

New information on the early Permian lanthanosuchoid *Feeserpeton oklahomensis* based on Computed Tomography (#37076)

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New information on the early Permian lanthanosuchoid *Feeserpeton oklahomensis* based on Computed Tomography

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The cave deposits of the Lower Permian Richards Spur locality in Oklahoma, USA, have produced an incredible number of terrestrial tetrapod taxa, many of which are currently only known from this locality. One of the many recent taxa to be described from the locality was the small lanthanosuchoid parareptile *Feeserpeton oklahomensis*. Represented by a well-preserved, near complete skull, *F. oklahomensis* would have been a small predatory sauropsid, likely preying upon arthropods, and contributes to the extensive tetrapod fauna that was present at Richards Spur. New computed tomography (CT) data of the holotype and only specimen has allowed us to visualize and describe previously obscured and inaccessible anatomy of this taxon. These areas include the mandibular ramus, the palate, the sphenethmoid, the epipterygoids, and the braincase. Furthermore, this new anatomical information allowed formerly unknown character codings to be updated, thus we also performed a new phylogenetic analysis that incorporated this new information. The results of this updated phylogenetic analysis are very similar to those of past studies, with *F. oklahomensis* being found as the sister taxon to all other lanthanosuchoids.

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Abstract

The cave deposits of the Lower Permian Richards Spur locality in Oklahoma, USA, have produced an incredible number of terrestrial tetrapod taxa, many of which are currently only known from this locality. One of the many recent taxa to be described from the locality was the small lanthanosuchoid parareptile *Feeserpeton oklahomensis*. Represented by a well-preserved, near complete skull, *F. oklahomensis* would have been a small predatory sauropsid, likely preying upon arthropods, and contributes to the extensive tetrapod fauna that was present at Richards Spur. New computed tomography (CT) data of the holotype and only specimen has allowed us to visualize and describe previously obscured and inaccessible anatomy of this taxon. These areas include the mandibular ramus, the palate, the sphenethmoid, the epipterygoids, and the braincase. Furthermore, this new anatomical information allowed formerly unknown character codings to be updated, thus we also performed a new phylogenetic analysis that incorporated this new information. The results of this updated phylogenetic analysis are very similar to those of past studies, with *F. oklahomensis* being found as the sister taxon to all other lanthanosuchoids.

Keywords: Parareptilia, Reptilia, Sauropsida, Cisuralian, Palaeozoic

67 Introduction

68 The Lower Permian (Cisuralian) Richards Spur locality of southwestern Oklahoma,
 69 represented by an extensive cave system, is known for its immense terrestrial tetrapod fauna
 70 (Sullivan & Reisz, 1999; MacDougall et al., 2017b). Over the last few decades, more than 30
 71 taxa have been described from the locality (MacDougall et al., 2017b), which includes various
 72 anamniotes, synapsids, and sauropsids. Among these tetrapods are numerous parareptile taxa,
 73 specifically: *Colobomycter pholeter* Vaughn, 1958, *Delorhynchus priscus* Fox, 1962, *Bolosaurus*
 74 *grandis* Reisz et al., 2002, *Microleter mckinzieorum* Tsuji et al., 2010, *Abyssomedon williamsi*
 75 MacDougall and Reisz, 2014, *Delorhynchus cifelli* Reisz et al., 2014, *Colobomycter vaughni*
 76 MacDougall et al., 2016. Most early Permian continental assemblages exhibit only a single
 77 parareptile taxon, Richards Spur is in stark contrast to this pattern, with eight parareptiles being
 78 known from the locality (MacDougall et al., 2017b), several of which belong to the clade
 79 Lanthanosuchoidea (Vaughn, 1958; Fox, 1962; Modesto, 1999; MacDougall & Reisz, 2012;
 80 Reisz, Macdougall & Modesto, 2014; MacDougall, Modesto & Reisz, 2016).

81 Lanthanosuchoidea is a small clade of sauropsids that includes various early and middle
 82 Permian forms. Currently, all early Permian lanthanosuchoids are only known from North
 83 America, whereas as the Middle Permian taxa are known only from Russia. There are also
 84 notable differences between the North American and Russian lanthanosuchoids. The early
 85 Permian North American taxa are considered to be small, fully-terrestrial, predatory taxa
 86 (Modesto, Scott & Reisz, 2009; Haridy, MacDougall & Reisz, 2017; MacDougall et al., 2017a),
 87 whereas the Middle Permian Russian taxa are larger and considered to be semi-aquatic
 88 (Sennikov, 1996; Reisz, 1997; Verrière, Brocklehurst & Fröbisch, 2016). Overall, this suggests
 89 that the clade could have potentially originated in western Laurasia and later dispersed to eastern

Laurasia, though the lack of Russian early Permian strata makes this biogeographic hypothesis difficult to test.

The lanthanosuchoid *Feeserpeton oklahomensis* is one of the more recently described taxa from Richards Spur locality and is currently only known from its holotype (MacDougall & Reisz, 2012). It is represented by a small, nearly complete skull, and is characterized by several enlarged maxillary teeth on the maxillae and dentaries, as well as large postorbitals and small squamosals. In the initial description, MacDougall and Reisz (2012) largely described the visible external anatomy of the skull, although CT data was used to examine the mandibular dentition. However, they did not examine any other areas of the skull that were obscured or inaccessible, which left some aspects of the anatomy of the skull unknown.

Herein, we describe the previously inaccessible anatomy of *Feeserpeton oklahomensis* using new CT data. Areas that were segmented and examined include obscured parts of the lower jaw and palate, the sphenethmoid, the epipterygoids, and elements of the braincase (Fig. 1). Furthermore, the new information obtained from this data also warranted updating the phylogenetic character codings of *F. oklahomensis*, thus an updated phylogenetic analysis was performed as well.

Institutional Abbreviations: OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA.

Materials & Methods

Specimen

The skull of *Feeserpeton oklahomensis* examined for this study is the holotype and currently only known specimen, OMNH 73541. It was previously studied and described by MacDougall and Reisz (2012).

Computed Tomography Scans

The skull of *Feeserpeton oklahomensis* was scanned using the x-ray computed tomography setup (Phoenix | x-ray Nanotom | s) at the Museum für Naturkunde in Berlin. Scan parameters were set to 57 kV voltage and 170µA current with 1440 images /360° at an exposure time of 1000ms/image and an effective voxel size of 0.0129 mm, resulting in a magnification rate of 3.857. Cone beam reconstruction was performed using datos | x-ray sensing 4 Inspection Technologies GmbH (phoenix | x-ray) with a correction value of 1.845. The elements were visualized and digitally segmented in VG studio Max 3.2.

Phylogenetic Analysis

The data matrix used in the phylogenetic analysis is based on the data matrix of MacDougall et al. (2018). The analysis itself was performed in PAUP 4.0a165 (Swofford, 2019), using parsimony as the optimality criterion. The outgroup was set to include the taxa *Seymouria*, *Limnoscelis*, and *Orobates*. Furthermore, minimum branch lengths of zero were set to collapse. A heuristic search (TBR) was then performed using these parameters. Both a bootstrap and Bremer decay analysis were conducted to determine support values for clades.

