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A new stegosaur (Dinosauria: Ornithischia) from the Middle Jurassic of Gansu Province, China

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Stegosaurs are a minor but iconic clade of ornithischian dinosaurs, yet due to a poor fossil record, their early evolution is poorly understood. Here, we describe a new stegosaur, *Baiyinosaurus baojiensis*, gen. et sp. nov. from the Middle Jurassic Wangjiashan Formation of the Pingchuan District, Baiyin City, Gansu Province, China. The frontal of *Baiyinosaurus* possesses a unique characteristic among Stegosauria: it is wider than long and contributes to both the medial and anterior margins of the supratemporal fenestra. The character combinations of dorsal vertebrae of *Baiyinosaurus* are also different to other stegosaurs: its neural arches are not greatly elongated, its parapophyses are well developed, and its neural spines are axially expanded in lateral. The features of the frontal and vertebrae of *Baiyinosaurus* are reminiscent of basally branching thyreophorans, indicating that *Baiyinosaurus* is transitional in morphology between early thyreophorans and early-diverging stegosaurs. Systematic analysis shows that *Baiyinosaurus* is an early-diverging stegosaur.

Keywords Dinosaur, Stegosaur, Middle Jurassic, Gansu

Abbreviations

IVPG	Institute of Vertebrate Paleontology, Gansu Agricultural University
MB	Museum für Naturkunde, Berlin, Germany
NHMUK	Natural History Museum, London, UK
ZDM	Zigong Dinosaur Museum, Zigong, Sichuan Province, People's Republic of China

The stegosaurs are characterised by the possession of two parasagittal rows of hypertrophied dermal armour plates and/or spines extending from the neck to the end of the tail and have been found on all continents except for Antarctica and Australia¹. The earliest stegosaurs are from the Middle Jurassic, they achieved a global distribution by the Late Jurassic and subsequently waned in diversity during the Early Cretaceous. Records of stegosaurs from the Middle Jurassic are rare, including only five taxa: *Loricatosaurus*² from the U.K., *Isaberrysaura*³ from Argentina, *Adratiklit*⁴ from Morocco, and *Huayangosaurus*⁵ and *Bashanosaurus*⁶ from China.

Dinosaur fossils are abundant in Gansu Province. Since the first dinosaur was discovered in Gansu Province in 1930⁷, seventeen dinosaurian taxa have been discovered and named. Among these named dinosaurs, there are five sauropods including *Gobititan shenzhouensis* (Titanosauriformes)⁸, *Huanghetitan liujiaxiaensis* (Titanosauriformes)⁹, *Daxiatitan binglingi* (Titanosauriformes)¹⁰, *Qiaowanlong kangxii* (Brachiosauridae)¹¹, and *Yongjinlong datangi* (Titanosauria)¹²; three theropods, including *Suzhousaurus megatherioides* (Therizinosauroidae)¹³, *Xiongguanlong baimoensis* (Tyrannosauroidae)¹⁴, and *Beishanlong grandis* (Ornithomimosauria)¹⁵, and nine ornithischians, including *Gongpoquanlong mazongshanensis* (Hadrosauroidae)¹⁶, *Archaeoceratops oshimai* (Ceratopsia)¹⁷, *Equijubus normani* (Hadrosauroidae)¹⁸, *Auroraceratops rugosus* (Ceratopsia)¹⁹, *Lanzhousaurus magnidens* (Iguanodontia)²⁰, *Jintasaurus meniscus* (Hadrosauroidae)²¹, *Archaeoceratops yujingziensis* (Ceratopsia)²², *Xuwulong yueluni* (Hadrosauroidae)²³, and *Taohelong jinchengensis* (Ankylosauria)²⁴. Recently, a stegosaurian specimen from the Lower Cretaceous Hekou Group of the Zhongpu area, Lanzhou-Minhe Basin, Gansu Province was reported, which is the first stegosaurian dinosaur from Gansu Province²⁵. In 2016, Dr. Li Daqing and his team discovered some dinosaurs, including a stegosaur, several large-sized theropod and sauropod remains and

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one small theropod track site in Pinchuan District of Baiyin City, Gansu Province. Thereafter, these specimens were excavated and prepared by the Gansu Zhendan Dinosaur Culture Communication Co. Ltd., and they were preserved at Gansu Agricultural University. We herein describe the new stegosaurian dinosaur from the Middle Jurassic of Gansu Province.

