Bizarre tail weaponry in a transitional ankylosaur from subantarctic Chile

Armoured dinosaurs are well known for their evolution of specialized tail weapons—paired tail spikes in stegosaurs and heavy tail clubs in advanced ankylosaurs. Armoured dinosaurs from southern Gondwana are rare and enigmatic, but probably include the earliest branches of Ankylosauria—here we describe a mostly complete, semi-articulated skeleton of a small (approximately 2 m) armoured dinosaur from the late Cretaceous period of Magallanes in southernmost Chile, a region that is biogeographically related to West Antarctica. Stegouros elengassen gen. et sp. nov. evolved a large tail weapon unlike any dinosaur: a flat, frond-like structure formed by seven pairs of laterally projecting osteoderms encasing the distal half of the tail. Stegouros shows ankylosaurian cranial characters, but a largely ancestral postcranial skeleton, with some stegosaur-like characters. Phylogenetic analyses place Stegouros in Ankylosauria; specifically, it is related to Kunbarrasaurus from Australia and Antarctopelta from Antarctica, forming a clade of Gondwanan ankylosaurs that split earliest from all other ankylosaurs. The large osteoderms and specialized tail vertebrae in Antarctopelta suggest that it had a tail weapon similar to Stegouros. We propose a new clade, the Parankylosauria, to include the first ancestor of Stegouros—but not Ankylosaurus—and all descendants of that ancestor.

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Thyreophora Nopcsa, 1928
Ankylosauria Osborn, 1923
Parankylosauria clade nov.
Stegouros elengassen gen. et sp. nov.

Etymology. Stegouros, after the Greek stego (roof) and the Greek uros (tail) in reference to the covered tail; elengassen, after the local Aónik’enk people.

Holotype. CPAP-3165 (Colección de Paleobiología de Antártica y Patagonia, at the Instituto Nacional Antártico Chileno, INACH) consists of a mostly complete skeleton (Fig. 1) of which the posterior half (tail, sacrum, pelvic girdle and hindlimbs) is largely articulated, with the remaining disarticulated skeleton including axis, cervical and dorsal vertebrae, sternal plates, coracoids, forelimbs (including a partially articulated right manus), osteoderms and several disarticulated cranial bones. Preservation reflects a single individual (Supplementary Information) and the ontogenetic fusion of elements is complete (neural arches, occipital bones, anterior and greater trochanters of the femur), discarded juvenile status (that is, an animal with no signs of impending maturity).

Locality and horizon. Río de las Chinas Valley, Estancia Cerro Guido, Magallanes Region, Chilean Patagonia (51°S). Lower section of the Dorotea Formation (upper Campanian—lower Maastrichtian), between 71.7 ± 1.2 million and 74.9 ± 2.1 million years ago (Supplementary Information).

Diagnosis. A small-sized (180–200-cm body length, including tail), slender-limbed, armoured dinosaur that differs from all other members of this clade by the presence of a short tail with no more than 26 vertebrae, covered distal to the 14th caudal vertebra by seven pairs of large osteoderms, the distalmost five of which are fused into a flat composite unit. Stegouros can be assigned to Ankylosauria on the basis of medially bowed dentary tooth rows; strongly medially inset maxillary tooth rows; maxilla with a medial process; and short cervical vertebrae. Otherwise, the postcranial skeleton lacks ankylosaurian synapomorphies. Stegouros differs from Antarctopelta in its smaller body size; proportionally larger neural canal; longer dorsosacral centra; higher and narrower sacral centra; teeth with six mesial denticles (versus seven to eight in Antarctopelta); and cingula lacking vertical furrows. Stegouros differs from Kunbarrasaurus in a more curved ulna and ischium (straight in Kunbarrasaurus) and a dorsal maxillo-lacrimal process that is narrow and posteriorly inclined.
Fig. 1 | Skeletal anatomy of the *S. elengassen* holotype (CPAP-3165).

a, Preserved elements of the skeleton in CPAP-3165: the mandible is reversed, and the position of osteoderms in grey shade is uncertain. b, c, Dorsal (b) and right lateral (e) views of the rostral portion of the premaxilla. d, Caudal view of the occipital complex. e, f, Digital reconstruction of cheek tooth (labial (e) and lingual (f) views). g, Anterior view of the mid dorsal vertebra. h, i, Lateral view of the left humerus. j, Lateral view of the left ulna. k, Dorsal view of the partial right hand. l, Dorsal view of the pelvis. m, Anterior view of the left femur. n, Anterior view of the left tibia and fibula. o, Articulated right foot (ventral view). p, Articulated tail with caudal weapon of paired osteoderms. Scale bars, 50 cm (a), 1 cm (b, c, g - k and m - o), 5 mm (e and f) and 10 cm (l and p).