The character codings of *Feeserpeton oklahomensis* were updated based on new information obtained from the CT data. The characters that were recoded are as follows: interpterygoid vacuity anterior extent (61) ?→0, alar flange of the vomer presence or absence

(64) ?→0, cultriform process present; (67) ?→1, pterygoid anterior extent (85) ?→0, cultriform process anterior extent (86) ?→1, sutural contact between paroccipital process and dermatocranium (92) ?→1, Meckelian fossa orientation (108) ?→0, Meckelian fossa anteroposterior length (109) ?→0, number of coronoids (113) ?→1, prearticular anterior extent (114) 1→0, coronoid process height (119) ?→0, high coronoid process composition (120) ?→-, single large tooth on anteriormost end of vomer (169) 1→0.

Furthermore, a few characters were recoded for other taxa to correct some coding errors; these changes are indicated in the data matrix. The updated data matrix and the full character list can be found in the supplementary info.

Description

The CT scans of *Feeserpeton oklahomensis* allowed for several previously inaccessible and obscured areas of the skull to be examined and segmented (Fig. 1). These areas include parts of the palate and the mandible, the sphenethmoid, the epipterygoids, and elements of the braincase.

The Palate

Many of the palatal elements of *Feeserpeton oklahomensis* are visible in the holotype, however, only the right side of the palate was prepared, and there are portions of it that are obscured by supportive matrix. Through segmentation of the CT data both sides of the palate are visible in their entirety (Fig. 2), some parts of the palate are damaged or not preserved, but it is largely intact. The most notable feature of the palate that is clarified by the scans is the extent of

the palatal dentition, in particular on the palatine. The left palatine appears to be largely complete and grants us a view of the element that was not available previously.

As was suggested by MacDougall and Reisz (2012), the palatine is a large element and makes up a considerable portion of the overall palatal surface. Anteriorly, the palatine contacts the vomer, whereas it contacts the pterygoid medially and posteriorly, the ectopterygoid is also contacted posteriorly. Laterally, there is a contact with the maxilla. MacDougall and Reisz (2012) note that there are two clusters of palatine teeth visible, though the full extent of these clusters could not be fully determined. The segmented left palatine clearly shows that there is a lateral and medial group of teeth on the element; they are roughly organized in the form of rows. The lateral row consists of seven large teeth and a few smaller ones, whereas the medial row consists of several smaller teeth.

The full anteroposterior extent of the vomer is also now apparent, the element is about the same length as the palatine, and ends anteriorly with a narrow, pointed medially positioned process. Likewise, the full lateral extent of the element reveals that the anterior end of the palatine is nestled between two posterior extensions of the vomer: a broad medial extension, and a narrower lateral one.

There are other features of the palate that are clarified with this new CT data. It is now clear that the interpterygoid vacuity extends quite far anteriorly, past the posterior edge of the palatines. Likewise, it is apparent that the cultriform process of the parasphenoid extends forward for much of the length of the vacuity. Furthermore, a suborbital foramen is not present, with the palate being unbroken at the intersection of the pterygoid, palatine, and ectopterygoid, as is the case in other lanthanosuchoids (deBraga & Reisz, 1996; Reisz, Macdougall & Modesto, 2014).

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183 The Mandibles

184 Due to the mandibular rami of *Feeserpeton oklahomensis* being occluded with the upper
185 jaw, only details of the ventral and labial surfaces can be clearly observed, with much of the
186 dorsal and lingual surfaces being obscured by the occlusion. However, segmentation of the entire
187 left mandibular ramus (Fig. 3) reveals new information regarding these previously inaccessible
188 areas. The left ramus is slightly damaged on its labial surface, which results in a small gap
189 through which the labial surface of the prearticular can be seen.

190 MacDougall and Reisz (2012) used CT scans to investigate the dentition of the dentary,
191 however, only the shape of the teeth was examined. The segmented mandibular ramus of the
192 holotype exhibits 21 teeth on the dentary, however, when empty alveoli are included the total
193 number of dentary teeth increases to 25. Furthermore, there are enlarged teeth found on the
194 anterior end of the element; there are two visible and an empty alveolus, suggesting that there
195 would have been three enlarged teeth, the same pattern that is observed on the maxilla
196 (MacDougall & Reisz, 2012).

197 One of the more notable features of the mandible are the coronoid elements (Fig. 3, 4). In
198 their investigation of multiple coronoids and coronoid dentition in Palaeozoic sauropsids, the
199 coronoid of *Feeserpeton oklahomensis* was examined by Haridy et al. (2017) using CT scans.
200 They identified the presence of two coronoids on each ramus, as well as the presence of coronoid
201 dentition. We are able to confirm that coronoid dentition is present in *F. oklahomensis* (Fig. 4),
202 though much of the dentition appears to not be preserved, there are three small teeth that are
203 clearly visible on the right coronoid. However, unlike what was observed by Haridy et al. (2017),

we find no trace of two coronoid elements (Fig. 3), suggesting that the presence of multiple coronoids in *F. oklahomensis* was likely a misinterpretation.

The coronoid itself is a relatively long element found lingual to the posterior end of the dentary. It extends from its posterior articulation with the surangular to the middle of the dentary, narrowing for most of its length. A posteroventral process of the coronoid curves posteriorly to meet with the prearticular.

The full extent of the prearticular, an element not described by MacDougall and Reisz (2012), is revealed in the segmented mandibular ramus (Fig. 2). It is a long element that extends from the articular to the posterior end of the splenial. It also articulates ventrally with the portion of the angular that wraps around to the lingual side of the ramus, whereas its anterodorsal edge contacts the coronoid and dentary. The dorsal portion of the prearticular forms the lingual margin of the large adductor fossa. Overall, the prearticular is quite similar in shape and position to that of other closely related taxa, such as *Delorhynchus* (Haridy, MacDougall & Reisz, 2017).

The Meckelian fossa, normally completely obscured by the occlusion of the jaws to the rest of the skull, is revealed in its entirety in the segmented mandibular ramus as well (Fig. 2). The Meckelian fossa of *Feeserpeton oklahomensis* is found on the posterior end of the mandibular ramus. The fossa faces dorsomedially and it is quite long, extending anterior for about a third of the length of the ramus, as is the case in *Delorhynchus* (Haridy, MacDougall & Reisz, 2017).

The Sphenethmoid

The sphenethmoid is a rarely described element in early sauropsids, usually because it is either not preserved or not visible. Due to the internal position of the sphenethmoid in the

holotype of *Feeserpeton* it was not noted or discussed in MacDougall and Reisz (2012), here we present the fully segmented sphenethmoid element (Fig. 5).

