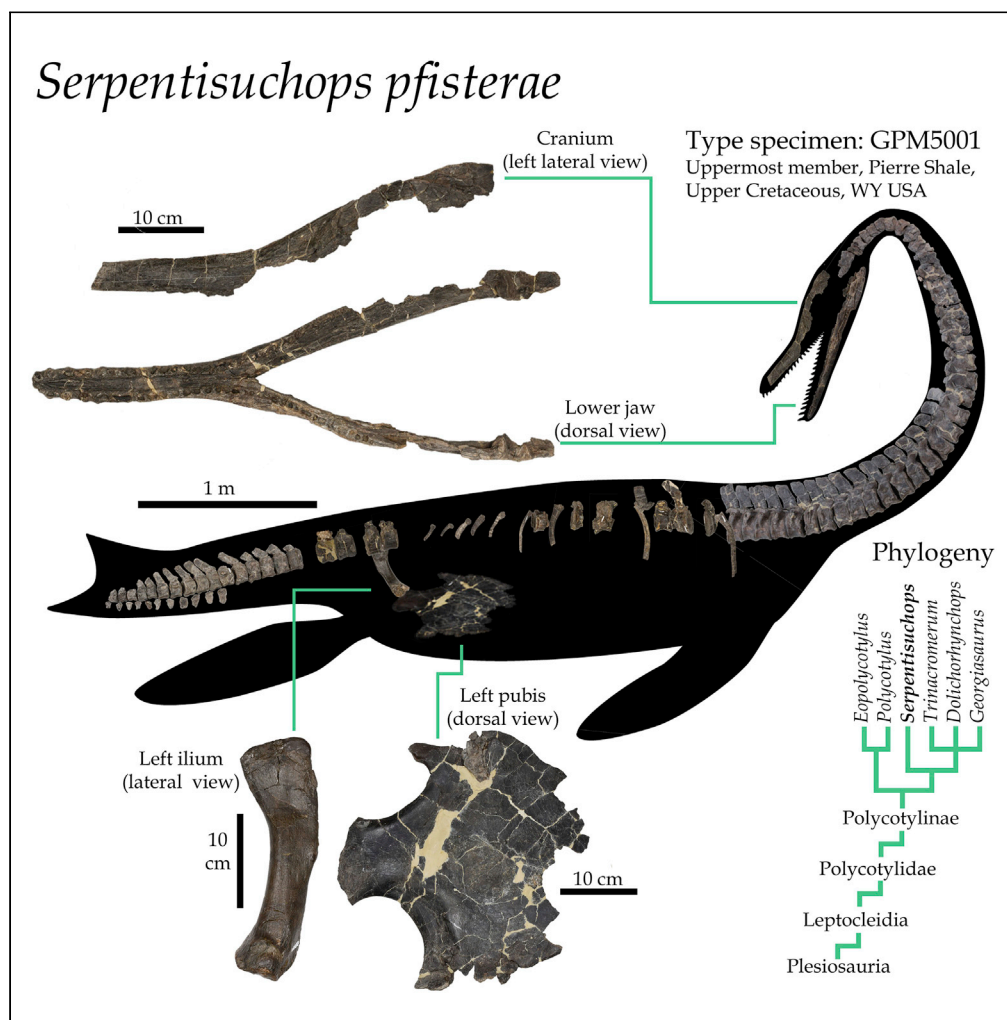


Article

A long-snouted and long-necked polycotyloid plesiosaur from the Late Cretaceous of North America



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Highlights

Serpentsuchops is a polycotyloid plesiosaur, from the Cretaceous of Wyoming

Unlike most plesiosaurs, it has both a long neck and large, elongated jaws

The partial skeleton indicates the animal was over seven meters long

The long jaws and neck likely aided in rapid lateral striking to snag fast, small prey



Article

A long-snouted and long-necked polycotyliid plesiosaur from the Late Cretaceous of North America

Walter Scott Persons IV,^{1,2,5,*} Hallie P. Street,³ and Amanda Kelley⁴

SUMMARY

Plesiosaurs are a group of Mesozoic marine diapsids. Most derived plesiosaurs fall into one of two typical body forms: those with proportionately small heads, short snouts, and elongated necks, and those with large heads, elongated snouts, and short necks. *Serpentisuchops pfisterae* is a polycotyliid plesiosaur from the Upper Cretaceous Pierre Shale that presents the trait combination of both an elongate snout and elongate neck (consisting of 32 vertebrae). Phylogenetic analysis places *Serpentisuchops* within the Polycotylinae, indicating that its long snout is an ancestral trait, while its long neck is secondarily derived and convergent with that of ancestral plesiosaurs, contemporaneous elasmosaurids, and some more basal members of the Polycotyliidae. The conical, recurved, and narrow teeth are consistent with a piscivorous diet. The tall and anteroposteriorly broad cervical neural spines indicate large epaxial muscles, suggesting that *Serpentisuchops* used both its neck and snout in fast lateral strikes aimed at proportionately small prey.

INTRODUCTION

Polycotyliidae is a derived group of plesiosaurs with a cosmopolitan distribution throughout the Late Cretaceous oceans. Although some more basal Turonian forms, such as the Moroccan *Thililia longicollis* and *Manemergus anguirostris*, are known to have long cervical series (30 and 25 vertebrae, respectively (Bardet et al., 2003; Buchy et al., 2005)) and elongated mandibles, all previously known polycotyline taxa are characterized by a reduced cervical series (≤ 26 vertebrae) and highly elongated, narrow snouts. We describe the polycotyliid *Serpentisuchops pfisterae*, from the upper Pierre Shale (Upper Cretaceous) of Wyoming, which possesses both an elongated cervical series and an elongated, narrow snout.

Plesiosauria de Blainville, 1835.

Plesiosauroidea Welles, 1943.

Polycotyliidae Williston, 1908.

Serpentisuchops pfisterae Persons, Street, and Kelley, 2022, gen. et sp. nov.

Etymology *Serpentisuchops* from *serpent* (Latin), snake, *suchus* (Latin), crocodile, and *ops* (Greek), face; and *pfisterae* for Anna Pfister, the landowner whose generosity afforded the scientific study and donation of the type specimen.

Holotype Specimen GPM5001 at the Glenrock Paleon Museum in Glenrock, Wyoming, USA, a partial skull, lower jaw, and vertebral column, plus left ileum and pubis (Figure 1).

Horizon and Locality Old Woman Anticline (Gill and Cobban, 1966), upper half of the upper member of the Pierre Shale, lower Maastrichtian (Upper Cretaceous), 69.59 (± 0.36) to 70.00 (± 0.45) million years ago (Ogg et al., 2012).