**Diagnosis of the genus.** As described for the type species.

**Description.** Preserved skull elements imply a proportionally large head, although depth versus width cannot be established (Fig. 1b–d and Extended Data Fig. 1). The premaxillae and maxillae preserve rostral portions only. The premaxillae are toothless, completely fused at the midline (with no suture or indentation), narrow, short and high, with a deep palatal surface (Fig. 1b, c). The maxillae are seamlessly fused to the lacrimals, which are posteriorly inclined. As in *Ankylosaurus*, the maxillae show a mediad process (secondary palate) and strongly inset tooth rows13. The maxillary tooth rows begin shortly anterior to the lacrimal, extending under the orbit. The supraoccpital is large, forming the entire upper margin of the foramen magnum, thickening above it into a distinct dorsal shelf (Fig. 1d). The basisphenoid is short (less than the basioccipital length). Two unidentified circumorbital skull roof fragments show strongly rugose surfaces ornamented by foramina and grooves, and clear sutures between bones as in *Kunbarrasaurus* (not obliterated as in other *Ankylosauria*13). The right dentary is sinuous in lateral view, with a medially bowed row of 14 alveoli; the last two of which show erupted teeth in position (Extended Data Fig. 1). These are leaf-like with high crowns that are mesiodistally asymmetric, and denticles continuous to enamel flutings that reach down to a bulged cingulum. The cingulum is asymmetric14: horizontal in labial view, but an arch in lingual view that tilts towards basomesial (Fig. 1e, f). The predentary is short and deep, with thin dorsal processes, longer than the ventral processes (Extended Data Fig. 1).

The axis is short as in *Ankylosaurus*, bearing a prominent odontoid process (Extended Data Fig. 2). The cervical centra are wider than long as in ankylosaurs, but laterally concave as in some stegosaurs15. Towards the posterior, the upward projection of the transverse processes increases, reaching 60° above horizontal in the dorsal vertebrae. Dorsal vertebrae have tall neural arches with high pedicles, tall neural spines and prezygapophyses that are fused into a U shape (Fig. 1g). Four true sacral vertebrae fuse anteriorly to two dorsosacrals, the `presacral rod'13. The ribs of the dorsosacrals are short and contact the ilium without fusing to it. Sacraudals are absent (Extended Data Fig. 2). The 13 more-proximal caudal vertebrae comprise the more flexible portion of the tail, with the remaining vertebrae encased in the large osteoderms of the caudal weapon. The 18th caudal is broken, and all of the vertebrae distal to it are missing (Figs. 1p and 2, Extended Data Fig. 2 and Supplementary Videos 1 and 2). From the remaining space within the caudal weapon, we estimate that there are no more than 8 missing vertebrae, suggesting at most 26 tail vertebrae, which is lower than documented in any armoured dinosaur (the lowest being 35 in *Scelidosaurus*22). The caudal centra are amphiplatyan to platycoelous. The transverse processes are long (about twice the neural spine) and are equally long than wide, but also very low. A digital endocast...
of the caudal weapon reveals a notably flattened interior space (Supplementary Video 3). Computed tomography (CT) scans show that the prezygapophyses of caudals 15–18 are short, while the postzygapophyses extend caudally over the following centrum, fusing medially into a structure that is wedge-like in dorsal view, with a corresponding V-shaped space between the prezygapophyses of the following vertebra (Fig. 2d–f). No ossified tendons are preserved.

The scapulae were not preserved. The coracoids have a well-preserved scapular margin, discarding fusion to the scapula. The sternal plates are unfused with a long tubular caudal lateral process (Extended Data Fig. 3). The humerus has a slender diaphysis but a mediolaterally expanded epiphyses, and a well-developed, anteriorly directed deltopectoral crest (Fig. 1h, l). A well-defined descending ridge along the caudolateral margin of the humerus includes a weak tubercle at its proximal end, at the same position as the triceps tubercle of Stegosauria17. The radius is slender, whereas the ulna is bowed and proximally expanded, with a well-developed olecranon (Fig. 1j). The hand of Stegouros presents definitive hoof-like unguals (in contrast to the comparatively sharp unguals of Scelidosaurus16). The partially articulated right hand shows a reduction to only two phalanges in digit II, as in Stegosauria18, with a flattened disc-like non-ungual (Fig. 1k). Other flat, disc-shaped phalanges were found disarticulated but associated with both hands. The left hand preserves a little U-shaped carpal attached to the fifth metacarpal, of which the anatomical position and shape suggest that it is an ulnare (Extended Data Fig. 3). The ilium shows a long preacetabular process that is strongly anterolaterally deflected (Fig. 1l and Extended Data Fig. 4). The shape and relative positions of the supracetabular shelf (lateral process) and postacetabular process are very similar to Stegosauria, suggesting medial rotation of the latter during ontogeny17. The ischium is long and lacking an obturator process and ischial symphysis. It tapers distally, bending slightly at mid-length (Extended Data Fig. 4). No pubes were preserved. The femora are straight and only slightly longer than the tibiae (Fig. 1m, n), with a reduced ridge-like fourth trochanter, and an anterior trochanter fused to the greater trochanter (Extended Data Fig. 4). Both feet are complete and articulated. They do not spread distally, showing more extensive proximal contact surfaces between metatarsals III and IV than Stegosauria and Ankylosauria11,18 (Fig. 1o). There is no reduction in the pedal phalangeal formula, although the distalmost non-unguals of digits III and IV are flattened and disc-shaped. All of the pedal unguals are hoof-like.