The sphenethmoid is found in its expected position, ventral to the frontals. It is a roughly Y-shaped element when viewed in anterior and posterior aspects, possessing a slender ventral process (often termed the keel) and two equally slender dorsal processes with a rounded trough between them. Lateral view of the element reveals that its anteroposterior length is about equivalent to its dorsoventral height. This sphenethmoid shape is similar to what has been observed in other early sauropsids, such as *Captorhinus* (Heaton, 1979; Modesto & Reisz, 2008).

The Epipterygoids

The epipterygoids are another example of rarely described elements of early sauropsids, largely due to their interior position within the skull. The new CT scans reveal the presence of both epipterygoids in the holotype of *Feeserpeton oklahomensis*, which were both fully segmented for the purpose of this study (Fig. 6). These elements were not described by MacDougall and Reisz (2012) as they are not exposed externally. Both epipterygoids appear to be disarticulated and not in their natural positions (Fig. 1), but overall they are similar in structure to those that have been described for other early sauropsids (Romer, 1956; Carroll & Lindsay, 1985), possessing a gracile dorsal columella that arches slightly posterior, and a ventral region that expands to form a more robust footplate with a broad anteroposterior length. The footplate also exhibits a process on its anteromedial surface, a characteristic that has also been observed in other early sauropsids, such as *Captorhinus* (Fox & Bowman, 1966). In their natural positions the dorsal columella of each epipterygoid would have contacted the supraoccipital and prootic, whereas the footplate would have presumably met with the quadrate process of the

pterygoid, as is the case in *Captorhinus* (Fox & Bowman, 1966) and the procolophonids
Leptopleuron and *Hypsognathus* (Sues et al., 2000; Cisneros, 2008).

The Braincase

The braincase of *Feeserpeton oklahomensis* was described externally by MacDougall and Reisz (2012), however, there was still substantial portions of its overall anatomy that could not be described due to being obscured. The fully segmented braincase presented here (Fig. 7) reveals several details that could not be observed in the original description of the holotype. It is also quite apparent that the braincase exhibits slight disarticulation of elements from their natural position, as well as some damaged areas.

The prootics of *Feeserpeton* are large, irregularly shaped anterior elements of the braincase and form an extensive portion of its overall structure. While MacDougall and Reisz (2012) were able to identify the prootics, they were only able to describe the exposed ventral surface of the elements, which is only a small portion of the overall element. The prootics are slightly disarticulated and not in contact with any of the other elements of the braincase, but they appear to be entirely intact. The posterior surface of the prootic would have articulated with the anterior surface of the opisthotic. The flattened posterolateral extension of the element, usually termed the paroccipital process of the prootic would have met with the paroccipital process of the opisthotic, with a large depression in this region of the prootic contributing to the fenestra ovalis. Dorsomedially, there is a small process that would have met with the supraoccipital. The medial portion of the element exhibits another smaller process that extends ventrally out from the main body of the prootic, which would likely have come close to contacting the basioccipital. The anterior part of the prootic is convex in shape. Overall, the structure of the prootic is largely

similar to what has been described for other parareptiles, such as *Leptopleuron* (Spencer, 2000), though in the case of *Leptopleuron* the prootic appears to be not quite as robust as that of *Feeserpeton*. Unfortunately, this is a rarely described element of closely related taxa, due to its often inaccessible position.

The opisthotics are another large component of the braincase, and like the prootics, they were also only partially described by MacDougall and Reisz (2012). The segmented braincase clearly illustrates that both of the opisthotics suffer from damage (Fig. 7), however, the left opisthotic is substantially more damaged than the right one, with a large posterior segment of the element being completely absent. The better preserved right opisthotic clearly exhibits a laterally expanded anterodorsal end, and a posterior portion that extends ventrally. The broad anterior end contributes to the paroccipital process of the opisthotic, which would have met with the paroccipital process of the prootics. Moving medially the posterior portion of the opisthotic expands dorsoventrally and meets with the lateral edge of the fused exoccipital-basioccipital complex, contributing to the posterior end of the braincase and forming the remaining portion of the paroccipital process.

The stapes was briefly described by (MacDougall & Reisz, 2012), and we expand upon **there** description here. The stapes of *Feeserpeton* is not in its natural position, being slightly disarticulated, it consists of a bifurcating laterally compressed distal end, and the broad proximally located footplate, which are connected by a short, slightly twisted shaft. In its natural position the footplate would have met with the fenestra ovalis of the paroccipital process, with the distal end extending laterally towards the quadrate. The distal end of the stapes bifurcates into two distinct processes, the distal facing columella, which appears to be broken, and prior to this process a dorsal extension. The stapes is similar in size and structure to the stapes of

296 *Acleistorhinus pteroticus* (deBraga & Reisz, 1996), but is quite distinct from the small gracile
297 stapes of *Leptopleuron lacertinum* (Spencer, 2000).

298

299

300 **Phylogenetic Analysis**

301 The phylogenetic analysis produced 27 optimal trees, each with a tree length of 667. As
302 in the original MacDougall and Reisz (2012) study, the strict consensus tree (Fig. 8) produced
303 from the optimal trees has *Feeserpeton oklahomensis* being recovered as the sister taxon of all
304 other lanthanosuchoids (it is in this position in all 27 of the optimal trees). The clade
305 Lanthanosuchoidea is recovered as the sister taxon to the clade that contains Bolosauria,
306 Procolophonoidea, Pareiasauridae, Nycteroletheridae, Nyctiphruretidae, and *Microleter*. This is
307 similar to what was recovered in the analysis of MacDougall and Reisz (2012), except for the
308 inclusion of *Microleter* within this clade. However, the position of Bolosauria in our analysis
309 differs from what was recovered by other studies (Modesto et al., 2015; MacDougall et al.,
310 2017a), where the clade was found to be more basal than Lanthanosuchoidea.

311 Similar to the results of MacDougall et al. (2018), the ophiacodontid (*Archaeothyris*) and
312 varanopid taxa (*Archaeovenator*, *Mycterosaurus*) included in the analysis were recovered as
313 being more closely related to the sauropsid taxa than to the synsapsids. This is an atypical result
314 that warrants further investigation in the future, but is at least partly in line with the results of
315 recent work that has recovered varanopids within Sauropsida (Ford & Benson, 2018). In the case
316 of our study this result could potentially be the result of the relatively narrow focus of our
317 analysis.

318

319

320 Discussion

321 New Information from CT Scans

322 The early Permian Richards Spur locality has produced a considerable amount of well-
 323 preserved fossil material, largely due to the unique preservational environment associated with
 324 the caves found there (MacDougall et al., 2017b). In particular near complete skulls are not
 325 uncommon at the locality, with many taxa being known almost solely from skulls (e.g. Modesto
 326 and Reisz, 2008; Anderson et al., 2009; Tsuji et al., 2010; Polley and Reisz, 2011; MacDougall
 327 et al., 2017b). These various well-preserved specimens provide substantial information regarding
 328 the anatomy of the taxa to which they belong, however, there are also various regions of these
 329 skulls that cannot be examined normally, either due to being obscured or not being exposed
 330 externally. CT scans are proving to be an ideal way to study these skulls and their difficult to
 331 examine areas, which will in turn provide more information regarding the Richards Spur
 332 assemblage and the taxa that compose it. The new CT scans of the holotype of *Feeserpeton*
 333 *oklahomensis* have allowed for the segmentation of several previously inaccessible areas,
 334 revealing more details regarding the anatomy of this taxon. Specifically, the dentition of the
 335 mandible and palate, and various elements of the skull that are largely internal.