Diagnosis A polycotyliid (Figure 2) having 36 dentary alveoli; a mandibular symphysis dominated by the dentaries and in which each angular extends for less than 0.3% of the total symphysis length (6 mm in

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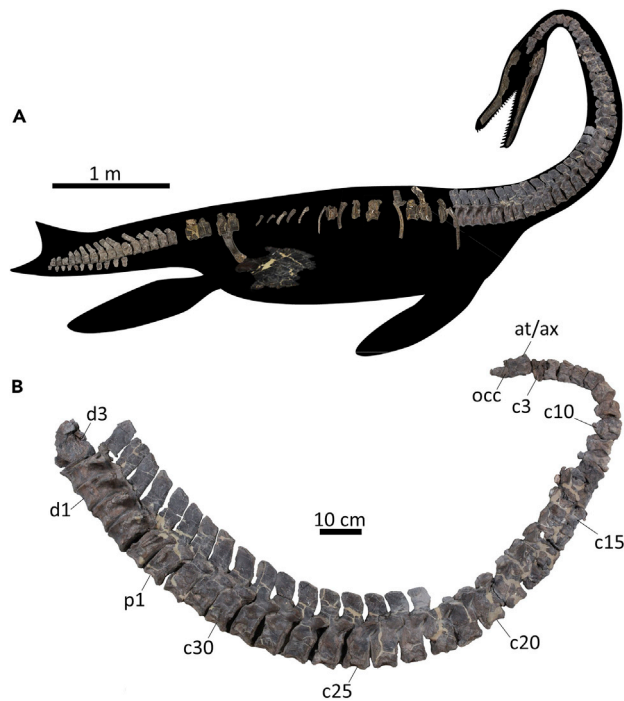


Figure 1. Holotype of *Serpentsuchops pfisterae*. Specimen GPM5001 from the Upper Cretaceous Pierre Shale Formation, of Wyoming

(A) Composite image of known skeletal material and interpretative body silhouette.

(B) Cervical, pectoral, and anterior dorsal vertebral series in articulation as preserved. Many of the neural spines abut one another, suggesting that (although all preserved zygapophyses remain in articulation) dorsal flexion of the neck much beyond the preserved condition would not have been possible in-life. The prepared side exposes the left lateral surface of the atlas-axis complex, the dorsal surface of cervicals 3–7, various intermediate surfaces of cervicals 8–13, and the right lateral surfaces of cervicals 14–32. The atlas-axis complex is preserved in articulation with the occipital condyle and the rest of the cervical series, and the final cervical is articulated with the first pectoral vertebrae, thus the completeness of the cervical series is certain. at/ax, atlas-axis complex; c, cervical vertebra; d, dorsal vertebra; occ, occipital condyle; p, pectoral vertebra.

the holotype); a pre-dorsal vertebra series of 32 cervical vertebrae and 4 pectoral vertebrae; posterior cervical vertebrae with neural spines that broaden anteroposteriorly into expanded dorsal tips; an ilium with a sacral end that is the anteroposteriorly widest and mediolaterally thinnest part of the ilium and is neither rounded nor tapered, but forms an abrupt and anteroposteriorly straight edge; and a pubis with a posterolateral edge that extends anteriorly and curves strongly to form a posterolateral projection that is hook-shaped in dorsal and ventral view. In addition, *Serpentsuchops* presents a unique combination of characters: as in *Polycotylus*, the splenial is not visible dorsally and the left and right angulars never converge on the ventral surface of the mandible; as in *Dolichorhynchops*, the dorsal vertebrae have anteroposteriorly elongate centra and neural spines with anteroposteriorly long and flat distal tips; the medioposterior edge of the pubis is strongly curved, but does not end in a prominent posterior projection (as it does in *Dolichorhynchops tropicensis*) and does not extend as far posteriorly as the ischial articulation facet.

DESCRIPTION

The specimen was embedded in fine gray shale, and all elements suffer mild deformation in the form of compaction. The first 38 vertebrae (32 cervicals, 4 pectorals, and 2 dorsals) were preserved in a fully articulated series, with the cranium articulated with the atlas axis complex and overlaying the mandible. The remaining elements were recovered *in situ* and in close association.

Cranium

The cranium suffers from strong taphonomic lateral compaction (Figure 3). The anterior end of the snout is missing, as are most of the braincase and palate elements ventral to the parietal. The left lateral face of the

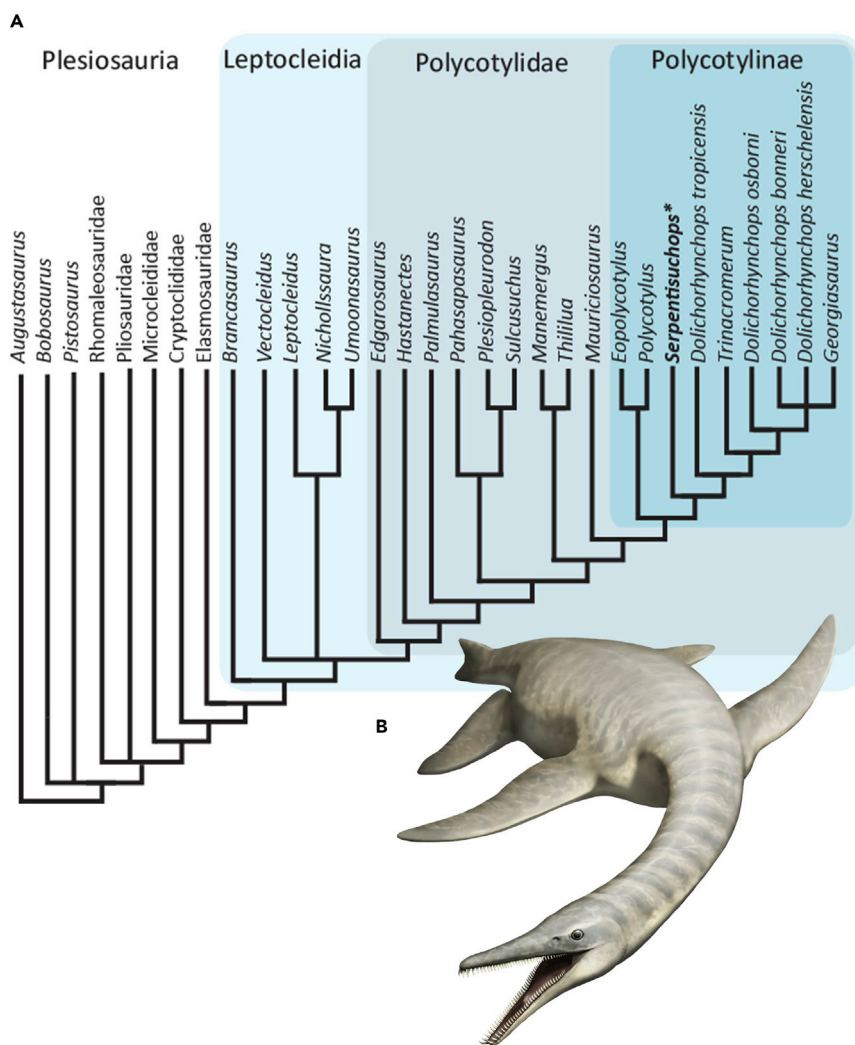


Figure 2. Simplified phylogeny showing genera within Leptocleidia and other clades within Plesiosauria

(A) The phylogeny resulting from an implied weight parsimony analysis of the data matrix (Fischer et al., 2018; Benson and Druckenmiller, 2014) in which *Serpentsuchops* is incorporated (see supplemental information). *Serpentsuchops* is resolved as the sister taxon to a clade containing all species of *Dolichorhynchops* plus *Georgiasaurus* and *Trinacromerum*. *Serpentsuchops* possesses three unambiguous synapomorphies of Polycotylidae: cervical vertebrae that are compressed anterodorsally, a mandibular symphysis that is long (measuring more than one-fourth of the entire mandibular length), and a splenial that is included in the mandibular symphysis. Symmetric resampling analysis returned results too low (<50) to present on the tree.