No cranial osteoderms were found. A small (19 mm) flat osteoderm was found near the axis. Eight medium-sized (40–50 mm) elliptical and keeled osteoderms (Extended Data Fig. 4) resemble flank scutes of other armoured dinosaurs20 but were not clearly associated with skeletal elements, except for one that was preserved near the neural arch of a dorsal vertebra. No large cervical osteoderms were found; four small osteoderms (15–20 mm) with higher, acuminate keels were found clustered together near the left manus. Numerous ossicles (small, 4–5 mm osteoderms) were scattered around all of the skeletal elements. These are almost square oblate spheroids ornamented by pitting in the external surface, and strong orthogonal fibres on the inner side. At the anterior sacrum, the dorsal space between the ilium and the tip of the sacral neural spines is covered by a continuous layer of thin dermal bone with vascular furrows and pits (Fig. II and Extended Data Fig. 4). Two pairs of small semiconical osteoderms with high, acuminate keels21 and concave inner surfaces were found associated with the anterior tail. The seven pairs of lateral osteoderms of the tail weapon are clearly in anatomical position. The first (most proximal) pair in the series has an acuminate keel with a caudo-laterally slanted apex, a flattened dorsal surface (more conical ventrally), and a markedly concave inner medial surface. Their posterior ventral aspect is fused to smaller semiconical osteoderms similar to those of the proximal tail, pointing ventrolaterally and posterior (Supplementary Video 1). The following pair of osteoderms is similar, but larger (covering two entire vertebrae), flatter and lacking the smaller ventral osteoderms (Fig. 2 and Supplementary Video 1). The next five pairs of osteoderms are flattened and fused to each other at their anterior–posterior contact surfaces, giving each osteoderm a roughly pentagonal appearance in the upper view, with laterally projecting apices. They conform a large frond-like structure covering the tail dorsolaterally, and also ventrally towards its distalmost end (Supplementary Videos 1 and 2). Two small knob-like structures at the distal tip probably represent an eighth pair of very small osteoderms. At the appendicular skeleton, a small rounded keeled osteoderm with a concave inner surface was found appressed to the upper right ulna, along with a flat subtriangular osteoderm (Extended Data Fig. 4). Keeled osteoderms were found at the lateral side of both feet (three on the left foot, two on the right; Fig. 1o).

Discussion

Stegouros shows ankylosaurian skull characters, but slender limbs; most postcranial characters are ancestral for Eurypoda (Stegosauria + Ankylosauria), and a few resemble Stegosauria. We carried out phylogenetic analyses with five different datasets modified from recent studies focusing on Ornithischia2, armoured dinosaurs23, Stegosauria24 and Ankylosauria3,25. In all of the datasets, Stegouros was found to be closer to Ankylosauria than to Stegosauria, and further grouped with the basal ankylosaur Kuniabarausaurus and Antarcticopelta, forming a monophyletic clade that split earliest from all other Ankylosauria. In all of the modified datasets3,22–24 supported Stegouros as sister of Ankylosauria (as in most studies2,17), including a dataset that had previously supported a different result23.

Before Stegouros, relationships among Gondwanan ankylosaurs have been enigmatic because only Kuniabarausaurus from the late Lower Cretaceous of Australia26,27 was represented by a well-preserved skeleton. Kuniabarausaurus includes a skull with ancestral characters3, but most of the tail and distal limbs are missing. Like Stegouros, Kuniabarausaurus is small-sized (around 2.5 m), maxillary tooth rows extend under the orbit4, osteoderms are present on the limbs28 and a thin layer of dermal bone covers the sacrum21. Stegourosia have a superficially similar sacral covering, but it is formed by the expanded transverse processes of the sacral vertebrae26, while the pelvic shield of other Ankylosauria
is also different, formed by a mosaic of fused osteoderms that also covers the ilium\(^28\). Both *Stegouros* and *Kunbarrasaurus* show a slender humerus with a descending ridge, and a supracetabular process that is semi-circular in the dorsal view\(^9\) that are usually found in Stegosauria\(^3\) and could therefore be ancestral characters for Eurypoda. *Antarctopelta* from the late Campanian age of the Antarctic peninsula is a larger ankylosaur (around 4 m) known from a very partial skeleton (approximately 15\%)\(^7\). Both *Stegouros* and *Antarctopelta* show ancestrally slender metatarsi and no sacrocaudals (Extended Data Fig. 7 and Supplementary Information). Some vertebrae of *Antarctopelta* are unusual for Ankylosauria, even leading to discussion that they could belong to marine reptiles\(^3,29\), but comparison to *Stegouros* confirms that they are caudal vertebrae. Both dinosaurs present uniquely specialized vertebrae with a flattened centrum and a ventral groove, which are found in the caudal weapon of *Stegouros* (Extended Data Fig. 5 and Supplementary Information). Large enigmatic osteoderms of *Antarctopelta* show a marked medial concavity and an acuminate keel and striae on the inner side that are unique among armoured dinosaurs\(^7,27,30\), and teeth that have denticles confluent with enamel ridges, reaching basally to a bulged and asymmetric cingulum (Extended Data Fig. 9). The North-American ankylosaur *Edmontonia* has similar teeth\(^10\), but this is probably convergent given the distant position of this ankylosaur in phylogenetic analyses.