336 Recently, there have been other parareptile taxa that have been examined using CT scans
 337 (Tsuji, Sobral & Müller, 2013; Zaher, Coram & Benton, 2018), which resulted in the discovery
 338 of new information about the examined taxa, however, there are still numerous parareptile taxa
 339 that have yet to be examined in comparable detail using CT scans. The new information that will
 340 be obtained from examining other parareptiles using CT scans will be important for resolving
 341 issues and testing existing hypotheses regarding early amniote relationships (Laurin & Piñeiro,

2017; Ford & Benson, 2018; MacDougall et al., 2018), as well as for better understanding the anatomy and evolution of these taxa (Zaher, Coram & Benton, 2018).

The Coronoid Process of *Feeserpeton*

One of the aspects of the anatomy of *Feeserpeton oklahomensis* that was clarified with CT scans is the composition of the coronoid process. The coronoid process of lanthanosuchoids has been shown to be quite complex, with the presence of multiple coronoids and dentition present on the elements (Haridy, MacDougall & Reisz, 2017; MacDougall et al., 2017a). Our identification of a single coronoid on the mandibular ramus of *F. oklahomensis* (Fig. 3), which is contrary to the observations of Haridy et al. (2017), does not dramatically change their interpretations about the evolution of the trait within Lanthanosuchoidea. The only potential change this reinterpretation introduces to their hypothesis is that multiple coronoids does not appear to be primitive for Lanthanosuchoidea, instead appearing later in the evolution of the clade. However, we were able to confirm that the coronoid of *F. oklahomensis* does indeed exhibit dentition (Fig. 4), thus it is clear that denticulate coronoids are the primitive condition for lanthanosuchoids, as was hypothesized by Haridy et al. (2017). Other lanthanosuchoid taxa, notably *Acleistorhinus pteroticus*, will have to be reexamined in the future to further elucidate details regarding the evolution of multiple and denticulate coronoids within the clade.

Conclusions

Through computed tomography scans and modern visualization techniques this study reveals new information regarding the anatomy of the early Permian sauropsid *Feeserpeton oklahomensis*. Notably, we were able to describe numerous details regarding the anatomy of the mandibular rami, the palate, the sphenethmoid, the epipterygoids, and the braincase. All of which are parts of the skull that cannot be fully examined normally in the holotype specimen. This new information also allowed for several previously unknown phylogenetic characters to be coded. The evolution and relationships of early amniotes is still an area of palaeontological research that is far from set in stone, and the investigation of normally inaccessible anatomy using CT data has been and will continue to be important for better understanding sauropsid, and more broadly, early tetrapod evolution.

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489

490 **Figure Captions**

491 Figure 1. The skull of *Feeserpeton oklahomensis*, OMNH 73541, showing the regions that were
492 reconstructed using CT data. Scale bar equals 3 mm. [Half page width]

493

494 Figure 2. The palate of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from CT data.
495 **A**, dorsal view, and **B**, ventral view. Abbreviations: **ec**, ectopterygoid; **m**, maxilla; **pal**, palatine;
496 **ps**, parasphenoid; **pt**, pterygoid; **v**, vomer. Scale bar equals 4 mm. [Half page width]

497

498 Figure 3. The left mandibular ramus of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed
499 from CT data. **A**, dorsal view, **B**, ventral view, **C**, labial view, and **D**, lingual view.

500 Abbreviations: **an**, angular; **ar**, articular; **c**, coronoid; **d**, dentary; **pra**, prearticular; **sa**,
501 surangular; **sp**, splenial. Scale bar equals 2 mm. [Half page width]

502

503 Figure 4. The right coronoid of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from
504 CT data. **A**, lingual view, and **B**, dorsal view. Scale bar equals 1 mm. [Half page width]

505

506 Figure 5. The sphenethmoid of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from
507 CT data. **A**, anterior view, **B**, posterior view, **C**, dorsal view, and **D**, lateral view. Scale bar
508 equals 1 mm. [Half page width]

509

510 Figure 6. The left epipterygoid of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from
511 CT data. **A**, lateral view, **B**, medial view, **C**, dorsal view, and **D**, ventral view. Scale bar equals 1
512 mm. [Half page width]

513

514 Figure 7. The braincase of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from CT
515 data. **A**, dorsal view, **B**, ventral view, **C**, right lateral view, and **D**, posterior view. Abbreviations:
516 **bo**, basioccipital; **eo**, exoccipitals; **op**, opisthotic; **pro**, prootic; **ps**, parasphenoid; **so**,
517 supraoccipital **st**, stapes; **?**, unknown fragment that may be part of the left stapes or the left
518 opisthotic. Scale bar equals 2 mm. [Half page width]

519

520 Figure 8. Strict consensus tree obtained from the phylogenetic analysis. Tree length =667,
 521 consistency index = 0.301, rescaled consistency index = 0.195, retention index = 0.647. Nodes of
 522 clades of interest are labeled: **A**, Amniota; **B**, **Sauropsida**; **C**, Parareptilia; **D**, Eureptilia; **E**,
 523 Lanthanosuchoidea; **F**, Bolosauria; **G**, Nyctiphruetidae; **H**, Nycteroleteridae; **I**, Pareiasauridae;
 524 **J**, Procolophonoidea. Bootstrap support values are found above nodes, if no value is indicated it
 525 was less than 50%. Bremer support values are found below nodes, if no value is indicated the
 526 clade collapsed with the addition of one extra step. [Half page width]

Figure 1

The skull of *Feeserpeton oklahomensis*, OMNH 73541, showing the regions that were reconstructed using CT data.

Scale bar equals 3 mm.