Results

Geological setting

The study area is located in the northwestern part of the Baojishan Basin, belonging to the Pinchuan District of Baiyin City, Gansu Province (Fig. 1a,b). The Baojishan Basin is at the eastern end of the Qilian Mountains. It is a fault-bounded subsiding basin, being a small part of the Hexi Corridor Basin, which developed in the Late Triassic and Jurassic. The Middle Jurassic strata of the area is composed of two lithostratigraphic units, the Longfengshan Formation and the Wangjiashan Formation. Underlying these Middle Jurassic strata is a disconformity with Upper Triassic rocks, while Upper Jurassic sediments conformably overlie them^{26,27}. The Straw-yellow Sandstone Member of the Wangjiashan Formation was deposited mainly in a lake deltaic setting, and the succession is characterized by its straw-yellow colour. It changes gradually upward from coarse sandstones at the base to fine sands with interbedded red mudstones in the upper part. The dinosaur fossils were collected from the sandstone of the upper part of the Straw-yellow Sandstone Member of the Wangjiashan Formation (Fig. 1c). Based on its megafossil plants and palynoflora, as well as the lacustrine invertebrate assemblage of the overlying Oil Shale Member, including conchostracans, charophytes, and bivalves, the Straw-yellow Sandstone Member of the Wangjiashan Formation is considered to be late Bathonian in age^{26–28}.

Systematic palaeontology

Dinosauria Owen²⁹

Ornithischia Seeley³⁰

Thyreophora Nopcsa³¹

Stegosauria Marsh³²

Baiyinosaurus baojiensis gen. et sp. nov.

