions by Huxley (1877) and Walker (1961) subsequent authors have assigned other species to *Stagonolepis robertsoni* based on similarities of the dorsal paramedian osteoderms (e.g., Murry & Long 1989; Long & Murry 1995; Lucas & Heckert 2001; Heckert & Lucas 2002; Lucas et al. 2007b). However, none of these authors have addressed the diagnostic status of the type specimen.

Ventral osteoderms are known from several other aetosaurian taxa including *Coahomasuchus kahleorum*, *Calyptosuchus wellesi*, *Scutarx deltatylus*, *Aetosaurus ferratus*, and even the non-aetosaurian *Revueltosaurus callenderi*. However, as described above presently the ornamentation in the ventral osteoderms of the holotype specimen (ELGNM 27R) of *S. robertsoni* differs from that of other aetosaurians in that it consists of randomly arranged oblong pits separated by a latticework of thin ridges. These pits are tightly packed and cover the majority of the osteoderm surface. This differs from what is seen in other aetosaurian taxa where the ornamentation consists of narrow grooves and oblong pits radiating from a central point on the osteoderm. Presently *Stagonolepis robertsoni* is currently valid based on this character as well as the unique combination of characters listed and discussed above.

CONCLUSIONS

Stagonolepis robertsoni is the oldest named aetosaurian and as such has long served as the standard for aetosaurian osteology. Despite this status the material is difficult to work with because of its preservation and because the only sites where *S. robertsoni* fossils have been recovered are no longer active. However, the holotype specimen, although fragmentary, is

presently diagnostic and Walker's (1961) description is extremely faithful to the existing material and still serves as the basis for our understanding of this taxon.

In this contribution we redescribe and note several features that have recently become important characters for the purpose of comparing aetosaurians taxonomically and phylogenetically. *S. robertsoni* has a paramedian osteoderm morphology that bears a unique combination of characters including a raised anterior bar with anteromedial, anterior, and anterolateral processes (projections), a 'scalloped' anterior edge of the anterior bar medial to the anterior process, a short anterolateral process, a posteriorly placed, pyramidal dorsal eminence, and an anastomosing pattern of pits and grooves radiating from the eminence that lacks elongate nearly parallel grooves. Furthermore, the posterior portion of the paramedian osteoderms are devoid of ornament. *S. robertsoni* is also the only aetosaurian to preserve and extremely elongate first cervical rib, which possibly is an autapomorphy of the taxon. Posterior cervical vertebrae are keeled ventrally and bear diapophyseal and zygapophyseal laminae. The parabasisphenoid is anteroposteriorly elongate with significant separation between the basitubera and the basipterygoid processes. The ventral osteoderms have an autapomorphic ornamentation.

These characters serve to differentiate *S. robertsoni* from all other aetosaurs include those who are or have been historically assigned to the same genus including "*Stagonolepis*" *olenkae*, *Calyptosuchus wellesi*, and *Aetosauroides scagliai*. These assignments were made based on general similarity and symplesiomorphies rather than synapomorphies, a practice that is widely discouraged in vertebrate paleontology.

INSTITUTIONAL ABBREVIATIONS

ELGNM Elgin Museum; Elgin, Scotland

MCP Museo de Ciencias e Tecnología, Porto Alegre, Brazil

559 **MACN** Museo Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos
560 Aires, Argentina;
561 **MCZD** Marischal College, Zoology Department, Aberdeen, Scotland
562 **MNA** Museum of Northern Arizona, Flagstaff, Arizona, USA
563 **NHMUK** Natural History Museum, United Kingdom
564 **PEFO** Petrified Forest National Park, Petrified Forest, Arizona, USA
565 **PVL** Paleontología de Vertebrados, Instituto "Miguel Lillo," San Miguel de Tucumán,
566 Argentina
567 **PVSJ** División de Paleontologia de Vertebrados del Museo de Ciencias Naturales y
568 Universidad Nacional de San Juan, San Juan, Argentina
569 **TMM** Texas Vertebrate Paleontology Collections, University of Texas, Austin, Texas,
570 USA
571 **UCMP** University of California Museum of Paleontology, Berkeley, CA, USA
572 **UMMP** University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA
573 **YPM** Yale Peabody Museum of Natural History, New Haven, Connecticut, USA
574 **ZPAL** Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland
575

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585
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760

761 **FIGURES**
762
763 Figure 1. Casts of bones of *Stagonolepis robertsoni*. A) NHMUK R4787a, 1885 cast which
764 represents much of the lower portion of a skull. B) NHMUK R4787, PVC cast of the same

765 specimen that shows more details of the braincase and dorsal portion of the skull. Scale bars
766 equal 1 cm. Abbreviations: **an**, angular; **art**, articular; **bpt**, basipterygoid process; **bs**,
767 parabasisphenoid; **bt**, basal tuber; **d**, dentary; **fr**, frontals; **l**, left; mx, maxilla; **mpr**, area of the
768 medial pharyngeal recess; **pa**, parietal; **pmx**, premaxilla; **pra**, prearticular; **pro**, prootic; **pt**,
769 pterygoid; **qu**, quadrate; r, right; **sa**, surangular. Elements from the left side have a prefix of **l.**;
770 elements of the right side have a prefix of **r.**.
771
772 Figure 2. NHMUK R4787, cast of a right maxilla of *Stagonolepis robertsoni* in lateral A) and
773 medial B) views. Scale bar equals 1 cm. Abbreviations: **a.**,articulation with listed element; **alv**,
774 alveoli; **aof**, antorbital fenestra; **ap.m**, ascending process of the maxilla; **ju**, jugal; **la**, lacrimal;
775 **ms**, medial shelf; **na**, nasal; **pac**, pneumatic accessory cavity; **pmx**, premaxilla; **tr**, transverse
776 ridge.
777
778 Figure 3. Cast of the anterior part of the right side of the skull of *Stagonolepis robertsoni* in
779 lateral view. Scale bar equals 1 cm. Abbreviations: **en**, external naris; **mx**, maxilla; **na**, nasal; **nr**,
780 nasal ridge; **pmr**, premaxillary ridge; **pmx**, premaxilla.
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782 Figure 4. NHMUK 4784a, casts of articulated sections of the presacral vertebral column in
783 lateral view including the rear of the skull through the fourth cervical position (A), and the
784 seventh through the twelfth presacral vertebrae (B). Scale bars equal 1 cm. Abbreviations: **cvr**,
785 cervical rib; **k**, ventral keel; **oc**, occipital condyle of the basicranium; **parp**, parapophysis; **pcdl**,
786 posterior centrodiapophyseal lamina.
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Figure 5. Casts of osteoderms of *Stagonolepis robertsoni*. A, left dorsal trunk paramedian (NHMUK R4790a) in dorsal view; B, right dorsal trunk lateral (NHMUK R4789a) in dorsolateral view. Scale bar equals 1 cm. Abbreviations: **a.**, articulation with listed element; **ab**, anterior bar; **alp**, anterolateral projection; **amp**, anteromedial projection; **de**, dorsal eminence; **df**, dorsal flange; **lf**, lateral flange; **sc**, scalloping of anterior bar margin.