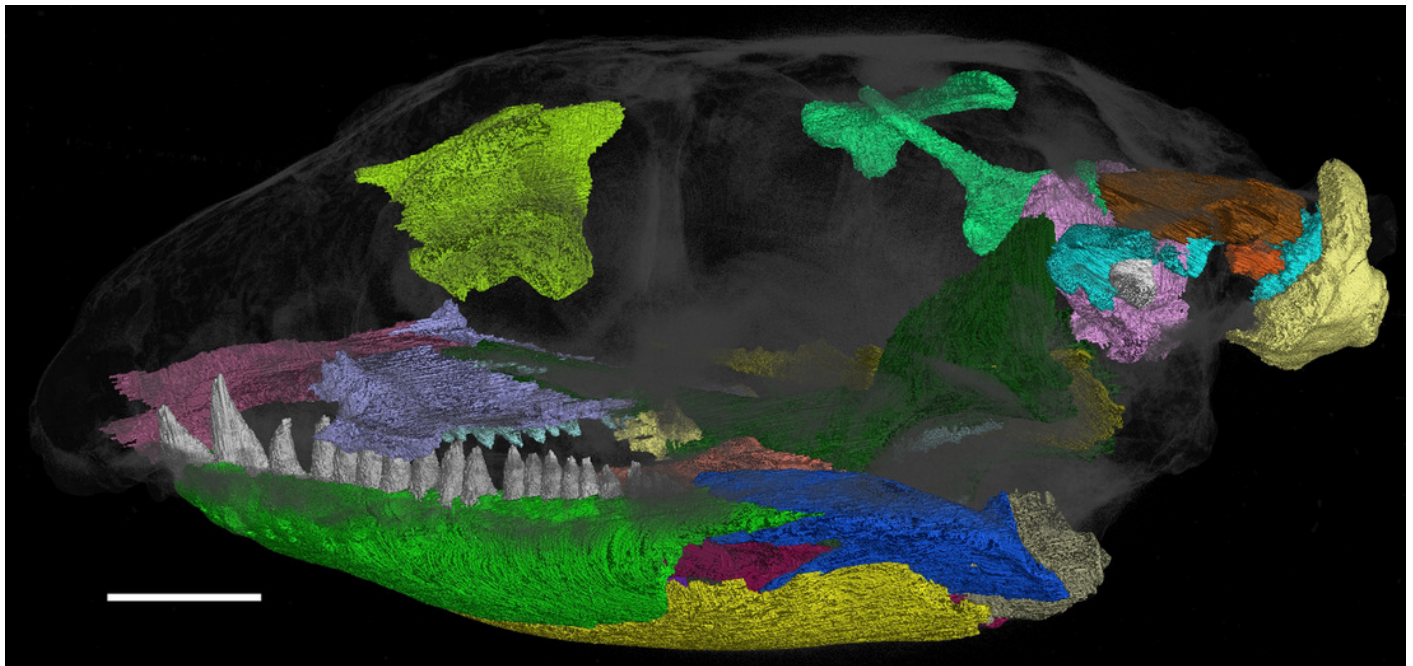


Figure 2

The palate of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from CT data.

(A) Dorsal view, and (B), ventral view. Abbreviations: **ec**, ectopterygoid; **m**, maxilla; **pal**, palatine; **ps**, parasphenoid; **pt**, pterygoid; **v**, vomer. Scale bar equals 4 mm.

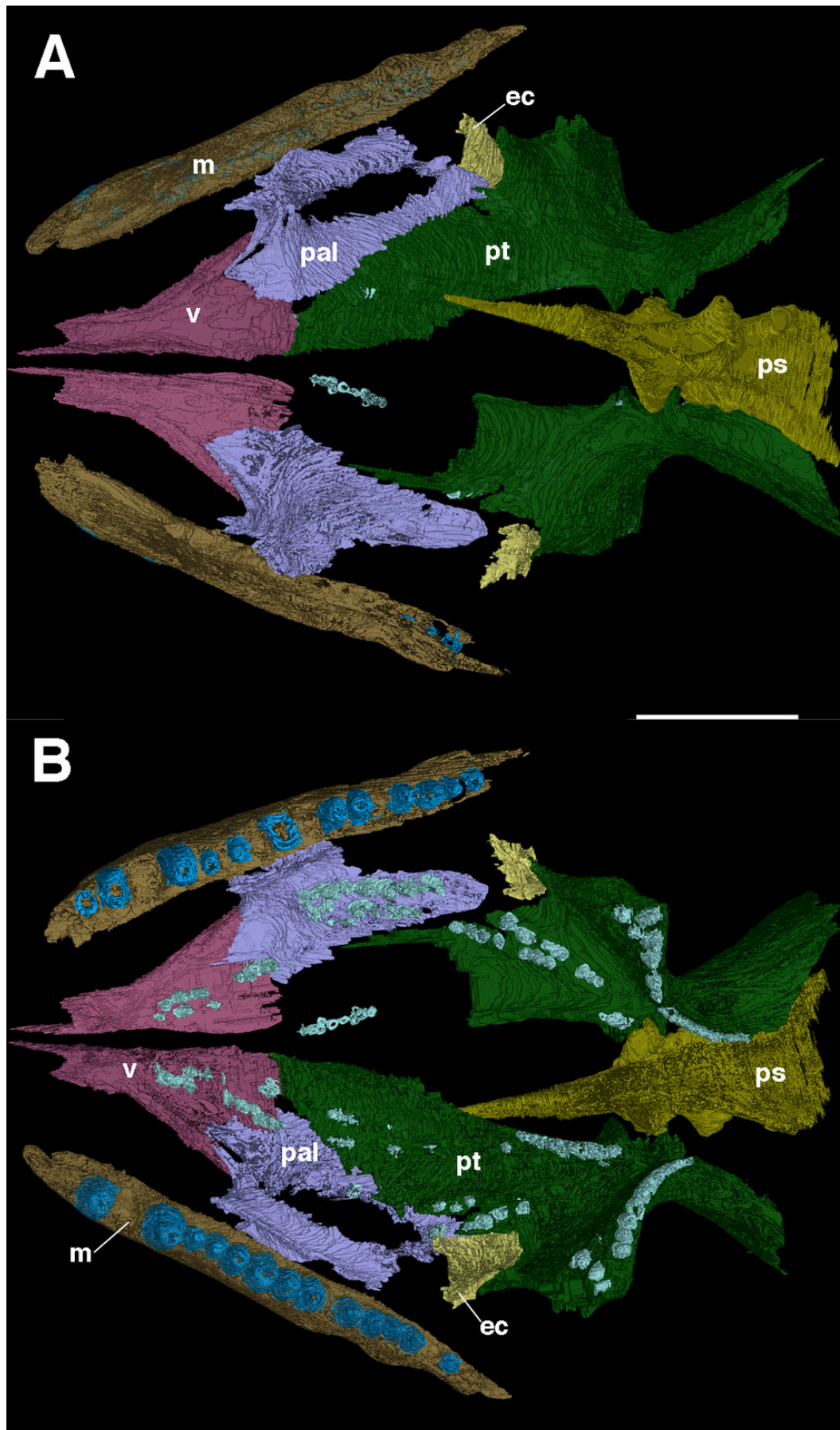


Figure 3

The left mandibular ramus of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from CT data.

(A) Dorsal view, (B) ventral view, (C) labial view, and (D) lingual view. Abbreviations: **an**, angular; **ar**, articular; **c**, coronoid; **d**, dentary; **pra**, prearticular; **sa**, surangular; **sp**, splenial. Scale bar equals 2 mm.