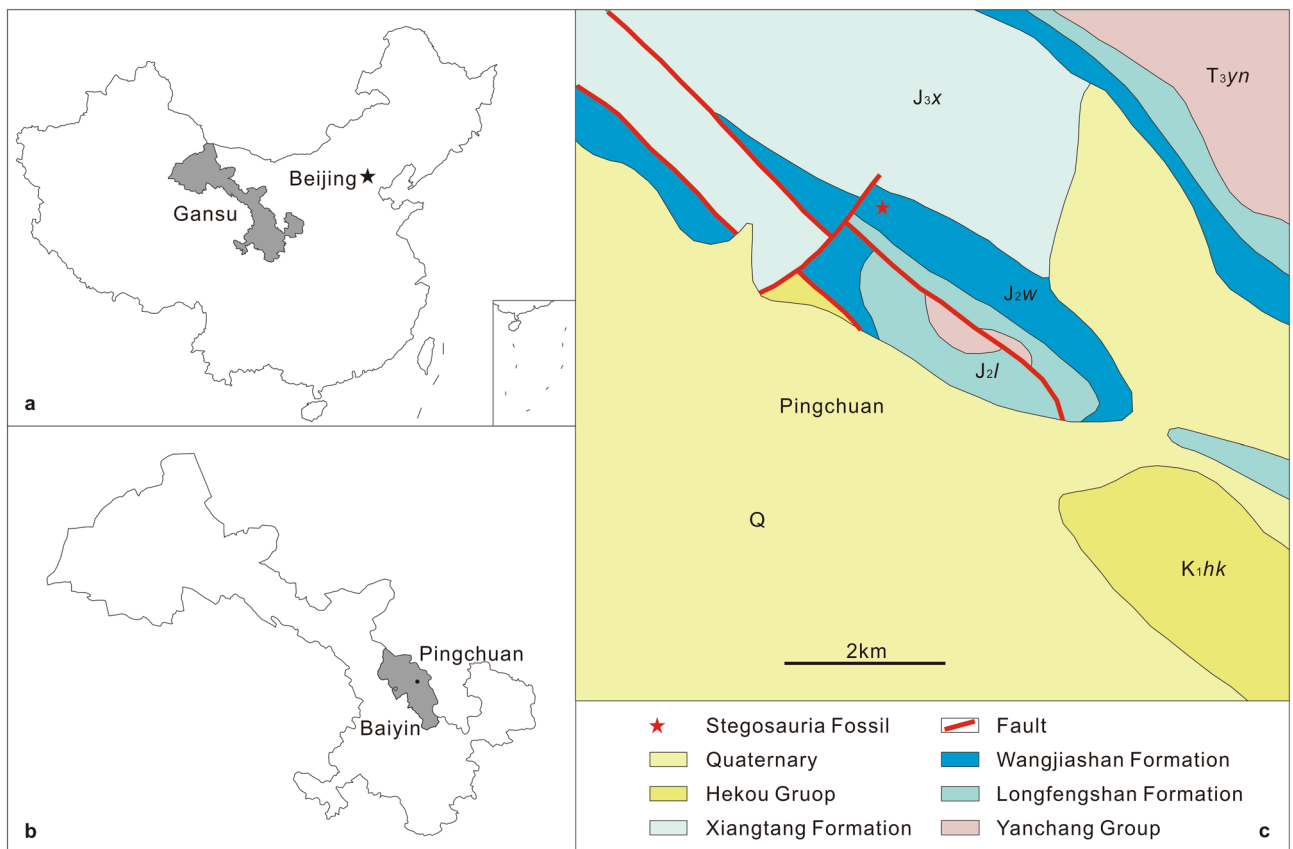


Figure 1. Locality and geological maps of the fossil locality. (a) map of China showing Gansu Province. (b) map of Gansu showing Baiyin City and Pingchuan District. (c) Geological map of Pingchuan District and the fossil locality.

Holotype

IVPG-D021. A partial skeleton comprising a partial cranium, one cervical vertebra, seven dorsal vertebrae and one caudal vertebra. The measurements of the vertebrae can be found in Table 1.

Etymology

Generic name is a combination of Baiyin (the city in which the type locality is located) and saurus (Greek, reptile). The specific name is derived from Baoji (the basin name of the type locality).

Locality and Horizon

Pingchuan District, Baiyin City, Gansu Province, China. GPS coordinates: N36° 44' 59.1", E104° 49' 53.2". The materials are from the upper part of the Straw-yellow Sandstone Member of the Wangjiashan Formation, whose age is considered to be Middle Jurassic, late Bathonian.

Diagnosis

Baiyinosaurus differs from all other stegosaurs by possession of the following autapomorphy: the frontal is wider than long (score 1 for character 32), and not only contributes to the medial margin of the supratemporal fenestra but also makes up a very great contribution to the anterior margin of the supratemporal fenestra. *Baiyinosaurus* also possesses the following character combination on dorsal vertebrae: (1) the neural arches are not greatly elongated dorsally: the ratio of neural arch height to neural canal height is 1.59 (character 6, a continuous character); (2) the parapophyses are well developed and project somewhat laterally on stalks in anterior view (score 0 for character 64); (3) the neural spines are anteroposteriorly broad and axially expanded in lateral view: the ratio of neural spine length (measured at the base) to centrum length is 0.75 (character 9, a continuous character).

Description and comparisons

Skull

Some parts of the skull are preserved incompletely, including the left premaxilla (Fig. 2a), frontal (Fig. 2b,c), left maxilla (Fig. 2d–f), right jugal (Fig. 2g,h), and right squamosal (Fig. 2i,j). The skull of *Baiyinosaurus* is reconstructed in Fig. 2k,l, which is modified from *Emausaurus*³³.

Premaxilla: only the posterior part of the left premaxilla is preserved (Fig. 2a). It is an oblique, slightly sinuous, gracile posterolateral process that wedges itself between the maxilla and nasal, similar to *Stegosaurus*³⁴, *Scelidosaurus*³⁵ and *Emausaurus*³³. The dorsal margin of the posterolateral process has an obvious transversely expanded contact surface for the nasal.

Maxilla: the anterior and middle parts of the left maxilla are nearly completely preserved, but the anteroventral and posterior parts are missing. The lateral surface of the maxilla is flat (Fig. 2d). The complete tooth row is inset medially from the lateral surface (Fig. 2f), similar to other stegosaurs and most other ornithischians^{36,37}. The dorsolateral surface of the maxilla is laterally compressed, forming a thin lamina that forms the lateral wall of the nasal cavity (Fig. 2e).

Frontal: although the frontal is incomplete (Fig. 2b,c), its overall form is shorter anteroposteriorly than most stegosaurs, but is similar to *Tuojiangosaurus*³⁸ and the basally branching thyreophorans *Scelidosaurus*³⁵ and *Emausaurus*³³. It is flat in dorsal view. Posteriorly, the sutural boundaries overlapped by the parietal are clear (Fig. 2b). The right part of the frontal is almost complete and the structure overlapped by the postorbital is visible (Fig. 2b). The end of this structure is narrower anteroposteriorly than *Huayangosaurus*³⁹ and *Stegosaurus*³⁴, but more similar to *Emausaurus*³³. Right laterally, the anterior margin has a structure overlapped by the nasal and the prefrontal, and the posterior margin is smooth forming the supratemporal fossae (Fig. 2b). The frontal not only contributes to the medial margin of the supratemporal fenestra but also makes up a much greater contribution to the anterior margin of the supratemporal fenestra than in other stegosaurs, such as *Huayangosaurus*³⁹, *Stegosaurus*³⁴ and *Kentrosaurus*⁴⁰.