Figure 6. Ventral osteoderms of *Stagonolepis robertsoni*. A) close-up of NHMUK R27404 (positive cast of EM 27R, the holotype specimen of *Stagonolepis robertsoni* Agassiz 1844) in ventrolateral view showing the detail of the overlapping osteoderms; B) NHMUK R4787a, referred ventral osteoderm in ventral view.

Figure 7. NHMUK R4789. Cast of medial side of right ilium in medial view. Scale bar = 2 cm. Abbreviations: **arsr2**, articulation for sacral rib 2; **ip**, ischiadic peduncle; **ost**, osteoderm; **poab**, postacetabular blade; **pp**, pubic peduncle; **prab**, preacetabular blade.

Figure 8. Phylogenetic analysis of the Aetosauria. The reduced strict consensus tree from Parker 2016a, with all named clades. Decay indices and bootstrap values are shown for all nodes, with bootstrap values under 70% (the confidence threshold of Hillis & Bull, 1993) shown in red.

Figure 9. Dorsal trunk paramedian osteoderms of *Stagonolepis*. A) NHMUK R4787a, left dorsal trunk paramedian in dorsal view; B) PAN ZPAL AbIII 57011, left dorsal trunk paramedian in dorsal view. Scale bars = 1 cm.

Figure 10. Alternate phylogenetic hypothesis of the Aetosauria of Hoffman, Heckert, and Zanno (2018) with clade names and decay indices for each node.

Figure 11. Cast of EM 27R, the holotype specimen of *Stagonolepis robertsoni* Agassiz 1844. A series of imbricated osteoderms from the ventral trunk region.

Figure 1

Casts of bones of *Stagonolepis robertsoni*.

(A) NHMUK R4787a, 1885 cast which represents much of the lower portion of a skull. (B) NHMUK R4787, PVC cast of the same specimen that shows more details of the braincase and dorsal portion of the skull. Scale bars equal 1 cm. Abbreviations: **an**, angular; **art**, articular; **bpt**, basipterygoid process; **bs**, parabasisphenoid; **bt**, basal tuber; **d**, dentary; **fr**, frontals; **l**, left; mx, maxilla; **mpr**, area of the medial pharyngeal recess; **pa**, parietal; **pmx**, premaxilla; **pra**, prearticular; **pro**, prootic; **pt**, pterygoid; **qu**, quadrate; r, right; **sa**, surangular. Elements from the left side have a prefix of **l.**; elements of the right side have a prefix of **r.**

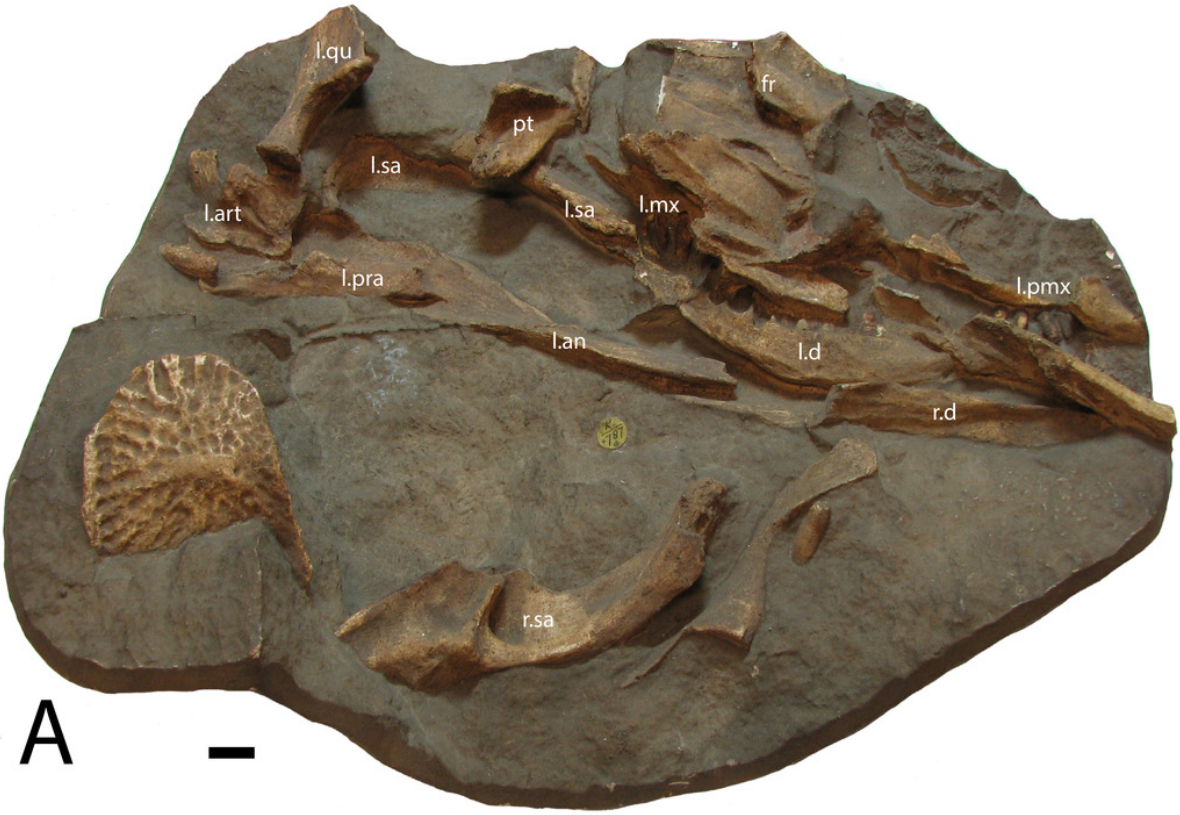
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Figure 2

NHMUK R4787, cast of a right maxilla of *Stagonolepis robertsoni*

Lateral (A) and medial (B) views. Scale bar equals 1 cm. Abbreviations: **a.**,articulation with listed element; **alv**, alveoli; **aof**, antorbital fenestra; **ap.m**, ascending process of the maxilla; **ju**, jugal; **la**, lacrimal; **ms**, medial shelf; **na**, nasal; **pac**, pneumatic accessory cavity; **pmx**, premaxilla; **tr**, transverse ridge.