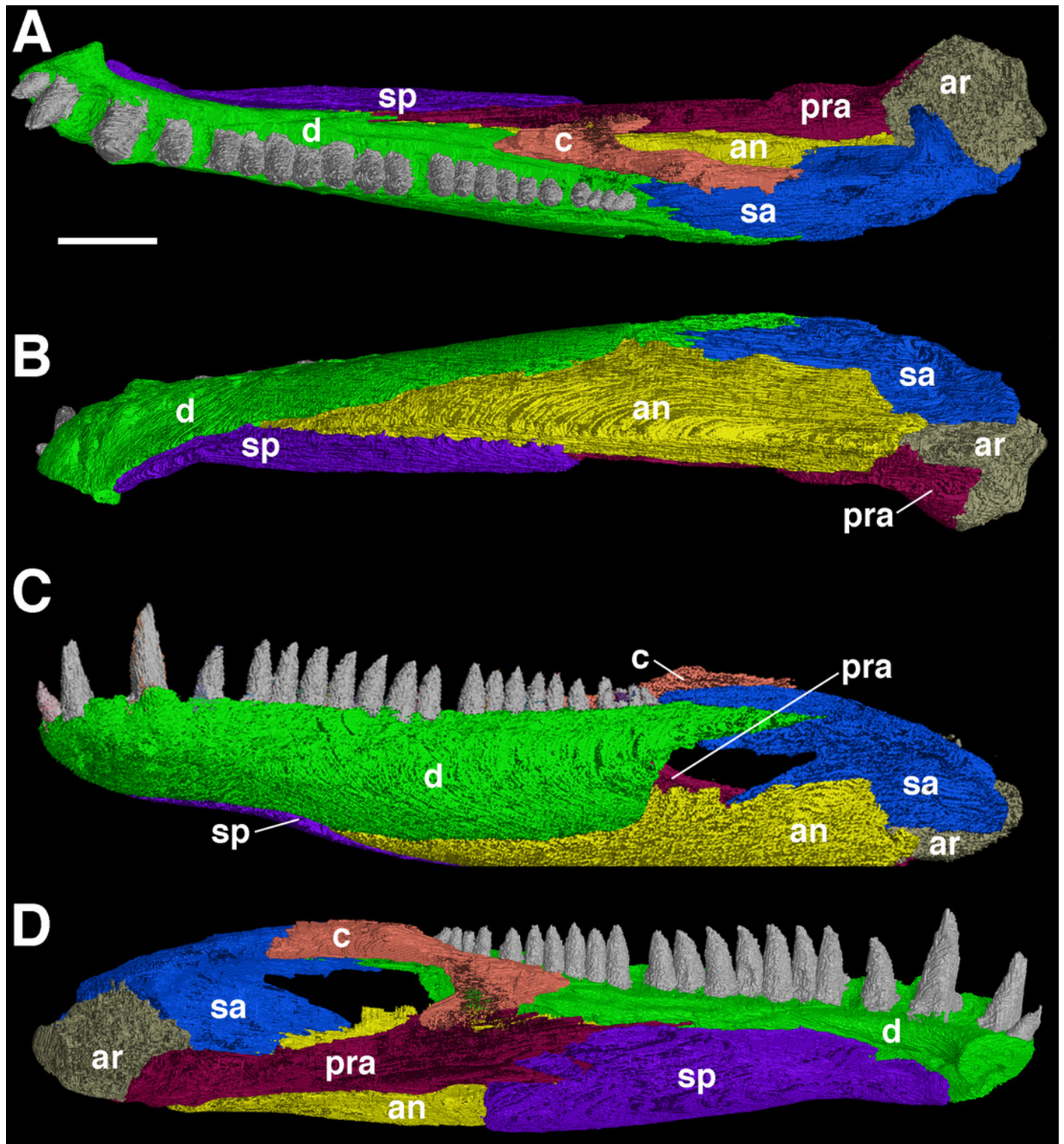


Figure 4

The right coronoid of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from CT data.

(A) Lingual view, and (B) dorsal view. Scale bar equals 1 mm.

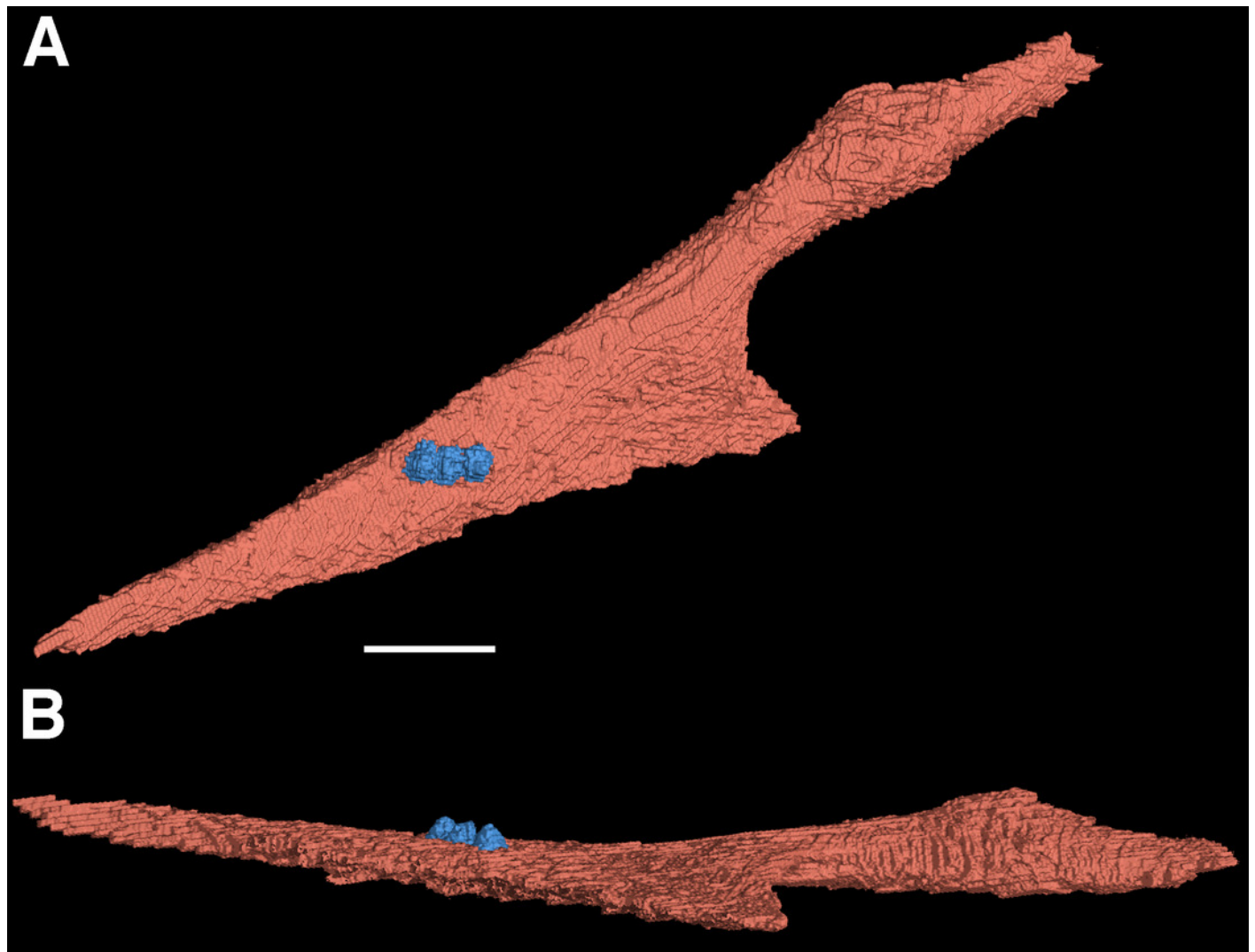


Figure 5

The sphenethmoid of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from CT data.