Element	Centrum length	Anterior facet width	Anterior facet height	Posterior facet width	Posterior facet height	Neural canal height	Neural arch height
Atlas (Fig. 4)	23	49	8	50	27	–	–
Second dorsal vertebra (Fig. 5e–j)	62	78	58	82	73	34	46
Third dorsal vertebra (Fig. 6a–f)	78	69	54	70	68	35	52
Fourth dorsal vertebra (Fig. 6a–f)	69	75	64	81	55	43	–
Fifth dorsal vertebra (Fig. 6g–l)	78	62	54	71	60	31	56
Sixth dorsal vertebra (Fig. 6m–r)	84	54	41	50	57	37	57
Seventh dorsal vertebra (Fig. 6s–x)	81	65	55	68	64	41	65
Caudal vertebra (Fig. 7a–f)	46	71	58	76	62	23	–

Table 1. Measurements (in mm) of vertebrae.

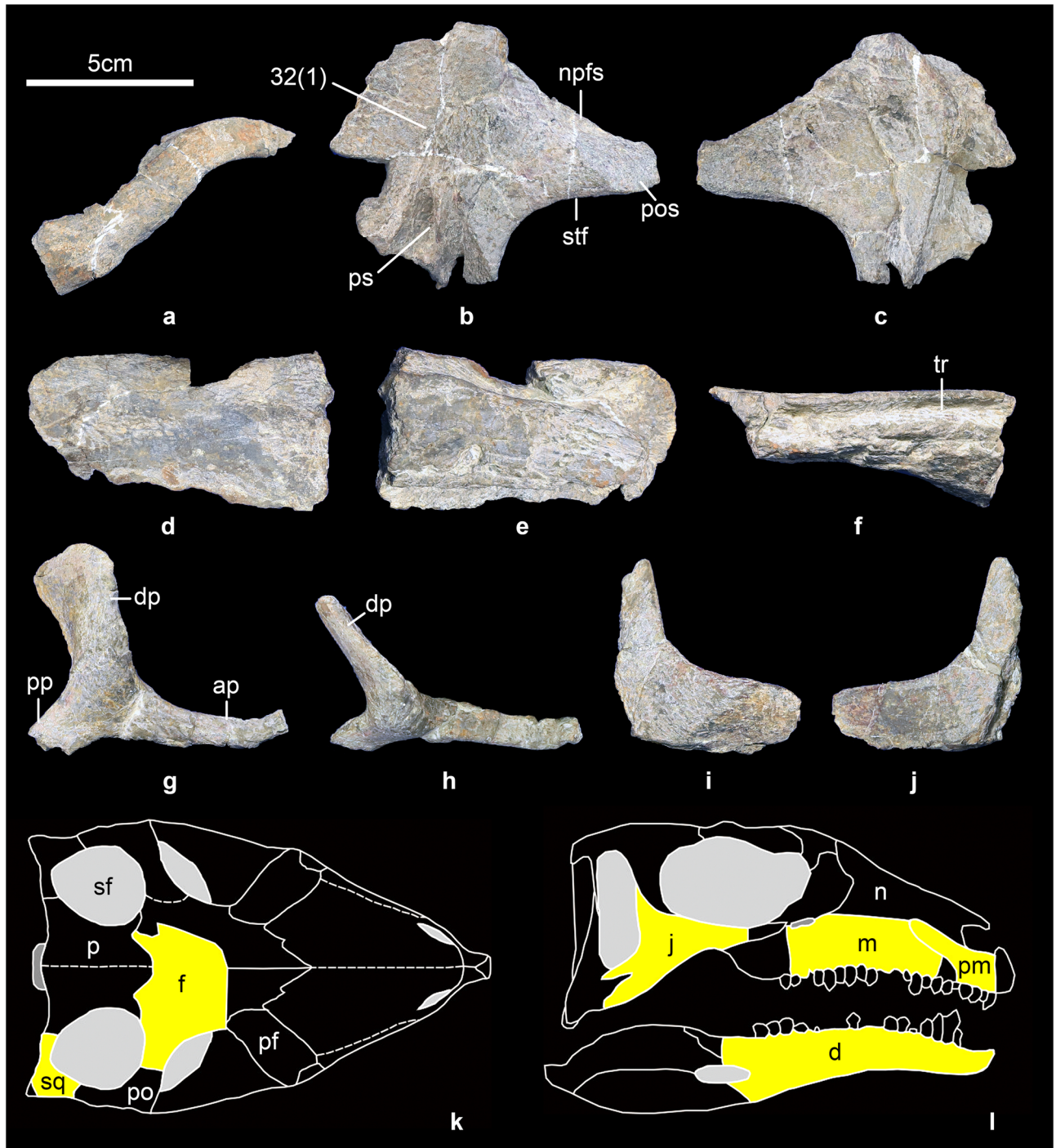


Figure 2. Skull of *Baiyinosaurus baojiensis*. (a) left premaxilla (IVPG-D021-01), (b, c) frontal (IVPG-D021-02), (d–f) left maxilla (IVPG-D021-03), (g, h) right jugal (IVPG-D021-04), (i, j) right squamosal (IVPG-D021-05). (a, d, g) lateral view, (b, h, i) dorsal view, (c, f, j) ventral view, (e), medial view. Reconstruction of the skull of *Baiyinosaurus* in dorsal (k) and lateral (l), modified from *Emausaurus*³³. The yellow areas represent preserved bones. Ap anterior process, d dentary, dp dorsal process, f frontal, j jugal, m maxilla, n nasal, npfs nasal and prefrontal suture, p parietal, pf prefrontal, pm premaxilla, po postorbital, pos postorbital suture, pp posterior process, ps parietal suture, sf supratemporal fossae, sq squamosal, stf margin of supratemporal fenestra, tr teeth row.

Jugal: a possible jugal is present. The jugal (Fig. 2g,h) is triradiate and contacts postorbital dorsally, maxilla anteriorly and quadratojugal posteroventrally. The end of the anterior process slightly curved dorsally because of fracture. The dorsal process is very broad and extends medially.