(B) Hypothetical flesh reconstruction of *Serpentsuchops pfisterae* by artist Nathan Rogers.

skull is the best preserved. Both the premaxilla and the maxilla are elongate and contribute to the snout. Along the section of snout that is preserved, the premaxilla is positioned dorsal to the maxilla (Figure 4). The premaxilla rises more steeply dorsally anterior to the orbit than is seen in *Dolichorhynchops* spp. (O'Keefe, 2008; Morgan and O'Keefe, 2019), forming a dorsally concave profile. This portion of the skull often suffers taphonomic damage, so it is difficult to be certain whether the relatively shallow incline of the premaxilla of *Dolichorhynchops* spp. is real or an artifact of preservation. *Edgarosaurus muddi* is a more basal polycotylid that does exhibit a similarly steeply inclined premaxilla (Druckenmiller, 2002), however, that taxon has a distinctly shorter snout than *Serpentsuchops*.

Posteriorly, the premaxilla overlaps the frontal along the midline and, dorsal to the frontal, the premaxilla tapers to a thin wedge that ends at a narrow contact with the anteroventral edge of the parietal. The maxilla also contacts the frontal, but the full extent of the contact is not preserved. There are seven maxillary alveoli

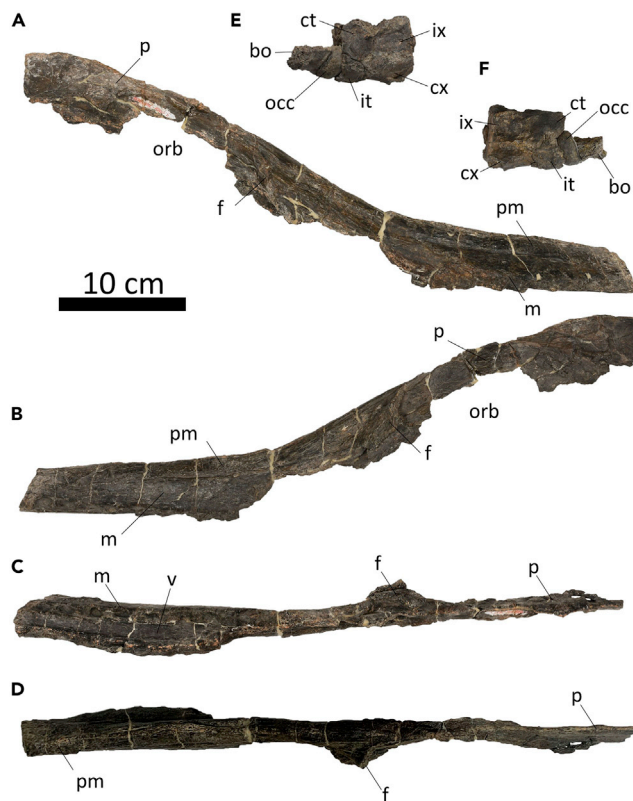


Figure 3. Details of the cranium and atlas-axis complex of the holotype

(A) Cranium in right lateral, (B) left lateral, (C) ventral view, and (D) dorsal view. Basicranium in articulation with the atlas-axis complex in (E), left lateral, and (F) right lateral view. bo, basioccipital; ct, atlat centrum; cx, axial centrum; f, frontal; it, atlat intercentrum; ix, axial intercentrum; m, maxilla; occ, occipital condyle; orb, orbit; p, parietal; pm, premaxilla; v, vomer.

preserved on the left side, and all show a circular form (consistent with the alveoli of the dentary). The parietal comprises a majority of the skull roof and the entire dorsal margin of the orbit. The orbit is large, spanning 113mm anteroposteriorly. The orbit appears to have a slightly ovoid shape, more elongated anteroposteriorly than dorsoventrally. Other long-necked Cretaceous plesiosaurs, including *Thalilua* and elasmosaurids, have convergently evolved dorsally oriented orbits (Fischer et al., 2018). There is no evidence that the orbits of *Serpentisuchops* differ in orientation from those of closely related short-necked polycotylines, like *Dolichorhynchops* and *Trinacromerum*; however, the strongly compacted form of the specimen makes this assessment tentative. Although the posterior of the parietal is not present, the anterior form of the sagittal crest affirms that it was low and long, as in *Trinacromerum* and unlike in *Dolichorhynchops* (McKean, 2012).

Overall, the mandible is anteroposteriorly elongate, short dorsoventrally, and has a triangular outline in the dorsal and ventral view (Figure 5). It obtains its greatest width (230mm) posteriorly and extends for 640mm anteroposteriorly. The anterior left and right halves of the mandible form a tightly fused symphysis, which accounts for over 40% of the total mandible length and spans 19 tooth positions. This symphyseal length is similar to those seen in *Dolichorhynchops bonneri* (19 tooth positions) (O'Keefe, 2008) and *D. herschelensis* (17–18 tooth positions) (Sato, 2005). The total tooth count of 36 also closely compares with those of *D. herschelensis* and *D. tropicensis* (37 for each) (Sato, 2005; McKean, 2012). The symphyseal portion of the mandible maintains a roughly consistent width of 40mm. Along the length of the mandibular symphysis, the lateral margin of the dentary bulges around each alveolus, giving the snout an undulating dorsolateral margin. Although all other alveoli have a roughly straight and dorsal orientation, the three anterior-most tooth positions are angled anteriorly, showing that the first three dentary teeth were strongly procumbent. Procumbent anterior teeth are also seen in *Edgarosaurus* (Druckenmiller, 2002). Small foramina are present along the lateral and ventral surfaces of the dentary. Anteriorly, these foramina are densely concentrated,

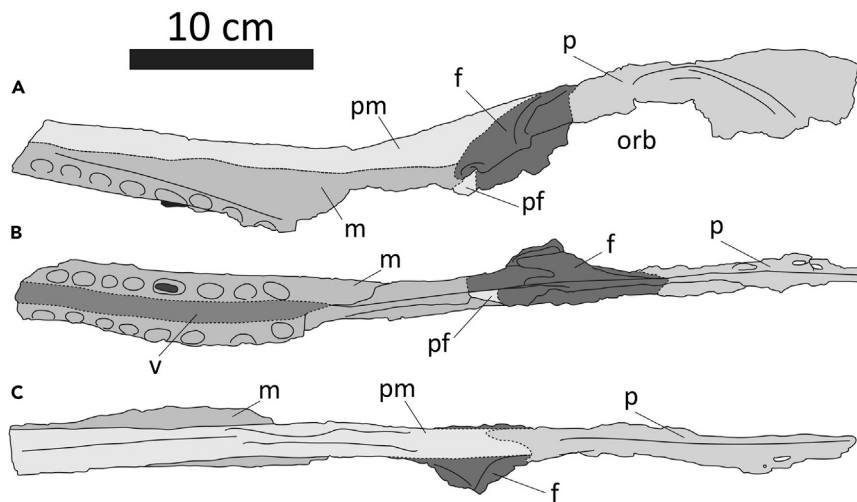


Figure 4. Interpretative illustration of the cranium

Skull in (A) left lateral, (B) ventral, and (C) dorsal view. Dotted lines denote visible sutures. f, frontal; m, maxilla; orb, orbit; p, parietal; pf, prefrontal; pm, premaxilla; v, vomere.

but that density decreases posteriorly. The foramina become absent on the ventral surface past alveolus seven and absent on the lateral surface past alveolus sixteen.