Taking into account that *Stegouros* is probably related to other basal ankylosaurs from southern Gondwana, we propose the clade Parankylosauria (‘at the side of Ankylosauria’) to include the first ancestor of *Stegouros*—but not *Ankylosaurus*—and all descendants of that ancestor. Conversely, we propose the clade Euankylosauria (‘true Ankylosauria’) for the first ancestor of *Ankylosaurus*—but not *Stegouros*—and all of its descendants (Fig. 3). The evidence for slender limbs in Parankylosauria suggests that stout limbs and broad feet (the namesake of Eurypoda) are actually convergent between Euankylosauria and Stegosauria. The generally ancestral postcranial of Parankylosauria also implies that ankylosaurian specializations evolved first in the skull. Tail clubs of Ankylosaurinae must have evolved independently from the tail weapon of *Stegouros*, as closer relatives of Ankylosaurinae such as Nodosauridae and even basal Ankylosauridae had no specialized tail weapon\(^7\) (Fig. 3). In Ankylosauridae, long prezygapophyseal articulations stiffen the distal tail, which becomes the handle of the tail club in Ankylosaurinae\(^3\). The tail of *Stegouros* reflects a different evolutionary pathway, with short prezygapophyses, and a notably shorter tail that is stiffened through osteoderm fusion (Fig. 3b). Among amniotes, herbivores with osteoderms and stiff trunks are more likely to evolve specialized tail
weapons, and armoured dinosaurs in particular are the only clade to have evolved three different kinds of tail weapons: paired spikes (thagomizers) in stegosaurs, clubs in ankylosaurines and the 'macuahuitl' of Stegosaurus (our suggested term, after the Aztec war club). The Parankyloursia must have originated before the earliest record of Eukynosaurus, some 167 million years ago, in the mid-Jurassic period (Fig. 3 and Supplementary Information). After the final separation of Laurasia and Gondwana in the late Jurassic, different clades of Ankylosauria may have prevailed in each supercontinent. These and other possibilities raised by Stegosaurus illustrate that much still remains unknown about the evolution of armoured dinosaurs, especially in Gondwana.

**Online content**

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-021-04147-1.

1. Arbour, V. M. & Zanno, L. E. The evolution of tail weaponization in amniotes. *Proc. R. Soc. B* 285, 20172299 (2018).
2. Thompson, R. S., Parish, J. C., Maidment, S. C. & Barrett, P. M. Phylogeny of the ankylosaurian dinosaurs (Ornithischia: Thyrreophora). *J. Syst. Palaeontol.* 10, 301–312 (2012).
3. Arbour, V. M. & Currie, P. J. Systematics, phylogeny and palaeobiogeography of the ankylosaurid dinosaurs. *J. Syst. Palaeontol.* 14, 385–444 (2016).
4. Wiersma, J. P. & Irims, R. B. A new southern Laramidian ankylosaurid, Akainacephalas johnsoni gen. et sp. nov., from the upper Campanian Kasparowits Formation of southern Utah, USA. *PeerJ* 6, e5016 (2018).
5. Reguero, M. A. & Goin, F. J. Paleogeography and biogeography of the Gondwanan final breakup and its terrestrial vertebrates: new insights from southern South America and the “double Noah’s Ark” Antarctic Peninsula. *J. South Am. Earth Sci.* 108, 103358 (2021).
6. Leahey, L. G., Molnar, R. E., Carpenter, K., Witmer, L. M. & Salisbury, S. W. Cranial osteology of the ankylosaurian dinosaur formerly known as Minmi sp. (Ornithischia: Thyrreophora) from the Lower Cretaceous Allai Mudstone of Richmond, Queensland, Australia. *PeerJ* 3, e1475 (2015).
7. Salgado, I. & Gasparini, Z. Reappraisal of an ankylosaurid dinosaur from the Upper Cretaceous of James Ross Island (Antarctica). *Geodiversitas* 28, 119–135 (2006).
8. Claraz, J. Diario de Viaje de Exploración al Chubut, 1865-1866 (Ediciones Marymar, 1988).
9. Howe, D. W. E., Farke, A. A. & Wedel, M. J. Ontogeny and the fossil record: what, if anything, is an adult dinosaur? *Biol. Lett.* 12, 20150947 (2016).
10. Gutierrez, N. M. et al. Tectonic events reflected by palaeocurrents, zircon geochronology, and palaeoecotopy in the Sierra Baguales of Chilean Patagonia. *Tectonophysics* 695, 76–99 (2017).
11. Manríquez, L. M., Lavinia, E. L., Fernández, R. A., Trevisan, C. & Leppé, M. A. Campanian-Maastrichtian and Eocene stratigraphic architecture, facies analysis, and paleoenvironmental evolution of the northern Magallanes Basin (Chilean Patagonia). *J. South Am. Earth Sci.* 93, 102–118 (2019).
12. Raven, T. J. & Maidment, S. C. The systematic position of the enigmatic thyreophoran dinosaur Paranthonodon africans, and the use of basal exemplars in phylogenetic analysis. *PeerJ* 6, e4529 (2018).
13. Vickaryous, M. V., Haysiata, T. & Weishampel, D. B. in *The Dinosauria* (eds Weishampel, D. B. et al.) 464–477 (Univ. California Press, 2004).
14. Coombs Jr W. P. in *Dinosaur Systematics: Approaches and Perspectives* (eds Carpenter, K. & Currie, P. J.) 269–279 (Cambridge Univ. Press, 1990).
15. Pereda-Suberbiola, X., Galton, P. M., Mallison, H. & Novas, F. A plated dinosaur (Ornithischia, Stegosauria) from the Early Cretaceous of Argentina, South America: an evaluation. *Alcheringa* 37, 65–78 (2013).
16. Norman, D. B. Scelesaurids from the Early Jurassic of Dorset, England: postcranial skeleton. *Zool. J. Linn. Soc.* 189, 47–157 (2020).
17. Sereno, P. C. The evolution of dinosaurs. *Science* 284, 2137–2147 (1999).
18. Maidment, S. C., Norman, D. B., Barrett, P. M. & Upchurch, P. Systematics and phylogeny of Stegosaurus (Dinosauria: Ornithischia). *J. Syst. Palaeontol.* 6, 367–407 (2008).
19. Carpenter, K., DiCroce, T., Kinneer, B. & Simon, R. Pelvis of Gorgosaurus (Dinosauria: Ankylosauria) and the origin and evolution of the ankylosaur pelvis. *PLoS ONE* 8, e79887 (2013).
20. Norman, D. B. Scelesaurids from the Early Jurassic of Dorset, England: the dermal skeleton. *Zool. J. Linn. Soc.* 190, 1–53 (2020).
21. Burns, M. E. & Currie, P. J. External and internal structure of ankylosaur (Dinosauria, Ornithischia) osteoderms and their systematic relevance. *J. Verteb. Paleon.* 34, 835–851 (2014).
22. Han, F., Forster, C. A., Xu, X. & Clark, J. M. Postcranial anatomy of Yimilong downsi (Dinosauria: Ceratopsidae) from the Upper Jurassic Shishugou Formation of China and the phylogeny of basal ornithischians. *J. Syst. Palaeontol.* 16, 1159–1187 (2018).
23. Norman, D. B. Scelesaurids (Dinosauria: Ornithischia) from the Early Jurassic of Dorset, England: biology and phylogenetic relationships. *Zool. J. Linn. Soc.* 191, 1–86 (2021).
24. Raven, T. J. & Maidment, S. C. A new phylogeny of Stegosaurus (Dinosauria, Ornithischia). *Palaeontology* 60, 401–408 (2017).
25. Loewen, M. A. & Kirkland, J. I. The evolution and biogeographic distribution of Ankylosaurus: new insights from a comprehensive phylogenetic analysis. *J. Verteb. Paleon.* (Program and Abstracts). 2013, 163–164A (2013).
26. Molnar, R. E. Preliminary report a new ankylosaur from the Early Cretaceous of Queensland, Australia. *Mem. Queensl. Mus.* 39, 653–668 (1996).
27. Molnar, R. E. In *The Armored Dinosaurs* (ed. Carpenter, K.) 341–362 (Indiana Univ. Press, 2001).
28. Arbour, V. M., Burns, M. E. & Currie, P. J. A review of pelvic shield morphology in ankylosaurians (Dinosauria, Ornithischia). *J. Vertebr. Palaeon.* 28, 298–302 (2019).
29. Lamanna, M. C. et al. Late Cretaceous non-avian dinosaurs from the James Ross Basin, Antarctica: description of new material, updated synthesis, biostratigraphy, and paleobiogeography. *Adv. Polar Sci.* 30, 228–250 (2019).
30. de Ricca, A., Suberbiola, X., Gasparini, Z. & Olivero, E. Histology of dermal ossifications in an ankylosaurian dinosaur from the Late Cretaceous of Antarctica. *Assoc. Paleon.* Argent. 7, 171–174 (2001).
31. Arbour, V. M. & Currie, P. J. Ankylosaurid dinosaur tail clubs evolved through stepwise acquisition of key features. *J. Anat.* 227, 514–523 (2015).
32. Arbour, V. M. & Zanno, L. E. Tail weaponry in ankylosaurs and glyptodonts: an example of a rare but strongly convergent phenotype. *Anat. Rec. C.* 303, 988–998 (2020).
33. Maidment, S. C., Raven, T. J., Ouarhache, D. & Barrett, P. M. North Africa’s first stegosaur: implications for Gondwanan thyreophoran dinosaur diversity. *Gondwana Res.* 77, 82–97 (2020).