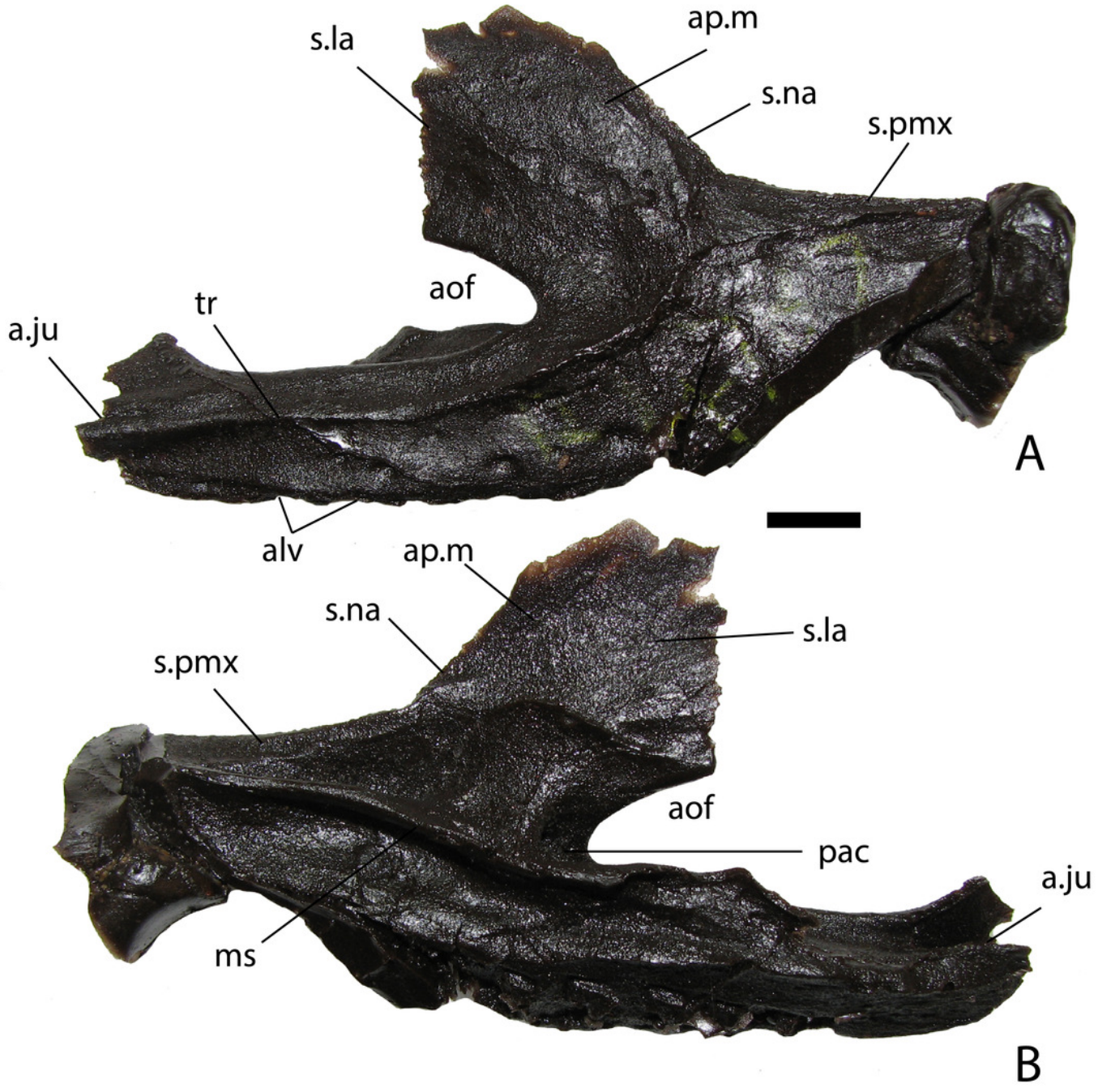
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Figure 3