The posterior-most portion of the right dentary is missing, but the left dentary is nearly complete (Figure 5). Dorsally and ventrally, the dentary-to-dentary fusion constitutes a majority of the mandibular symphysis. Dorsally, medial to the dentary, the coronoid extends into the mandibular symphysis until alveolus thirteen. We observe no contribution to the dorsal surface of the mandibular symphysis by the splenials. As in *Polycotylus*, but unlike *Dolichorhynchops* spp. (Morgan and O’Keefe, 2019; O’keefe, 2008), the left and right angulars never converge on the ventral surface (Figure 6). Instead, each angular extends into the mandibular symphysis for only a short distance (less than 6mm) and the splenials converge and extend for a more substantial distance (73mm), terminating ventrally to tooth position 11. Both surangulars are badly damaged and neither coronoid process is present. The articular bears a deep socket for the upper jaw articulation that is rimmed by thin bone along the anterior edge. Posterior to the jaw articulation surface, the articular tapers more gradually than in *Dolichorhynchops* spp. or *Polycotylus* (O’keefe, 2008; Schumacher and Martin, 2016).

A single complete tooth is preserved still within its socket (left dentary alveolus seven). This tooth has suffered compaction such that it lies flat on the dorsal surface of the dentary and points anteriorly. Broken teeth are present in the right dentary alveolus one and the left dentary alveoli five and eighteen. Nineteen disarticulated teeth were found in close association with the skeleton. The presence of roots rules out the possibility that the disarticulated teeth were shed by another plesiosaur, and the form of the teeth matches that of the articulated teeth. Given the lack of elements from any other animals discovered in association with the skeleton, the disarticulated teeth are here considered to belong to GPM5001. Which of these teeth belongs to the lower or upper jaw is unknown. All recovered teeth have a singular tall, narrow, conical, and posteriorly curved form, which is typical of polycotylids such as *Dolichorhynchops osborni* (Williston, 1907), but differs from that of *Polycotylus latipinnis* (Schumacher and Martin, 2016). However, the alveoli for the anterior three tooth positions are larger than all remaining alveoli. Whether this is merely the result of the procumbent nature of these teeth producing oblique alveoli, or if these anterior teeth were the largest in the mandible is unclear without the corresponding teeth preserved *in situ*. No serrations are present and the teeth lack carinae. The lack of carinae differentiates *Serpentisuchops* from *Palmulasaurus* and *Eopolycotylus*, which have weak posterior carinae (Albright et al., 2007), and the Moroccan taxa *Thililua* and *Manemergus*, which exhibit mesiolabial carinae on the anterior teeth (Fischer et al., 2018). The enamel surfaces of the crowns bear abundant, fine longitudinal ridges. In one case, the anterior enamel surface of a crown is worn, likely from where it lightly contacted another tooth when the jaws were closed (Figure 7). In combination with the tight spacing of most of the alveoli and the height of the teeth, this evidence of wear indicates that the teeth of the upper and lower jaws tightly interlocked. That interpretation is further supported

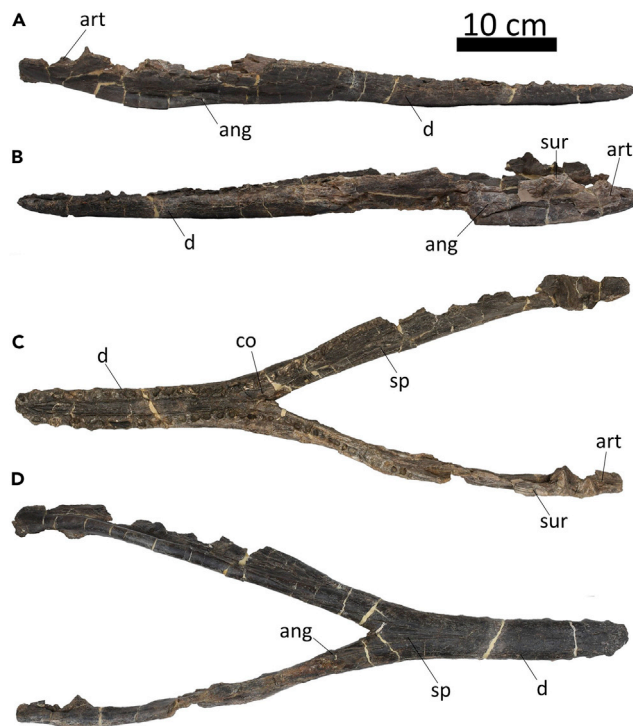


Figure 5. Details of the lower jaw of the holotype

Mandible in (A) right lateral, (B) left lateral, (C) dorsal, and (D) ventral view. ang, angular; art, articular; co, coronoid; d, dentary; sp, splenial; sur, surangular.

by the presence of lateral interdental pits between alveoli three and four and between four and five, which would have accommodated tight occlusion. Evidence of tight interdigitation is also reported for tooth positions three through eight of *Edgarosaurus muddi* (Druckenmiller, 2002), though the teeth of that taxon are more robust than those of *Serpentisuchops pfisterae*.

In overall form, the skull and lower jaw of GPM5001 are similar to that of the polycotyline *Dolichorhynchops*, *Polycotylus*, and *Trinacromerum*, which are also known from Late Cretaceous Western Interior Seaway deposits. Like these taxa, GPM5001 has a post-snout skull region that is anteroposteriorly compact, with the orbits positioned close to the posterior skull margin, and with a strongly dorsally sloping skull roof anterior to the sagittal crest. The result is an extended snout that is both mediolaterally and dorsoventrally narrow. This is as opposed to the general skull form seen in most non-polycotyline polycotylids, such as *Manemergus* (Buchy et al., 2005), *Plesiopleurodon* (Carpenter, 1996), and *Thililua* (Bardet et al., 2003; Fischer et al., 2018), which have more extensive post-orbital regions (sometimes described as “box-like” (Buchy et al., 2005)) and more gradually sloping foreheads. Similarly, the lower jaw of GPM5001 is thin dorsoventrally. This includes a surangular that is dorsoventrally short, as in *Dolichorhynchops* (Morgan and O’Keefe, 2019), *Georgiasaurus* (Storrs et al., 2003), and *Polycotylus* (Schumacher and Martin, 2016), and proportionately shorter than in *Plesiopleurodon* (Carpenter, 1996), *Sulcusuchus* (O’gorman and Gasparini, 2013), and *Thililua* (Bardet et al., 2003).