**Publisher’s note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.
Phylogenetic analyses

**Parsimony analyses.** The phylogenetic relationships of thyreophoran dinosaurs were investigated using TNT (v.1.5) through five different matrices available in literature\(^{34,35}\), following the same procedure described in the original data sources. The first data matrix is a modified version of that in ref.\(^{36}\) and is composed of 383 characters and 74 taxa. Characters 2, 23, 31, 39, 123, 163, 196, 203, 204, 222, 227, 238, 243, 247, 268, 292, 296, 302, 306, 320 and 361 were treated as ordered\(^{37}\). The second set for most parsimonious trees (MPTs) was performed using a traditional search (heuristic) with 1,000 replicates of tree bisection and reconnection (TBR) holding 100 trees per replicate. The trees obtained were used as the starting point for a second round of TBR by traditional search. The second data is a modified version of that in ref.\(^{35}\) and is composed of 127 characters (12 new characters were added) and 10 taxa. A traditional search was carried out with 10,000 replicates holding 10 trees. The third data matrix is a modified version of that from refs.\(^{34,35}\) and is composed of 131 characters (10 new characters were added) and 28 taxa. Characters 1–24, 29, 112 and 113 were treated as ordered\(^{37}\). A new technology search analysis (sectorial, ratchet, drift and tree fusing) was made with ten random-addition sequences, and the trees obtained were used for a second round of TBR using traditional search. The fourth data matrix is a modified version of that from refs.\(^{34,35}\) and is composed of 189 characters (12 new characters were added) and 65 taxa. In this matrix all of the characters were treated as unordered, and the search for MPTs was performed using TBR with 1,000 replicates, holding 10 trees per replica, and then a second search was performed with the trees saved in memory. The fifth data matrix is a modified version of that from refs.\(^{34,35}\) and is composed of 306 characters (13 new characters were added) and 37 taxa. The characters 1, 2, 3, 7, 10, 13, 16, 18, 23, 25, 30, 36, 38, 48, 49, 54, 64, 87, 98, 101, 103, 104, 105 140, 141, 143, 145, 148, 149, 156, 162, 165, 174, 177, 194, 201, 205, 209, 217, 229, 231, 232, 236, 237, 238, 268 and 279 were treated as ordered. For the search of MPTs, traditional search was used, with 10,000 TBR replicas with 10 trees saved per replica. Character argumentation and list changes are available in the Supplementary Information. For all of the analyses, standard bootstrap values were calculated with 1,000 pseudoreplicates and Bremer support values were calculated using the script bremer.run\(^{36}\).