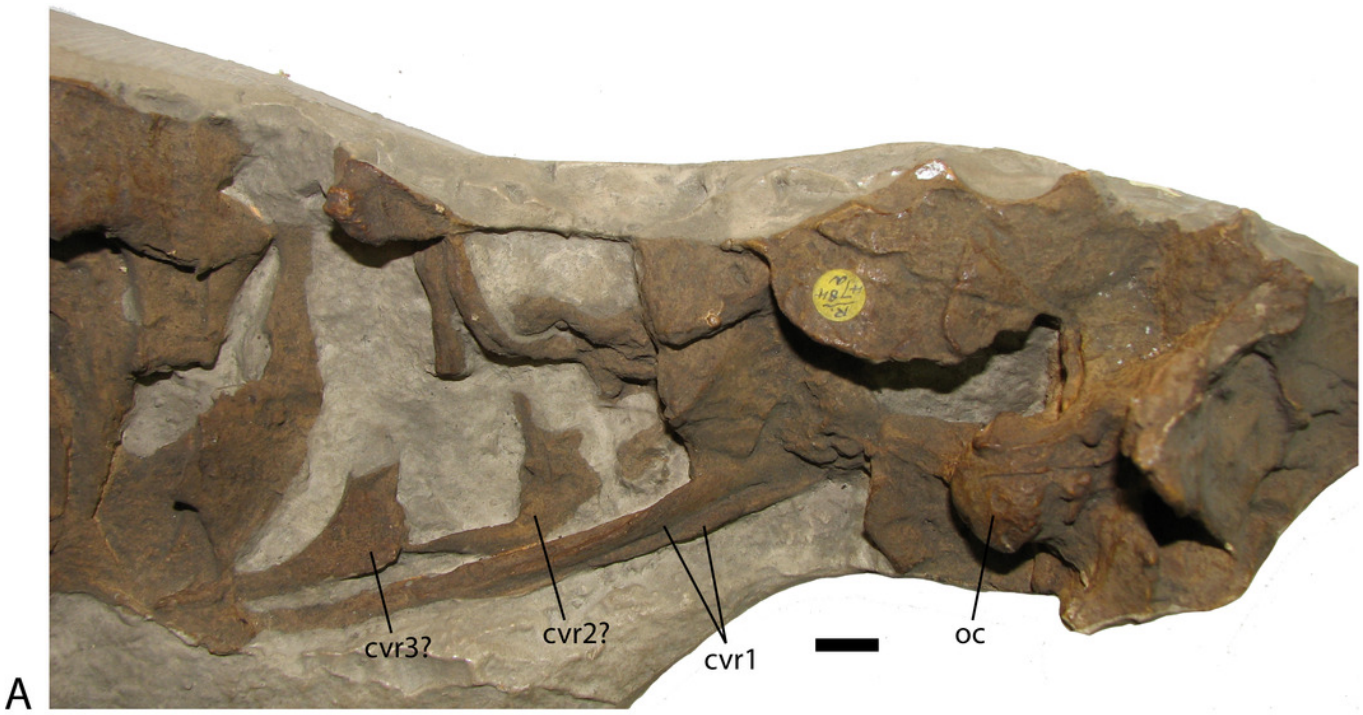
Skull of *Stagonolepis robertsoni.*

Cast of the anterior part of the right side of the skull of *Stagonolepis robertsoni* in lateral view. Scale bar equals 1 cm. Abbreviations: **en**, external naris; **mx**, maxilla; **na**, nasal; **nr**, nasal ridge; **pmr**, premaxillary ridge; **pmx**, premaxilla.

Figure 4

Presacral vertebrae of *Stagonolepis robertsoni*.

NHMUK 4784a, casts of articulated sections of the presacral vertebral column in lateral view including the rear of the skull through the fourth cervical position (A), and the seventh through the twelfth presacral vertebrae (B). Scale bars equal 1 cm. Abbreviations: **cvr**, cervical rib; **k**, ventral keel; **oc**, occipital condyle of the basicranium; **parp**, parapophysis; **pcdl**, posterior centrodiapophyseal lamina.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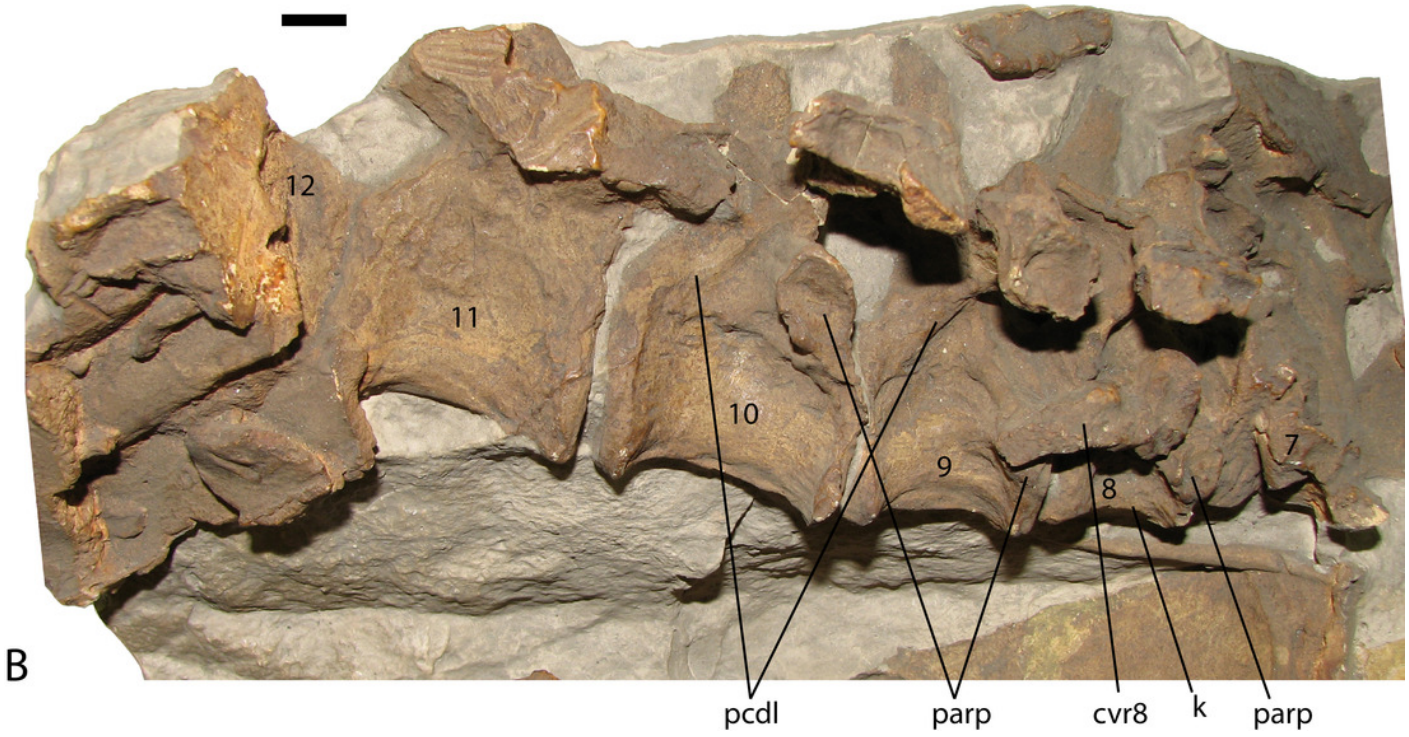
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Figure 5

Casts of osteoderms of *Stagonolepis robertsoni.*

(A) left dorsal trunk paramedian (NHMUK R4790a) in dorsal view; (B) right dorsal trunk lateral (NHMUK R4789a) in dorsolateral view. Scale bar equals 1 cm. Abbreviations: **a.**, articulation with listed element; **ab**, anterior bar; **alp**, anterolateral projection; **amp**, anteromedial projection; **de**, dorsal eminence; **df**, dorsal flange; **lf**, lateral flange; **sc**, scalloping of anterior bar margin.