Postcranium

Typical of derived polycotylids, the vertebrae are amphicoelous and the lateral surfaces of the centra bear concavities (Carpenter, 1996; Morgan and O’Keefe, 2019). The cervical series is fully articulated. The atlas and the axis are solidly fused to each other. The left transverse process of the atlas is present and has a short-rounded form. The cervical vertebrae (totaling 32) are strongly amphicoelous. Only a few broken cervical ribs remain articulated. However, the ventrally positioned articulation facets for the cervical ribs are large and easily discerned. The neural arches of cervicals 3–13 are missing or badly damaged. Starting at cervical 14, prezygapophyses are present. The prezygapophyses are large and wide, such that they project laterally beyond the margins of the centrum. The postzygapophyses are

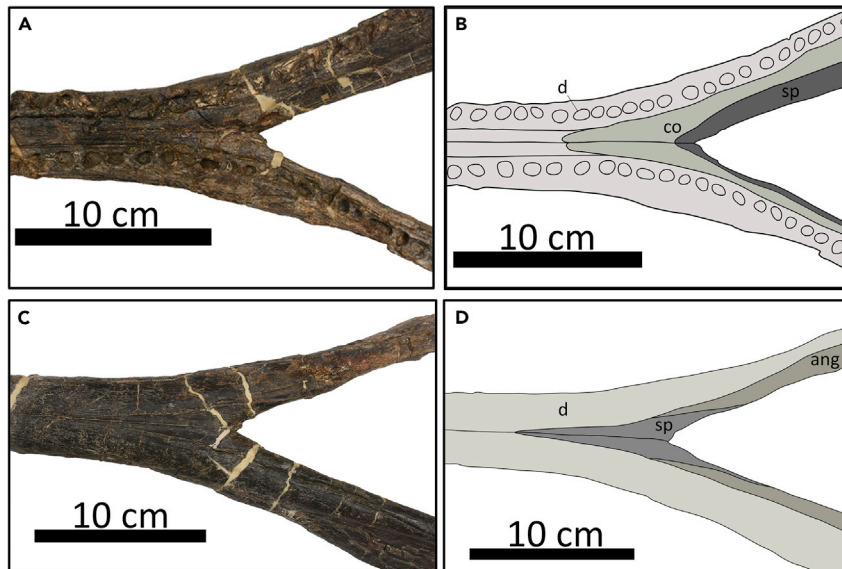


Figure 6. Details of the mandibular symphysis of the holotype

Closeup of the mandible in (A) dorsal and (C) ventral view. (B and D) respective interpretative illustration. ang, angular; co, coronoid; d, dentary; sp, splenial.

equally wide, with a roughly horizontal orientation. Preserved neural spines are absent until cervical 22; after which, they increase in height relative to the centrum. The neural spines are flat laterally, broad anteroposteriorly, and project at a slight posterior angle. The neural spines have a posterior position relative to the centrum, such that the posterior edge of the neural spines extends beyond the posterior centrum edge. Unlike the form recorded in other polycotylines, including *Eopolycotylus* (Albright et al., 2007), *Polycotylus* (Schumacher and Martin, 2016), and *Trinacromerum* (Thurmond, 1968), the posterior cervical neural spines do not taper dorsally, rather they increase in anteroposterior length and end in a roughly straight horizontal edge.

A complete series of four pectoral vertebrae is preserved in articulation, immediately following the cervicals. Following the standardized definition of Sachs et al. (Sachs et al. (2013), pectoral vertebrae are here considered to be vertebrae posterior to the cervical series with rib facets that originate entirely on the lateral surfaces of the centra and not yet from a portion of the neural arches (note that this definition is not always adhered to in the taxon scores of some recent phylogenetic datasets, e.g., Fischer et al. (Fischer et al. (2018), and scores have been adjusted accordingly). The centra are strongly amphicoelous and spool shaped, with anterior and posterior faces that are wider mediolaterally, relative to the anteroposterior centrum length, than those of the cervicals. A small foramen is present just ventral to the base of each rib facet. Additional foramina are present on the ventral centrum surface. The transverse processes of pectorals 1 and 2 are broken, but their bases indicate a narrow form that was much taller dorsoventrally than wide anteroposteriorly. Pectorals 3 and 4 have transverse processes with an anteroposteriorly wider and more typical form. The neural arches are short. Relative to the zygapophyses of the cervicals, the pectoral zygapophyses are reduced, with both the post- and prezygapophyses projecting a shorter anteroposterior distance and being less wide mediolaterally. The neural spines are mediolaterally thin and anteroposteriorly long. The posterior slant of the neural spines is reduced, relative to that of the posterior cervicals.

The first two dorsal vertebrae are part of the articulated series. The third dorsal vertebra was preserved out of alignment but adjacent to the second. Six additional disarticulated dorsal vertebrae were recovered, but their position within the dorsal series is indeterminate. Assuming a dorsal series roughly equivalent to that of other derived polycotylids (~22) (Thurmond, 1968), slightly more than half of the dorsal vertebrae are absent. The centra of the dorsal vertebrae are spool-shaped with round and amphicoelous anterior and posterior faces. The articular facets for the rib heads are slightly inclined, indicating that the ribs are extended at a posterior angle. The dorsal vertebrae of *Serpentisuchops* differ noticeably from those of

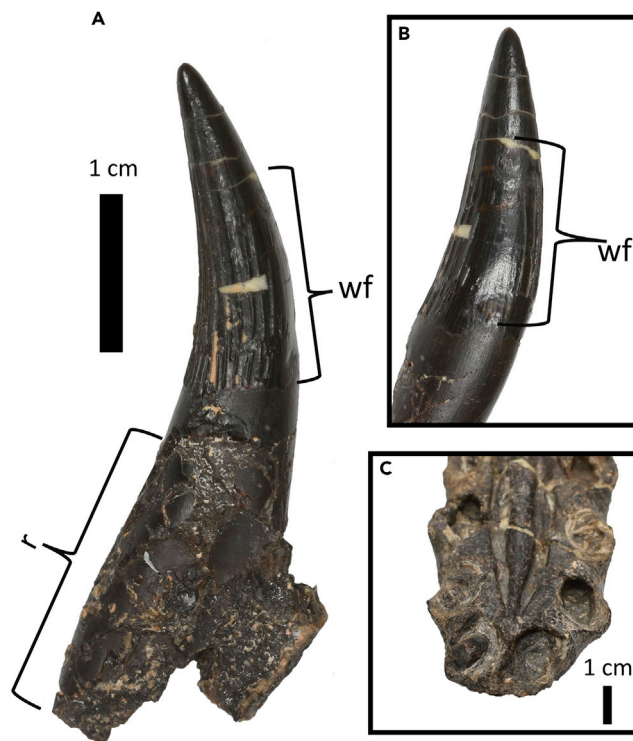


Figure 7. Details of the dentition the holotype

(A) Overview of the most complete and best-preserved tooth and (B) details of the worn surface.

(C) Anterior tip of the dentary, showing anterodorsally angled alveoli, indicating strongly procumbent dentition. r, root; wf, wear facet.

Polycotylus in having anteroposteriorly longer centra and neural spines with anteroposteriorly long and flat tips. In both these respects, *Serpentisuchops* more closely matches the morphology of *Dolichorhynchops* (Adams, 1997; Sato, 2005).

A set of two closely associated vertebrae are identifiable as the sacra, based on the absence of chevron facets and the presence of broken but attached sacral rib bases (Figure 8). The two sacral vertebrae are still amphicoelous but less strongly spool shaped than the other vertebrae, with the lateral and ventral surfaces of the centrum being less indented. The transverse processes are fused to the bases of the sacral ribs and originate primarily from the dorsal portion of the lateral centrum surface but also from the ventral portion of the neural arch. A large foramen is present at roughly the dorsoventral and anteroposterior midpoint of the lateral centrum surface. Additional smaller foramina are present on the lateral and ventral centrum surfaces, but their number and arrangement vary between the two sacra and between the left and right halves of the same centrum.