**Statistical analysis**

We used a Templeton test to assess the significance of whether the phylogenetic position of *Stegouros* was closer to Ankylosauria than to Stegosauria (Extended Data Table I). For this, we used randomly chosen MPTs from the tree space of the unconstrained analysis (AI) and a forced topology, where *Stegouros* is closer to Stegosauria than to Ankylosauria (A2), and applied a one-sided Wilcoxon signed-rank test to the differences in character transformations between these trees. Templeton tests were performed using TNT v.1.5 and the script is available online (http://www.anbg.gov.au/cpbr/tools/templeton-test.tnt).

**Estimation of divergence times**

The stratigraphic adjustment and estimation of the divergence times of the calibrated phylogenies was performed by calculating the Manhattan stratigraphic measure and gap excess ratio\(^{37–40}\) using the TNT script implemented in ref.\(^{41}\). Divergence times were not estimated for the data matrix of ref.\(^{35}\), which comprises only a small sample of armoured dinosaurs.

**Nomenclatural acts**

This published Article and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The LSID for this publication is urn:lsid:zoobank.org:pub:4D3ABFEE-5F21-4632-96F9-FE8C1542ACF7; the LSID for the new genus (*Stegouros*) is: urn:lsid:zoobank.org:act:5306DD47-2130-4866-8DB4-09092C632A4A, and the LSID for the new species (*Stegouros elengassen*) is: urn:lsid:zoobank.org:act:992A295B-75EE-4206-89FB-6666fBCBDF6A.

**Data availability**

All data supporting the findings of this study are available in the paper and its Supplementary Information. Raw data from all CT scans are available online (https://www.morphosource.org/?concern/biological-specimens/000382748). The LSID for this publication is urn:lsid:zoobank.org:pub:4D3ABFEE-5F21-4632-96F9-FE8C1542ACF7. The LSID ZooBank code for the new genus (*Stegouros*) is: urn:lsid:zoobank.org:act:5306DD47-2130-4866-8DB4-09092C632A4A. The LSID ZooBank code for the new species (*Stegouros elengassen*) is: urn:lsid:zoobank.org:act:992A295B-75EE-4206-89FB-6666fBCBDF6A. TNT files for phylogenetic analysis are provided on Zenodo (https://zenodo.org/record/5706422#.YZQ7Kr3Q8-R).
maximum-parsimony analyses. C.S.-G. and V.M. carried out taphonomic studies. M.A.L., L.M.E.M., R.A.F., J.P.P., H.M., C.T., D.R. and L.F.H. carried out geological and palaeoenvironmental studies. A.O.V. and S.S.-A. wrote the bulk of the manuscript; S.S.-A., C.S.-G., V.M. and J.P.P. made figures. All of the authors collected data and contributed to the writing, discussion and conclusions.

Competing interests The authors declare no competing interests.