Squamosal: a fragment that may represent the dorsal part of the right squamosal is preserved (Fig. 2i,j). It is flat on the dorsal surface and concave on the ventral surface. In dorsal view, the left part has a suture overlapped by the parietal and the right part has a structure overlapped by the postorbital.

Dentary

The left dentary is almost complete and curves medioventrally (Fig. 3a–d). Anteriorly, there are concave facets for the prementary on both the medial and lateral surfaces (Fig. 3a,d). The first dentary tooth arises immediately posterior to these facets for the prementary, with no diastema, similar to the condition in *Huayangosaurus*³⁹, *Gigantospinosaurus* (ZDM 0019) and *Kentrosaurus* (MB.R.3806.1), but in contrast to *Stegosaurus*⁴¹ and *Jiangjunosaurus*⁴², where there is a diastema of several tooth-widths between the prementary and the first dentary tooth. A large vascular foramen, the anterior dentary foramen, opens laterally on the dentary and posterior to the prementary area (Fig. 3a). In lateral, the tooth row is visible and sinuous, as in *Huayangosaurus*³⁹, *Gigantospinosaurus* (ZDM 0019) and *Jiangjunosaurus*⁴² but different to *Stegosaurus*³⁴, where a lateral lamina in lateral view obscures the tooth row. An external mandibular fenestra is present at the posterior end of the dentary (Fig. 3a). In dorsal view, the tooth row is strongly offset medially and the tooth alveoli face dorsomedially, similar to *Stegosaurus*³⁴ and *Gigantospinosaurus*⁴³. There is a row of nutrient foramina lateral to the tooth row in both dorsal and ventral views. The dentary contains eighteen alveoli, in some of which there are teeth in various stages of eruption. In medial view, replacement teeth within resorption pits, lingual to the empty alveoli, are present.