Two anterior caudals were recovered in close association with each other and appear to be a sequential set. The first of these two anterior caudals is close in size to the second sacral vertebra; however, it has both posterior and anterior chevron facets, indicating that it is not the first vertebra in the caudal series (in *Trinacromerum*, the first three caudal vertebrae lack chevron facets entirely (Thurmond, 1968)). Sixteen more posterior caudal vertebrae are preserved in a fully articulated series and with associated chevrons (Figure 9). The last and smallest of the posterior caudal vertebrae still has a posterior chevron facet and an associated chevron, indicating that it is not the terminal vertebra. Thus, there are three missing sections in the preserved caudal series (two anterior and one posterior) and the total number of vertebrae in the tail was at minimum 21.

All the caudal vertebrae are amphicoelous and bear prominent anterior and posterior chevron facets. The lateral surfaces of the centrum of the anterior-most preserved caudal lack any large sulcus. However, the



Figure 8. The sacral vertebrae of the holotype
(A) Anterior and (B), posterior view.

lateral centrum surfaces of the second of the preserved anterior caudals and all the posterior caudals are dominated by a large sulcus that is positioned ventral to each caudal rib articulation. In the thirteenth-most-posterior caudal and in all more posterior caudals, the caudal rib articulation has migrated ventrally onto the lateral centrum surface, and a second large sulcus is present dorsal to the caudal rib articulation (however, the articulation is never so dorsal as to be partially born by the neural arch). The ventral surface of each centrum is flat and bears a midline ridge. Posteriorly, the neural spines become reduced in height and also become proportionately narrower anteroposteriorly. The neural spines are mediolaterally flat and strongly angled posteriorly. The zygopophyses are greatly reduced and altogether absent on the five most posterior caudals. Most of the caudal ribs are broken, making their form and lateral extent impossible to judge. The fifth most posterior vertebra bears the final caudal rib set.

The eleven sequential chevrons are anteroposteriorly short. They suffer from lateral compression, which obscures details of the haemal arch. The haemal spines are dorsoventrally short, mediolaterally thin, and each forms an anteroposteriorly broad surface.

Both the left ilium and pubis are preserved (Figure 10). Polycotyloid ilia are highly variable across taxa and commonly utilized in taxonomic diagnoses (Schumacher and Martin, 2016). The acetabular half of the ilium is club shaped. The ilium shaft has a mediolaterally thick and roughly straight proximal half and a distal half that thins mediolaterally and widens anteroposteriorly. In these regards, the ilium closely resembles that of *Dolichorhynchops tropicensis*, *Polycotylus latipinnis*, and *Trinacromerum kirki* (Schumacher and Martin, 2016). However, the sacral end is distinct with an abrupt and anteroposteriorly straight edge.

Two articulation facets are present on the posterior end of the pubis. The facet for the ischium is smaller (roughly 50mm wide mediolaterally) and triangular. The facet that contributed to the acetabulum is larger (roughly 65mm wide mediolaterally). The neck supporting the articular head is more constricted than is seen in other polycotyloids (Albright et al., 2007; Carpenter, 1996), with *Dolichorhynchops herschelensis* being the most similar (Sato, 2005). The medioposterior edge is strongly curved, but does not end in a prominent posterior projection (as it does in *Dolichorhynchops tropicensis* (McKean, 2012)) and does not extend as far posteriorly as the ischial articulation facet. The medial edge is comprised of a large straight symphysis for articulation with the right pubis, while the posterolateral edge extends anteriorly and curves strongly to form a posterolateral projection – resulting in a prominent hook shape in the dorsal and ventral view. This pubic hook is a form not previously reported in the pelvis of any polycotyloid; however, a less prominent projection is present at the same position on the pubis of the *Dolichorhynchops bonneri* specimen KUV 40002 [pers. obs.].



Figure 9. Detail of the posterior caudal vertebrae and chevrons of the holotype

The articulated sequential series of 16 posterior caudal vertebrae and 11 chevrons in (A) right lateral and (B) left lateral view.

Phylogenetic analysis

The data matrix used to analyze the phylogenetic relationships of GPM5001 (*Serpentisuchops pfisterae*) to other polycotyliids was based on the taxon and character lists from Fischer et al. (Fischer et al. (2018), which in turn was based on the matrix developed originally by Benson and Druckenmiller (Benson and Druckenmiller (2014). The preserved elements permitted 76 of the 270 characters to be scored. The four new characters proposed by Morgan and O’Keefe (2019) were not incorporated, because those characters are not applicable to the material preserved in GPM5001.

The purpose of the phylogenetic analyses was not to extensively investigate the relationships within Polycotyliidae. Other researchers have done this work in recent years (McKean, 2012; Albright et al., 2007). Rather, our phylogenetic analyses were conducted to ascertain whether quantitative assessments would support our qualitative interpretations of the specimen.

RESULTS

In all trees, *Serpentisuchops pfisterae* was found to be the sister taxon to a clade within Polycotyliinae including *Dolichorhynchops* spp., *Trinacromerum bentonianum*, and *Georgiasaurus penzensis*. The new technology search resulted in a best score of 68.85340, which was hit one time, and 237 trees were retained. The traditional TBR search found 8,580 trees, with a consistency index of 0.2924 and a retention index of 0.6975. The resulting values of the symmetric resampling were too low within Polycotyliidae to report on the tree (<50). Among the 8,580 trees, Polycotyliidae remained relatively stable. The only differences were found to be the relationships between *Sulcusuchus erraini*, *Plesiopleurodon wellsi*, and the ‘Richmond pliosaur’ and the relationships between *Dolichorhynchops* ROM 29010, *D. bonneri*, *D. herschelensis*, and *Georgiasaurus penzensis*.

In all trees, *Edgarosaurus muddi* is found to be the basal-most species within Polycotyliidae, followed successively by *Hastanectes valdensis* and *Palmulasaurus quadratus*. Our analysis found *Pahasapasaurus haasi* to be the sister taxon of Occultonectia (sensu Fischer et al., 2018), and a sister taxon relationship between *Manemergus anguirostris* and *Thililua longicollis*. We recovered *Mauriciosaurus fernandesi* as the sister taxon of Polycotyliinae, and the sister pairing of *Eopolycotylus rankini* and *Polycotylus latipinnis* as the basal-most taxa within the subfamily. The characters that unite *S. pfisterae* with the *Dolichorhynchops* clade are posterior cervical neural spines, height relative to centrum: substantially taller [equal to or greater than 1.2 times centrum height] (ch.159, s.2); height of dorsal neural spines in lateral view: conspicuously taller than the centrum (ch.178, s.1); and caudal ribs facet location in proximal–middle caudal vertebrae: located dorsally, contacting or almost contacting neural arch (ch. 188, s.0). There is also one character that unites *S. pfisterae* with all of Polycotyliinae: pubis, ratio of anteroposterior length to minimum mediolateral width: >1.3 (ch. 229, s.1), a state also shared with Pliosauridae and Rhomaleosauridae. *S. pfisterae* also differs from the rest of Polycotyliinae for fourteen characters (chs. 23, 49, 62, 117, 119, 120, 123, 126, 142, 144, 167, 222, 225, and 226). However, there are missing data among those species and characters, so the list of differences is probably exaggerated by incomplete specimens.