Additional information
Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41586-021-04147-1.
Correspondence and requests for materials should be addressed to Sergio Soto-Acuña or Alexander O. Vargas.
Peer review information Nature thanks James Kirkland and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.
Reprints and permissions information is available at http://www.nature.com/reprints.
Extended Data Fig. 1 | Cranial bones of *S. elengassen* holotype (CPAP-3165). a, skull in lateral view (with left? supraorbital reversed). b, posterior skull in dorsal view. c, premaxilla in ventral view. d, left maxilla lateral view. e, f, both maxillae in ventral view. g, left? supraorbital dorsal view. h, i, predentary in occlusal and ventral views. j, basisphenoid in palatal view. k, right dentary in lingual view. Scale bars, 10 cm.
Extended Data Fig. 2 | Postcranial axial skeleton of *S. elengassen* holotype (CPAP-3165). a–c, axis in anterior and right lateral views. d–f, anterior cervical vertebra in anterior, right lateral and ventral views. g–i, posterior cervical vertebra in anterior, right lateral and dorsal views. j–l, anterior dorsal vertebra in anterior, right lateral and dorsal views. m, n, posterior dorsal vertebra in anterior and right lateral views. o, synsacral vertebrae in right lateral view. p, anterior caudal vertebrae in right lateral view. q, posterior caudal vertebrae in right lateral view. Scale bar 10 cm.
Extended Data Fig. 3 | Sternal, pectoral girdle and forelimb bones of *S. elengassen* holotype (CPAP-3165). a, b, sternal plates in ventral view. c–e, right coracoid in lateral, medial and glenoideal views. f–i left humerus in anterior, posterior, proximal and distal views. j, left radius in lateral view. k, left ulna in anterior view. l, m, left hand in proximal and dorsal views. n, originally semiarticulated right hand in dorsal view. o, fully prepared right hand in dorsal view. Scale bars, 10 cm.
Extended Data Fig. 4 | Pelvic girdle, hindlimbs and dermal armour of *S. elengassen* holotype (CPAP-3165). a, right ilium in lateral view. b, pelvis in ventral view. c, d, left pubis in lateral and medial views. e–h, left femur in proximal, distal and posterior views. i, right femur in lateral view. j, left foot in dorsal view. k, right foot in lateral view. l, m, isolated mid-sized ovalate keeled osteoderm in dorsal and lateral views. n, o, sacral covering in dorsal and ventral views. p, keeled osteoderm with deeply excavated inner surface associated with right ulna in ventrolateral view. q, flat osteoderm associated with right radius in dorsal view. Scale bars, 10 cm (a–k, n, o) 2 cm (l, m, p, q).
Extended Data Fig. 5 | Paired comparisons of the axial skeleton between *S. elengassen* holotype CPAP-3165 (left) and *A. oliveroi* holotype MLP 86-X-28-1 (right). Synsacral complex in a, b, anterior, c, d, posterior and e, f, ventral views; anterior caudal vertebrae (6th in *Stegouros elengassen*) in h, i, posterior and j, k, right lateral views; posterior caudal vertebrae (17th in *Stegouros elengassen*) in l, m, dorsal and n, o, posterior views. Scale bars, 2 cm (a, c, h, j, l, n), 5 cm (b, d, f, g, i, k, m, o).
Extended Data Fig. 6 | Anatomy of caudal weapon osteoderms in *S. elengassen* holotype (CPAP-3165) and *A. oliveroi* holotype (MLP 86-X-28-1). a, digital reconstruction and b, photograph of *Stegouros elengassen* caudal weapon cross section (at level of first osteoderm pair and 14th caudal vertebra) in anterior and left lateral views. c, d, *Antarctopelta oliveroi* dorsal osteoderm of the first pair in left lateral and anterior views. e, *Stegouros elengassen*, 3D reconstruction of the left second osteoderm in dorsal and internal views. f, *Antarctopelta oliveroi* left second osteoderm fragment in dorsal and internal views. g, h, *Stegouros elengassen*, digital reconstruction of the caudal weapon cross section (at level of second pair and 17th caudal vertebra) in anterior and posterior views. i, j, proposed configuration of the caudal weapon of *Antarctopelta oliveroi* in anterior and posterior views. Scale bars 10 cm.
Extended Data Fig. 7 | Comparison of cervical and pedal bones between *S. elengassen* holotype (CPAP-3165) and *A. oliveroi* holotype (MLP 86-X-28-1). a–d, *Stegouros elengassen* posterior cervical vertebra in anterior, right lateral, posterior, and dorsal views. e–h, *Antarctopelta oliveroi* posterior cervical vertebra in anterior, right lateral, posterior, and dorsal views. i–l, *Stegouros elengassen* right foot in dorsal and ventral views. k, l, *Antarctopelta oliveroi* right metatarsal in dorsal and ventral views. m, *Antarctopelta oliveroi* isolated pedal phalanx in dorsal, proximal and ventral views. Scale bars 5 cm.
Extended Data Fig. 8 | Comparison of dermal skeleton between S. elengassen holotype (CPAP-3165) and A. oliveroi holotype (MLP 86-X-28-1). a, Stegouros elengassen dermal ossicles in internal view. b, Antarctopelta oliveroi disarticulated dermal ossicles. c, Antarctopelta oliveroi dermal ossicle close-up exposed in internal view. d–f, sacral covering fragments of Antarctopelta oliveroi. Scale bars, 5 mm (1, b), 1 mm (c), 10 cm (d–f).
Extended Data Fig. 9 | Comparison of teeth and dentary of *S. elengassen* holotype (CPAP-3165) and *A. oliveroi* holotype (MLP 86-X-28-1).

**a–d.** Stegouros elengassen digital reconstruction of cheek tooth in labial, mesial, lingual, and distal views. **e–h.** Antarctopelta oliveroi tooth (reversed) in labial, mesial, lingual, and distal views. **i–k.** Stegouros elengassen right dentary (mirrored for better comparison) in labial, lingual and occlusal views. **l–n.** Antarctopelta oliveroi right dentary fragment in labial, lingual and occlusal views. Scale bars 5 mm (a–d), 10 mm (e–h), 10 cm (i–n).
Extended Data Table 1 | Results of phylogenetic analysis

|                        | Han et al. matrix | Norman matrix | Raven and Maidment matrix | Arbour et al. matrix | Loewen and Kirkland matrix |
|------------------------|------------------|---------------|---------------------------|----------------------|-----------------------------|
|                        | A1               | A2            | A1                        | A2                   | A1                          | A2                         | A1       | A2       |
| Tree length (steps)    | 1255             | 1263          | 272                       | 282                  | 336.370                     | 342.260                    | 693      | 701      | 687      | 705      |
| CI index               | 0.363            | 0.36          | 0.665                     | 0.642                | 0.554                       | 0.544                       | 0.359    | 0.355    | 0.479    | 0.468    |
| RI index               | 0.711            | 0.708         | 0.83                      | 0.812                | 0.647                       | 0.633                       | 0.651    | 0.645    | 0.745    | 0.733    |
| RC index               | 0.26             | 0.25          | 0.55                      | 0.52                 | 0.36                        | 0.34                        | 0.23     | 0.23     | 0.36     | 0.34     |
| Templeton test result  | significant      | significant   | not significant           | not significant      | not significant             | significant                  |
| P value                | < 0.025          | < 0.05        | > 0.05                    | > 0.05               | > 0.05                      | < 0.01                      |
| Bootstrap value        | 63               | 46            | 51                        | 13                   | 87                          |
| Bremer support value   | 2                | 2             | 0                         | 5                    | 4                            |