Teeth

The two complete teeth have seven denticles on either side of two apical denticles (Fig. 3e,f). *Tuojiangosaurus* also has seven denticles on each side of the tooth crown⁴⁴. In *Stegosaurus*, the number of denticles is variable between teeth, and varies between five and nine on either side of two to four apical denticles³⁴ (NHMUK PV R 36730), while in *Paranthodon* there are four to five denticles on either side of a central one⁴⁵ (NHMUK PV OR 47338; NHMUK PV R 4992). Striations on the tooth crown are not confluent with marginal denticles, as in most stegosaurs except *Paranthodon*⁴⁶. The cingulum is present similar to other stegosaurs except *Huayangosaurus*, where a swelling at the base of the crown is present, but this is not developed into a distinct cingulum³⁹. Compared to the replacement tooth (Fig. 3e), the functional tooth is slightly worn (Fig. 3f), and its wear facet is inclined

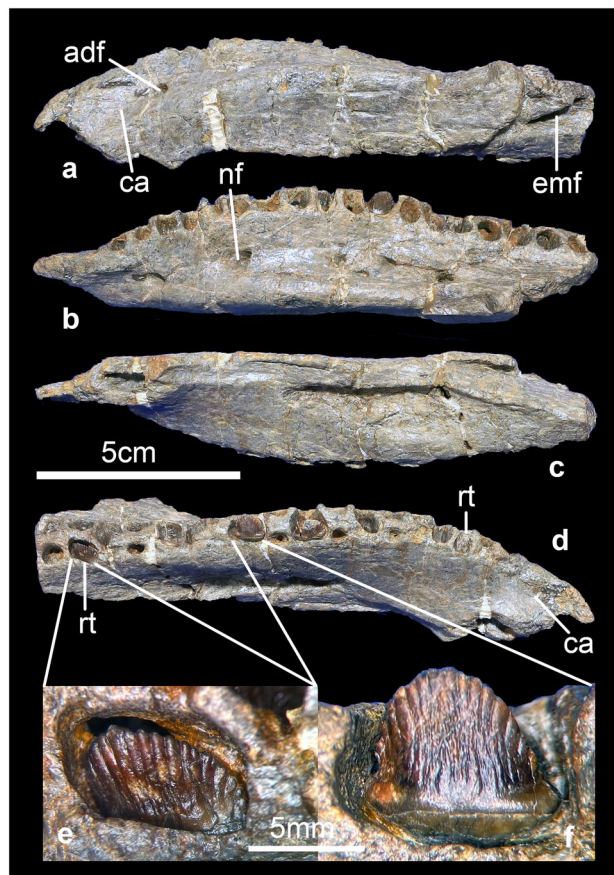


Figure 3. Dentary of *Baiyinosaurus baojiensis* (IVPG-D021-06). (a–d) left dentary, (e–f) teeth. (a) lateral view, (b) dorsal view, (c) ventral view, (d) medial view, (e, f) lingual view. *Adf* anterior dentary foramen, *ca* concave area, *emf* external mandibular fenestra, *nf* nutrient foramina, *rt* replacing teeth.

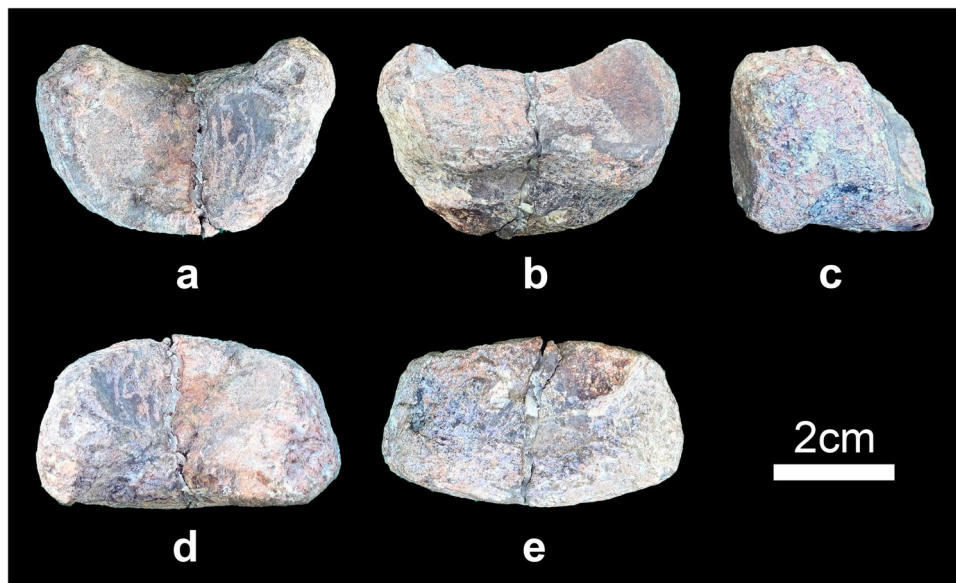


Figure 4. Atlas of *Baiyinosaurus baojiensis* (IVPG-D021-07). (a) anterior, (b) posterior, (c) right lateral, (d) dorsal view, (e) ventral view.