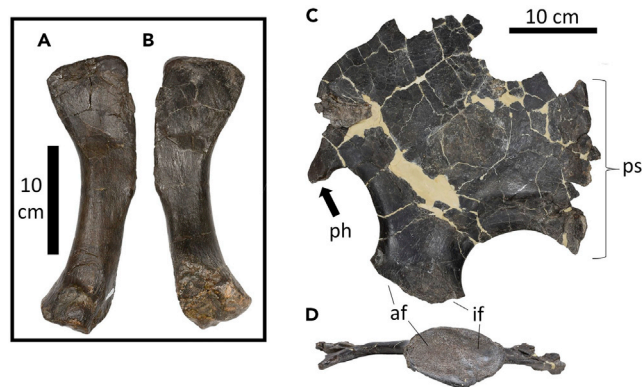


Figure 10. Details of the pelvic anatomy of the holotype

(A) Left ilium in lateral and (B) medial view.

(C) pubis in dorsal and (D) posterior view af, acetabular facet; if, ischial facet; ph, “pubic hook”; ps, pubic symphysis. The anterior edge of the pubis is not preserved. The lateral edge of the pubis presents the distinct trait of a hook-shaped projection. There is no osteological articulation associated with this region of the pelvis and the “pubic hook” presumably served as an enhanced attachment for musculature.

The results of this phylogenetic analysis agree with our morphological observations. Even though the holotype of *Serpentisuchops pfisterae* is incomplete, the preserved cranial and mandibular elements showed resemblances to *Dolichorhynchops* spp. most particularly *D. herschelensis*. However, despite the similarities in the configuration of the mandibular elements, the morphology of *S. pfisterae* displayed differences from the species of *Dolichorhynchops*. These morphological discrepancies, along with the autapomorphic cervical count and unique pubic shape suggested to us that this new specimen did not belong within the genus *Dolichorhynchops*. The morphology of the mandibles resembles species of *Dolichorhynchops* (McKean, 2012; O’keefe, 2008; Schumacher, and Martin, 2016; McKean, 2012), particularly *D. herschelensis* (Sato, 2005). The possibility that GPM5001 could be a longer-necked species of *Dolichorhynchops* was considered, but the morphological differences exhibited across the preserved skeleton are sufficiently distinct to merit a separate genus. The phylogenetic results found GPM5001 to be outside the *Dolichorhynchops* + *Trinacromerum* + *Georgiasaurus* clade, supporting our morphological interpretations. [See the [STAR Methods](#) section for details on the phylogenetic analysis and the [supplemental information](#) for the character matrix.]

DISCUSSION

The holotype skeleton of *Serpentisuchops pfisterae* possesses several autapomorphies that differentiate the taxon from other polycotyliids that it resembles. The hook-shaped projection on the posterolateral edge of the pubis extends the pelvic region associated with the puboischiofemoralis externus and puboischiofemoralis internus muscles (Carpenter et al., 2010) and also potentially the ambiens and pubotibialis muscles (Krahl and Witzel, 2021). This ‘pubic hook’ may be an adaptation for increasing the available muscle-attachment surface area and providing the attaching musculature with a more acute angle of pull with respect to hindlimb abduction. Debate surrounds the swimming styles of plesiosaurs. If *Serpentisuchops* swam using simple rowing motion (Lingham-Soliar, 2000), then this adaptation enhanced the recovery stroke. Alternatively, if, as recent experimental work suggests (Carpenter et al., 2010; Liu et al., 2015; Muscutt et al., 2017), plesiosaurs engaged in subaqueous flight, then the adaptation contributed to the hindlimb’s upstroke and, thereby, to direct generation of propulsive thrust.

The jaws and teeth of *Serpentisuchops* fall towards an extreme end of the known polycotyliid morphology (Table 1), with the teeth being gracile and the jaws long and thin (the mandibular symphysis spans 19 tooth positions – the same as in *Dolichorhynchops* and slightly more than the 18 of *Polycotylus*, the 12 of *Trinacromerum*, and the 15 of *Eopolycotylus*). Occlusive wear is uncommon among plesiosauroids with similarly tall and narrow teeth. In elasmosaurids, this absence of wear has been interpreted as supporting evidence for middle-trophic-level generalist feeding (Kear et al., 2017). Conversely, extensive wear and tooth pathologies have been used to argue for macrophagous diets in many large-skulled plesiosaurians (Kear, 2006; Massare, 1987). However, the observed wear on the single GPM5001 tooth does not extend to the tooth tip,

Table 1. Polycotyliid cervical and mandibular data

Symphysial relative length	0.42	0.45	0.49	0.4	?	0.47	0.45	0.28	?	0.43	0.37	?	0.44-
Symphysial tooth density	0.071	0.04	0.039–0.041	0.068	0.053	0.039	0.03–0.036	0.103	?	0.068	0.036	?	0.052
Symphysial tooth positions	19	19	18–19	17	15	18	12-8	15	?	9	12	8	15
Mandibular symphysis length	266	471	466	251	284	465	335	145	?	133	333	?	290
Mandible length	640	1050	942	627	???	980	745	520	?	312	900	760	663+
Total cervicals	32	21	20–21	21+	?	26	20	26	20–23	25	21+	?	30
Data source	Pers. obs.	O'Keefe, 2007*	Morgan and O'Keefe (2019)	McKean (2012)	Albright et al. (2007)	Schumacher, 2007	Schumacher, 2007; McKean (2012)	Druckenmiller (2002)	Benson et al., 2013	Buchy et al. (2005)	Schumacher, 2007	Carpenter, 1996*	Bardet et al. (2003)
Specimen	GPM5001	KUVP 40002	KUVP 4001	MNA V10046	MNA V9445	SDSM 23020	KUVP 5070	MOR 751	NHMUK R609	SMNK-PAL 3861	AMM 98.1.1	CM 2815	MNHGr. PA.11710
Taxon	<i>Serpentisuchops pfisterae</i>	<i>Dolichorhynchops bonneri</i>	<i>Dolichorhynchops osborni</i>	<i>Dolichorhynchops tropicensis</i>	<i>Eopolycotylus rankini</i>	<i>Polycotylus latipinnis</i>	<i>Trinacromerum bentonianum</i>	<i>Edgarosaurus muddi</i>	<i>Hastanectes valdensis</i>	<i>Manemergus anguirostris</i>	<i>Pahasapasaurus haasi</i>	<i>Plesiopleurodon wellsi</i>	<i>Thililua longicollis</i>
Classification	Polycotyliinae, Polycotyliidae	Polycotyliinae, Polycotyliidae	Polycotyliinae, Polycotyliidae	Polycotyliinae, Polycotyliidae	Polycotyliinae, Polycotyliidae	Polycotyliinae, Polycotyliidae	Polycotyliinae, Polycotyliidae	Polycotyliidae	Polycotyliidae	Polycotyliidae	Polycotyliidae	Polycotyliidae	Polycotyliidae

Symphysial tooth density = symphysial tooth positions/symphysial length, this ratio has been used to infer the preferential use of the anterior portion of the jaw in prey capture (Fischer et al., 2020; Massare, 1987); symphysial relative length = symphysial length/mandible length, this ratio has been used to characterize the overall jaw form and to infer the mechanical strength of the anterior region of the jaw (Fischer et al., 2020; Massare, 1987; Walmsley et al., 2013); *denote instances where measurements were not directly provided but were made from provided figures.

implying it is not the result of piercing and abrading prey. Rather the wear is limited to one side and appears to be the result of tooth-on-tooth contact as the widest portion of the crown base interfingered with another. This implies a tightly interlocking bite, but not one that routinely dispensed robust or particularly durable prey.