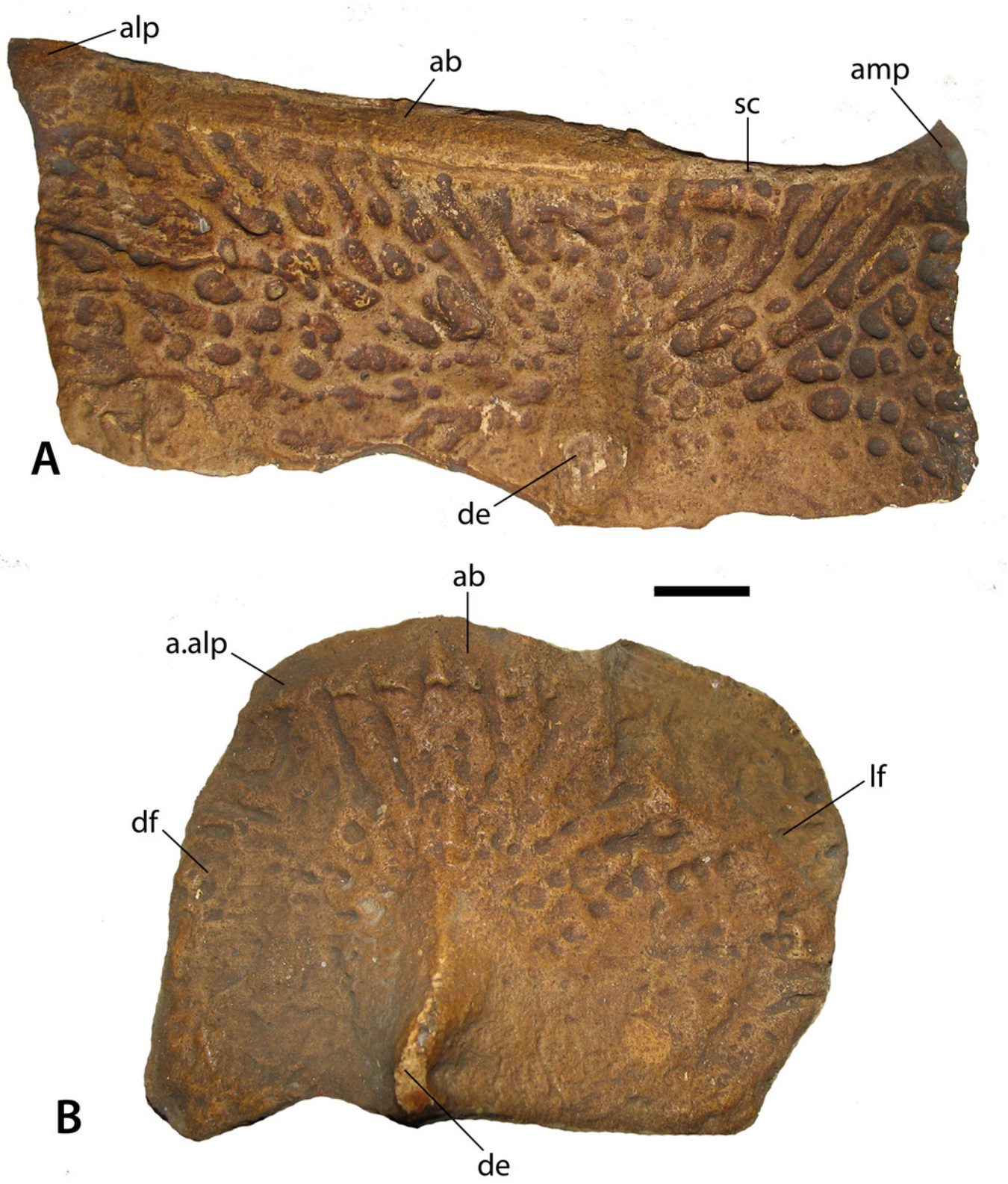
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Figure 6

Ventral osteoderms of *Stagonolepis robertsoni*.

(A) close-up of NHMUK R27404 (positive cast of EM 27R, the holotype specimen of *Stagonolepis robertsoni* Agassiz 1844) in ventrolateral view showing the detail of the overlapping osteoderms; (B) NHMUK R4787a, referred ventral osteoderm in ventral view. Scale bar = 1 cm.