(A) Anterior view, (B) posterior view, (C) dorsal view, and (D) lateral view. Scale bar equals 1 mm.

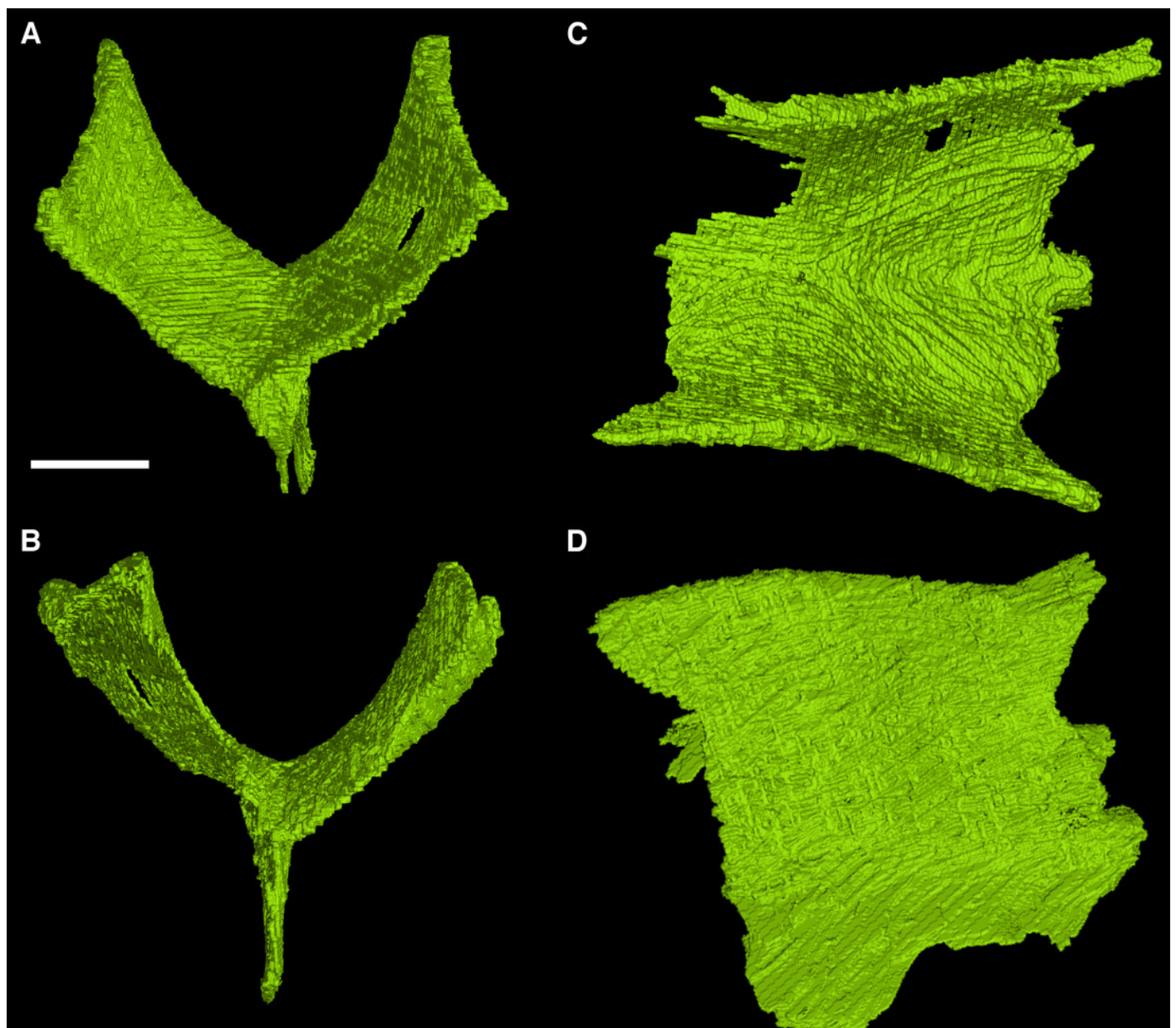


Figure 6

The left epipterygoid of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from CT data

(A) Lateral view, (B) medial view, (C) dorsal view, and (D) ventral view. Scale bar equals 1 mm.