Summary of phylogenetic analyses for five modified data matrices, indicating number of steps, consistency, retention and rescaled consistency indexes, and support values for Paranyaklosauria in the strict consensus of the most-parsimonious trees (A1) and in a forced topology of Stegouros closer to Stegosauria than to Ankylosauria (A2), with Templeton tests to assess its significance.
Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

- n/a
- Confirmed
- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
- Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted Give P values as exact values whenever suitable.
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection
CT volumes were segmented and analyzed in VGSTUDIO MAX 3.2, no additional software was used for data collection.

Data analysis
PAST 4.0 (Taphonomic directional analysis); TNT 1.5 (Phylogenetic analysis)

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:
- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

The authors declare that all data supporting the findings of this study are available in the paper and its Supplementary Information. Raw data from all CT-Scans is available at https://www.morphosource.org/concern/biological_specimens/000382748. LSID ZooBank code: urn:lsid:zoobank.org:act:992A259B-75EE-4206-89FB-6666F8C8DB5A. TNT files for phylogenetic analysis are provided at doi:10.5061/dryad.pk0p2ngpj
Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences
Behavioural & social sciences
Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

- **Study description**
  The present study comprises the description, taphonomic assessment and phylogenetic analysis of a new Ankylosaur fossil specimen. Given the limited nature of the data no replicates were included.

- **Research sample**
  The research sample consists exclusively of the holotype of Stegouros engelgassen. Additionally the phylogenetic analyses use five Ankylosaur character matrices published in Han et al. (2018), Raven and Maidment (2018), Arbour et al (2016), Wiersma and Irmis (2018) and Norman (2020a). Additional characters were coded for all these matrices.

- **Sampling strategy**
  A single holotype specimen was available

- **Data collection**
  The morphological data of the fossil specimen was collected and codified as discrete characters by Sergio Soto-Acuña. Morphology of the specimen was assessed directly and through 3D reconstructions based on the digital segmentation of CTscan volumes generated by José Palma-Liberona.

- **Timing and spatial scale**
  The timing of data collection is irrelevant for the present study.

- **Data exclusions**
  No data was excluded from this study.

- **Reproducibility**
  The present study does not include experimental procedures. As such, no measures were taken to verify the reproducibility of experimental findings.

- **Randomization**
  Given that the present study considers the description and phylogenetic analysis of a single fossil specimen, no randomization procedure was applicable besides the bootstrap methods applied in the phylogenetic analyses.

- **Blinding**
  Since the present study describes a single fossil specimen, no blinding procedure was used.

Did the study involve field work?  □ Yes  □ No

Field work, collection and transport

- **Field conditions**
  Annual rainfall is 307.5 mm and mean annual temperature is 6.5°C. These are not relevant for paleontological fieldwork studies (taphonomy, stratigraphy)

- **Location**
  50° 42' 42.72'' S / 72° 32' 29.08'' W. Altitude 1128 M

- **Access & import/export**
  Access and collection was carried out with permission of landowners of Estancia Cerro Guido and of the Chilean government through permit CMN° 6079 (18.12.2017) extended to Marcelo Leppe by the National Monuments Council (CMN, Consejo de Monumentos Nacionales), Government of Chile.

- **Disturbance**
  Only transient disturbance was carried out by digging in soils and rocks not covered by vegetation (the study area consists of cold steppe, with sparse vegetation cover of altitudinal cushions and grasslands). Excavation sites were covered to protect them from erosion and left with a similar appearance as before the intervention.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.
Materials & experimental systems

| Involved in the study |
|-----------------------|
| Antibodies          |
| Eukaryotic cell lines|
| Palaeontology and archaeology |
| Animals and other organisms |
| Human research participants |
| Clinical data |
| Dual use research of concern |

Methods

| Involved in the study |
|-----------------------|
| ChIP-seq              |
| Flow cytometry        |
| MRI-based neuroimaging|

Palaeontology and Archaeology

Specimen provenance: The site of provenance (SP17) is located in the Río de Las Chinas Valley, which is part of the Cerro Guido farm, Última Esperanza Province, Magallanes Region, southern Chile. The fossil-bearing level is located within the lower to mid section of Dorotea Formation.

Specimen deposition: CPAP-3165 is housed in the Palaeontological Collection of Antarctica and Patagonia of the Instituto Antártico Chileno (INACH), Punta Arenas, Chile.

Dating methods: No new dates are provided. Datation is based on previously published studies: U-Pb maximum depositional age above and below the fossil-bearing horizons provides values between 71.7 ± 1.2 Ma and 74.9 ± 2.1 Ma (Gutiérrez et al., 2017) [http://dx.doi.org/10.1016/j.tecto.2016.12.014](http://dx.doi.org/10.1016/j.tecto.2016.12.014)

[ ] Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

Ethics oversight: No ethical approval or guidance was required. Ethical aspects deal with access and collection of fossils which was carried out with the appropriate legal permits detailed above.

Note that full information on the approval of the study protocol must also be provided in the manuscript.