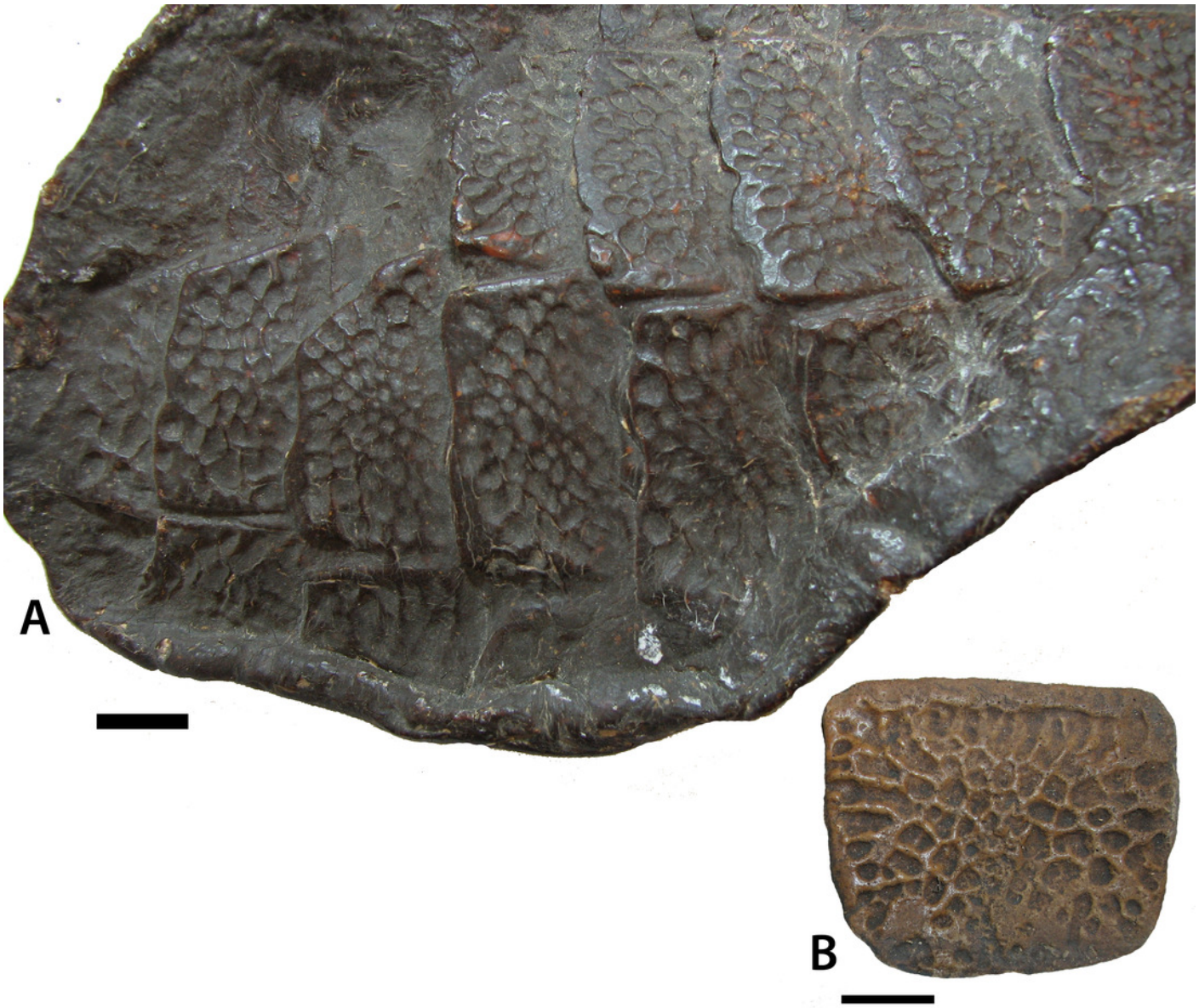

Figure 7

Ilium of *Stagonolepis robertsoni*

NHMUK R4789. Cast of medial side of right ilium in medial view. Scale bar = 2 cm.

Abbreviations: **arsr2**, articulation for sacral rib 2; **ip**, ischiadic peduncle; **ost**, osteoderm; **poab**, postacetabular blade; **pp**, pubic peduncle; **prab**, preacetabular blade.

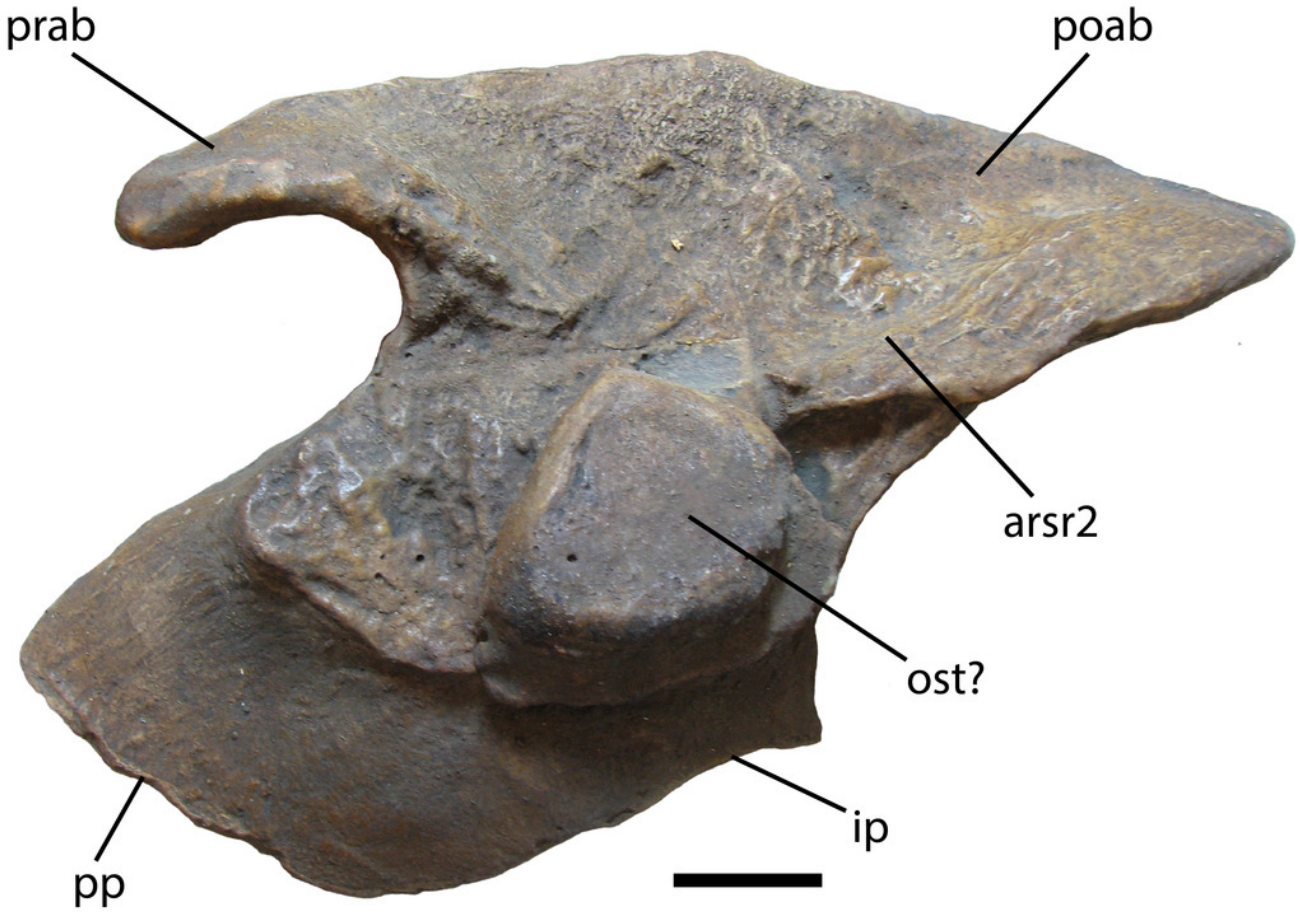

Figure 8

Phylogenetic Analysis of the Aetosauria.