Long necks, with an excess of 30 cervical vertebrae, are the basal condition among early plesiosaurs. Paleontologists have long recognized the tendency of derived plesiosaurs to conform to one of two basic morphotypes: those with short snouts, small heads, and elongated necks (as exemplified by elasmosaurids and microcleidids) and those with long snouts, large heads, and short necks (as in many pliosaurids and most other polycotyliids) (Carpenter, 1996; O'Keefe, 2002; O'Keefe, 2001). Among polycotyliids, only the African-derived non-polycotyline *Thililua longicollis* approaches *Serpentisuchops* in this form. As a polycotyline, *Serpentisuchops* calls into question the reliability of assuming a conservative post cranium in polycotyliids for which the skull but not the complete cervical series is known, as in the case of *Eopolycotylus* (Albright et al., 2007) and *Dolichorhynchops herschelensis* (Sato, 2005). Nonetheless, the form of *Serpentisuchops* clearly represents a departure from the polycotyline norm. Among long-snouted and short-necked plesiosaurs, specialization for larger prey has been recognized in association with the subsequent development of greater body size, more robust teeth, and proportionately wider (latirostrine) skulls (Fischer et al., 2020). Polycotyliids generally retain medium body size and narrow (longirostrine) skulls, indicating a diet of small to medium-sized prey. The elongated and narrow jaws of *Serpentisuchops* would have reduced hydraulic resistance and, in combination with the anteriorly procumbent, tall, and tightly interlocking teeth, are consistent with a predation style aimed at seizing small aquatic prey (presumably the fish and cephalopods that were abundant in the Western Interior Seaway (Landman et al., 2008; Parris et al., 2007)) through the rapid lateral acceleration of the snout tip.

This raises the question of whether the evolutionary reversion to an elongate neck was an aid to such a lateral-striking feeding strategy. Certainly, the neck contributes to the effective forward reach of the jaws and, if swung, to the lateral reach and acceleration. Across the cervical series, the zygapophyses remain horizontally oriented, indicating a high degree of lateral flexibility (Nagesan et al., 2018). Similarly, the presence of large epaxial neck muscles is affirmed by the neural spines of the pectoral and posterior cervical vertebrae, which are proportionately tall and anteroposteriorly broader than in other polycotyliids. *Serpentisuchops* seems, then, to have been anatomically well equipped for swinging its neck sideways. Although the long-necked and narrow long-snouted form of *Serpentisuchops* is unique among polycotyliines, these traits also evolved in tandem among less derived polycotyliids (Bardet et al., 2003; Fischer et al., 2020) and in other marine reptiles, including some nothosaurids (Diedrich, 2012) and askeptosaurids (Müller, 2005). During the Late Cretaceous, the Western Interior Seaway hosted an ecologically complex assemblage of large marine reptiles. *Serpentisuchops* coexisted with numerous mosasaurids, long-necked elasmosaurid plesiosaurs, and its fellow derived polycotyliid *Dolichorhynchops*. None shared a form similar to *Serpentisuchops*, and its trait combination may have evolved as a result of ecological niche partitioning.

Limitations of the study

The diagnosis of *Serpentisuchops pfisterae* is based on a single specimen, and that specimen is incomplete. Of particular note is the absence of the pectoral girdle and any limb material. The future discovery of additional specimens with these elements would greatly help assess the locomotive capabilities of the taxon and has the potential to affirm or refute the locomotive inferences made herein. The large percentage of missing data (>70%) for the new specimen also weakens the robustness of the phylogenetic analyses. Even though symmetric resampling and bootstrap resampling were run, neither of these a posteriori analyses resulted in support values above 50% within Leptocleidia. Although the specimen shows no signs of ontogenetic immaturity (such as incompletely fused sutures) no histological investigations have been conducted. As such, the specimen's age is unknown, as is whether or not it represents an individual at or below adult size.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- Materials availability
- Data and code availability
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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2022.105033>.

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AUTHOR CONTRIBUTIONS

W.S. Persons measured the specimen and created all anatomical figures. H.P. Street performed the phylogenetic analyses. A. Kelly photographed the specimen and assisted with data collection. All authors contributed to the anatomical interpretations and to the writing of the main text.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Phylogenetic character matrix	See Fischer et al., 2018 , in the reference list.	NA
Software and algorithms		
TNT – phylogenetic analysis program	Created by Goloboff et al., 2003 . TNT is a freely available for download at: http://www.lillo.org.ar/phylogeny/tnt/	NA

RESOURCE AVAILABILITY

Lead contact

Further information and requests for related data should be directed to and will be fulfilled by the lead contact, W. Scott Persons (personss@cofc.edu).

Materials availability

GPM5001 is curated at the Glenrock Paleon Museum, specimen access is available to all qualified researchers upon request.

Data and code availability

- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request. This paper analyzes existing, publicly available data and access information for the datasets is listed in the [key resources table](#).
- This paper does not report original code.

METHOD DETAILS

To conduct the phylogenetic analyses, characters scores for *Serpentisuchops pfisterae* were added to the data matrix used in Fischer et al. ([Fischer et al. \(2018\)](#)), which in turn was based on the matrix originally developed by Benson and Druckenmiller ([Benson and Druckenmiller \(2014\)](#)).

Analysis was performed using a new technology search in TNT ([Goloboff et al., 2008](#)) using implied weighting ([Goloboff, 2014](#)). Implied weighting analysis was selected because this method has been found to provide the best performance when using morphological data ([Goloboff et al., 2018](#)). The memory was increased to hold 99,999 trees, and this analysis was conducted with the weighting strength (K) increased to 12 from the default of 3, following the work of Goloboff et al. ([Goloboff et al. \(2018\)](#)), which found more robust results when using higher K values. The new technology search was run using sectorial search, drift, and tree fusing. For the sectorial search, random sectorial search, consensus sectorial search, and exclusive sectorial search were all selected. The default settings were kept for random sectorial search, but the rounds were increased to 100 for both consensus and exclusive sectorial searches. For the drift search, cycles were set to 100, the maximum fit difference was set to 20 and the maximum relative fit difference was also set to 20. For the tree fusing search, the rounds were set to 100. Random addition sequences was selected (and set to 1,000) instead of driven search, and all found trees were kept. The resulting trees were saved to the RAM and a traditional tree-bisection-reconnection search was run. The results of this analysis were used to filter out suboptimal trees more than 10 steps longer than the best trees found. Strict and majority rule consensus trees were found, and a symmetric resampling analysis was conducted.