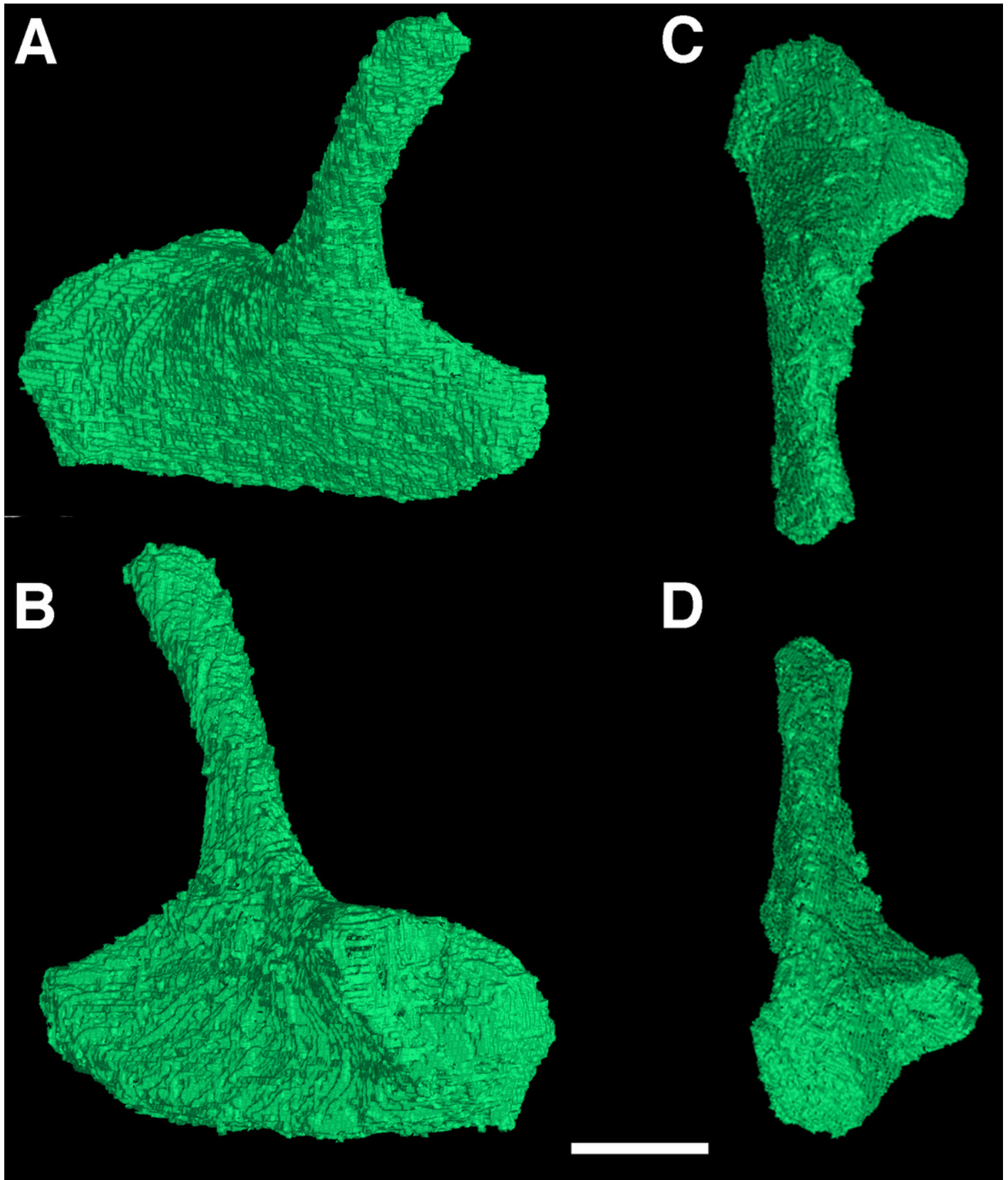


Figure 7

Figure 7. The braincase of *Feeserpeton oklahomensis*, OMNH 73541, reconstructed from CT data.

(A) Dorsal view, (B) ventral view, (C) right lateral view, and (D) posterior view. Abbreviations: **bo**, basioccipital; **eo**, exoccipitals; **op**, opisthotic; **pro**, prootic; **ps**, parasphenoid; **so**, supraoccipital; **st**, stapes; **?**, unknown fragment that may be part of the left stapes or the left opisthotic. Scale bar equals 2 mm.

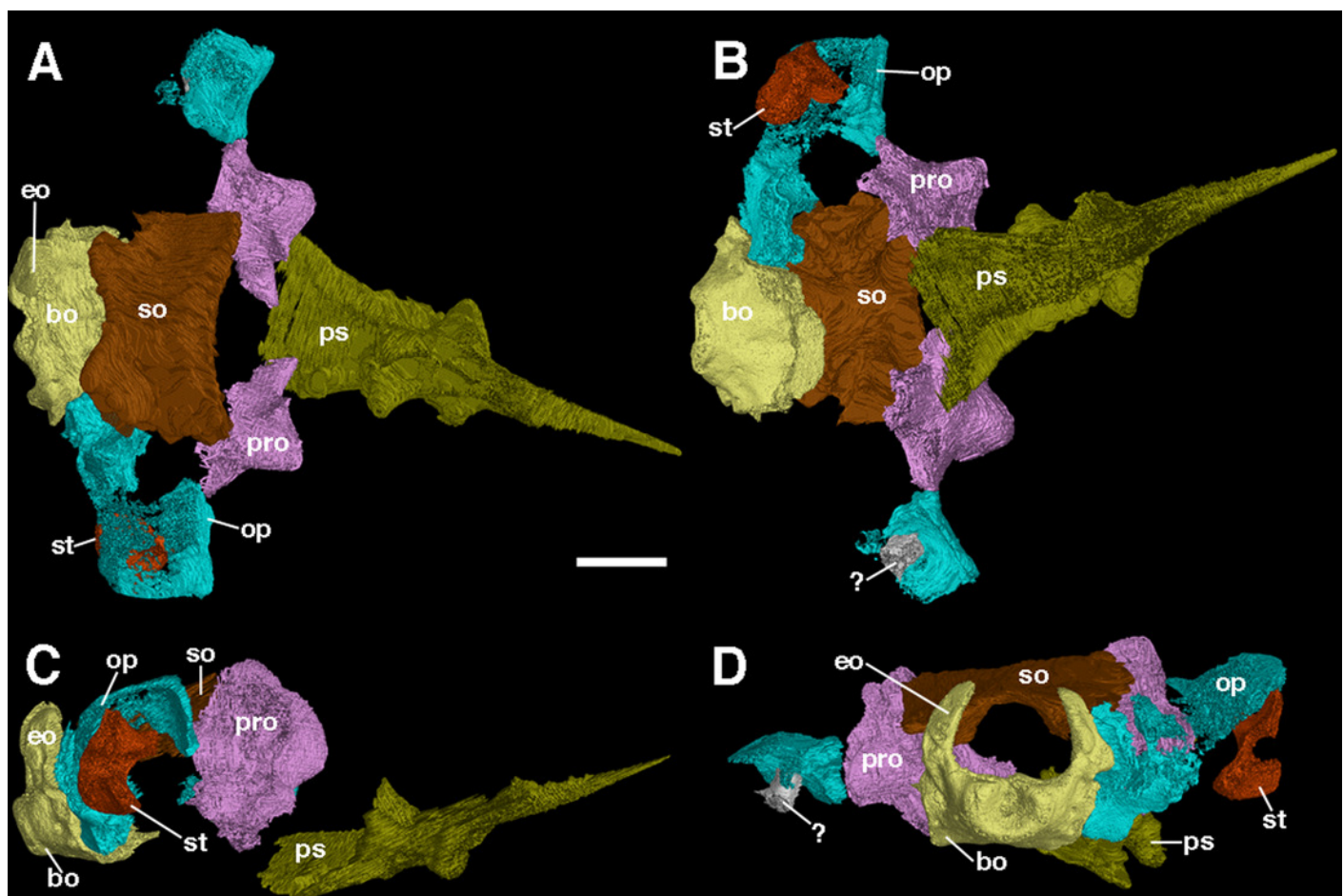


Figure 8

Strict consensus tree obtained from the phylogenetic analysis.

Tree length =667, consistency index = 0.301, rescaled consistency index = 0.195, retention index = 0.647. Nodes of clades of interest are labeled: **A**, Amniota; **B**, Sauropsida; **C**, Parareptilia; **D**, Eureptilia; **E**, Lanthanosuchoidea; **F**, Bolosauria; **G**, Nyctiphruretidae; **H**, Nycteroleteridae; **I**, Pareiasauridae; **J**, Procolophonoidea. Bootstrap support values are found above nodes, if no value is indicated it was less than 50%. Bremer support values are found below nodes, if no value is indicated the clade collapsed with the addition of one extra step.