The reduced strict consensus tree from Parker (2016a), with all named clades. Decay indices and bootstrap values are shown for all nodes, with bootstrap values under 70% (the confidence threshold of Hillis & Bull, 1993) shown in red.

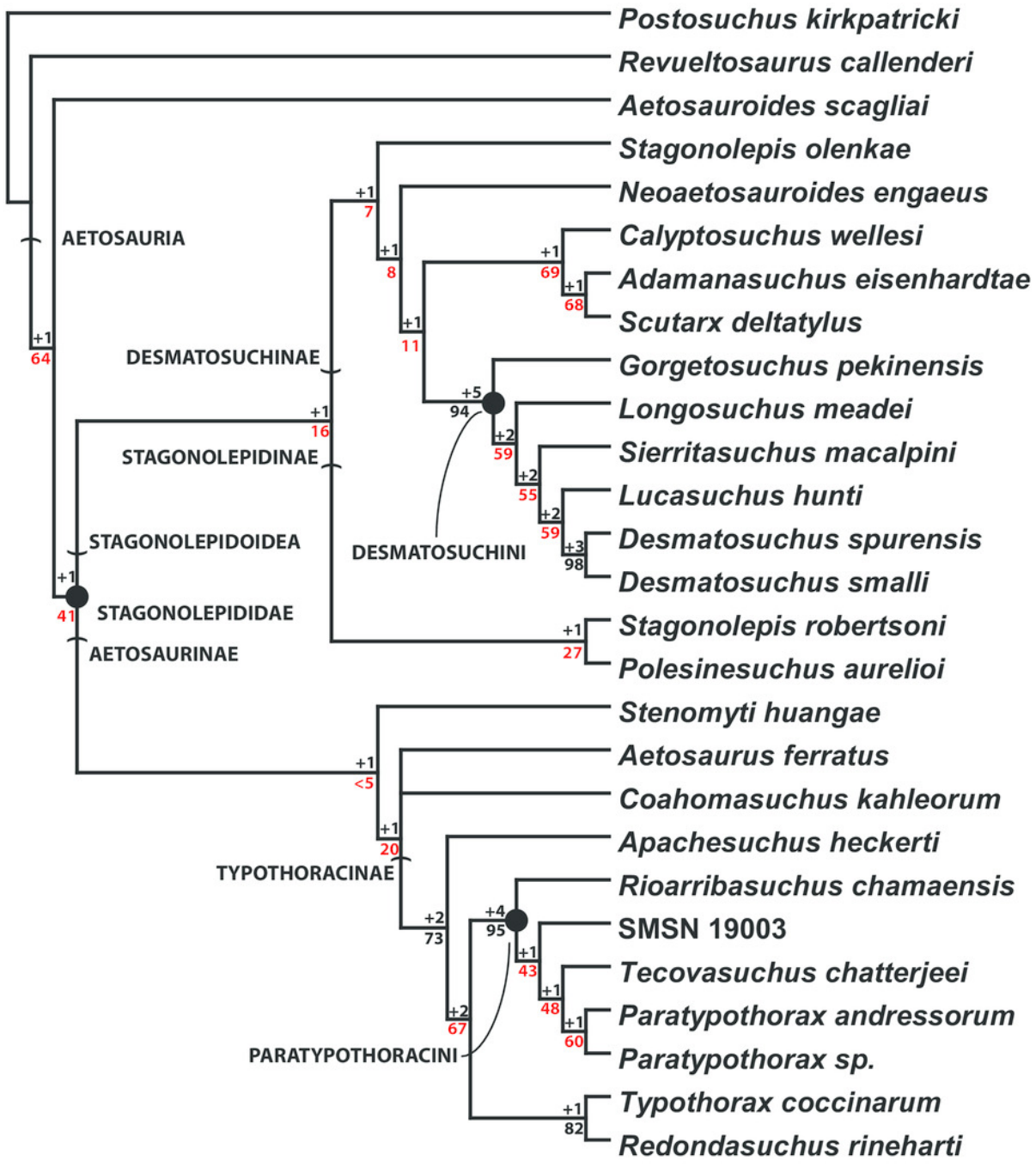

Figure 9

Dorsal trunk paramedian osteoderms of *Stagonolepis*.

(A) NHMUK R4787a, left dorsal trunk paramedian in dorsal view; (B) PAN ZPAL AbIII 57011, left dorsal trunk paramedian in dorsal view. Scale bars = 1 cm.

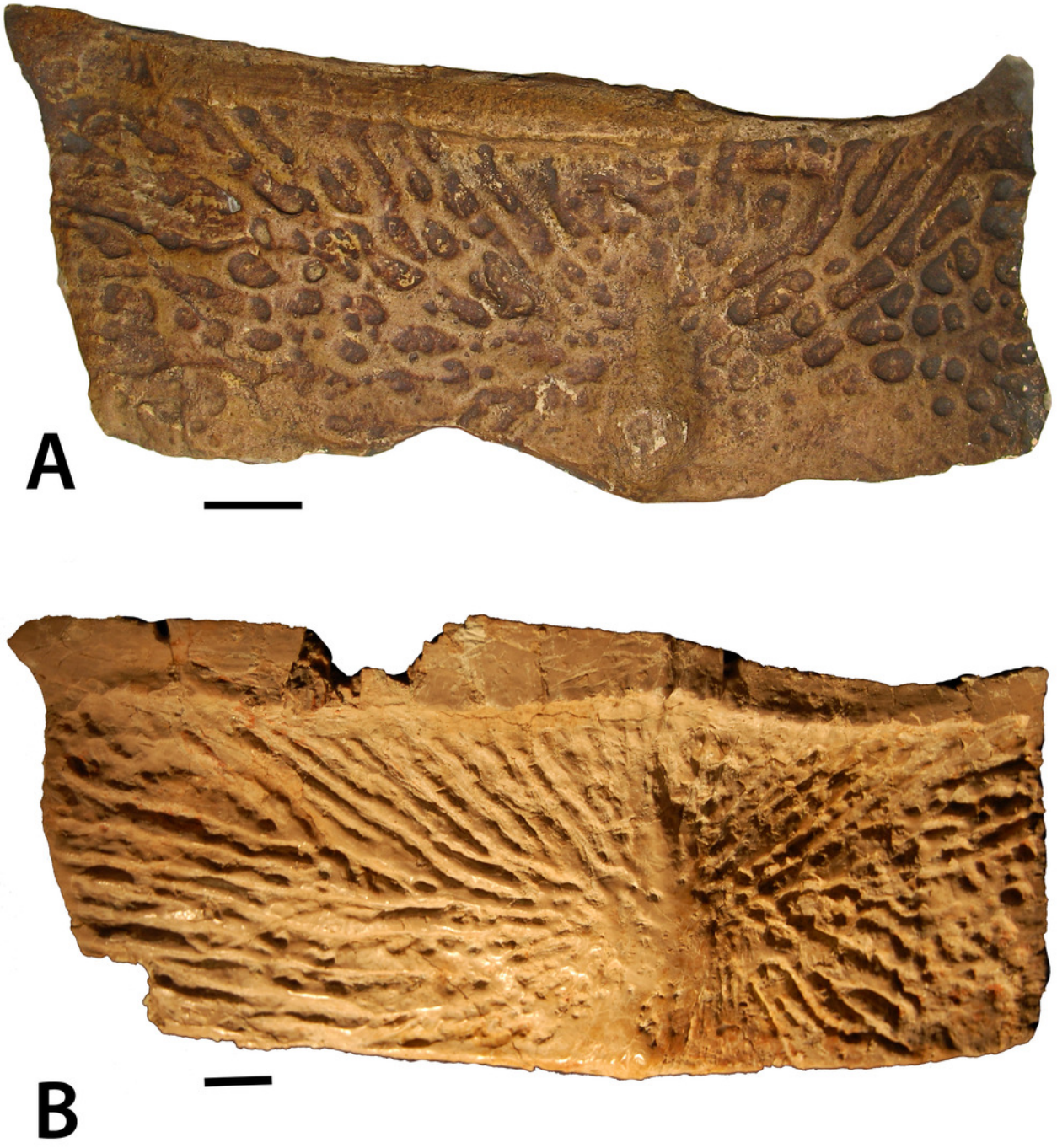
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Figure 10

Alternate phylogenetic analysis of the Aetosauria.

Alternate phylogenetic hypothesis of the Aetosauria of Hoffman, Heckert, and Zanno (2018) with clade names and decay indices for each node.

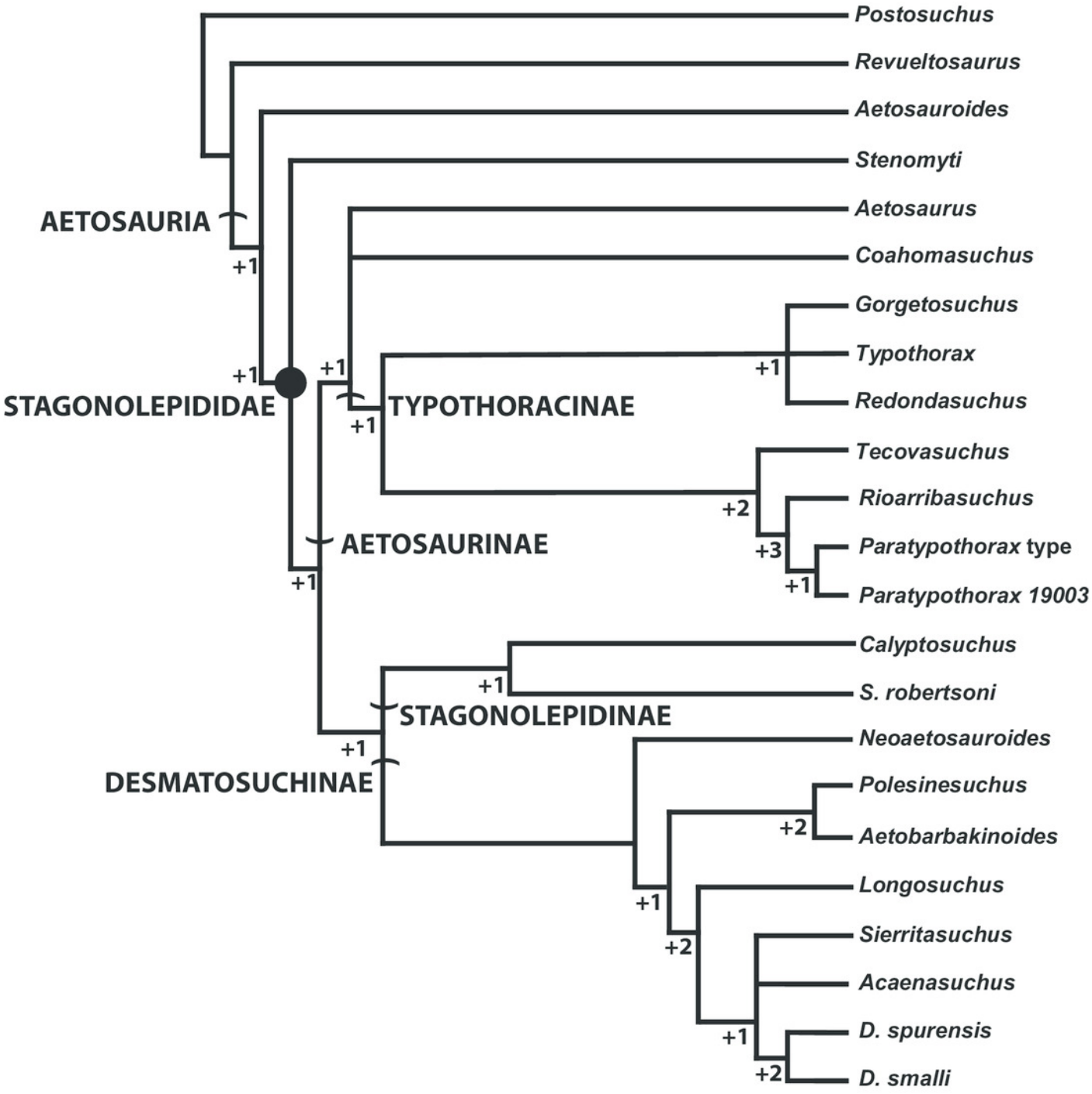

Figure 11

Holotype specimen of *Stagonolepis robertsoni*.

Cast of EM 27R, the holotype specimen of *Stagonolepis robertsoni* Agassiz 1844, a series of imbricated osteoderms from the ventral trunk region.


5 cm