anteroventrally or posteroventrally. The microwear of the tooth is similar to *Kentrosaurus*⁴⁰, but some stegosaurs have a higher degree of tooth wear, such as in *Huayangosaurus*³⁹ and *Gigantspinosauros*⁴³, and especially the stegosaurian teeth discovered in Montana, USA⁴⁷ and Yakutia, Eastern Russia⁴⁸. The higher degree of tooth wear may indicate that the tooth itself is more mature and does not represent an individual's maturational status⁴⁷.

Cervical vertebra

The only cervical vertebra preserved is the atlas (Fig. 4a–e). The atlas only preserves the intercentrum. It is saddle-shaped in anterior view (Fig. 4a) and its posterior margin is elevated dorsally in posterior view (Fig. 4b). In *Stegosaurus*, there are two ridges on the ventral surface of the intercentrum⁴⁹ which are not present in *Baiyinosaurus*.

Dorsal vertebrae

Seven dorsal vertebrae are preserved including two anterior dorsal vertebrae (Fig. 5a–j) and five middle or posterior dorsal vertebrae (Fig. 6a–x). Only one dorsal vertebra is preserved completely (Fig. 6s–x), and two of the dorsal vertebrae are associated (Fig. 6a–f). The centra of all these dorsal vertebrae are almost amphiplatyan, similar to most stegosaurs. Both the anterior and posterior articular surfaces of the centra are round in outline. The centrum is wider transversely than long anteroposteriorly in the anterior dorsal vertebra (Fig. 5e–h), but are longer than wide in middle and posterior dorsal vertebrae (Fig. 6a–x). The ventral surfaces of the centra are smooth and the ventral margin of the centra is gently concave upwards in lateral view. The neural arch is not greatly expanded dorsally, similar to early-diverging stegosaurs such as *Huayangosaurus*⁵⁰ and *Gigantspinosauros*⁴³, but different to most other stegosaurs such as *Stegosaurus*⁴⁹, *Kentrosaurus*⁵¹ and *Tuojiangosaurus*⁴⁴. The neural canal has a sub-ovate outline in anterior and posterior views. The parapophyses of the dorsal vertebra (IVPG-D021-08) are situated at the base of the neural arch and the parapophyses of the dorsal vertebra (IVPG-D021-09) have migrated entirely onto the lateral surface of the neural arch, which is similar to the first and second dorsal vertebrae of *Stegosaurus*⁴⁹. However, the parapophyses of the third dorsal vertebra of *Stegosaurus*⁴⁹ have migrated onto the upper part of the neural arch, indicating the two anterior dorsal vertebrae of *Baiyinosaurus* may be the first and second dorsal vertebrae. The parapophyses of five middle or posterior dorsal vertebrae are situated at the base of the diapophyses. In the anterior dorsal vertebrae, the parapophysis has a concave articular surface (Fig. 5a,h). However, the parapophysis is elevated on a short stalk in middle or posterior dorsal vertebrae (Fig. 6a,g,m,s), similar to the early-diverging stegosaur *Bashanosaurus*⁶. In the anterior, the prezygapophyses are joined ventrally and face dorsomedially. The articular surfaces of prezygapophyses are flat. In anterior view, the diapophyses extend dorsolaterally at a high angle to the horizontal, similar to most stegosaurs such as *Stegosaurus*⁴⁹ and *Huayangosaurus*⁵⁰. From the anterior to posterior dorsal vertebrae, the angle to the horizontal of the diapophyses increases. The diapophysis is compressed dorsoventrally. In posterior view, the postzygapophyses are triangular in outline and linked to the neural canal by a ridge, similar to *Stegosaurus*⁴⁹. The neural spine projects posterodorsally in lateral view and is a transversely compressed plate in anterior view. The neural spine is significantly elongated anteroposteriorly, similar to *Gigantspinosauros*⁴³, but this is developed to a greater degree than in most stegosaurs such as *Huayangosaurus*⁵⁰, *Stegosaurus*⁴⁹ and *Bashanosaurus*⁶.

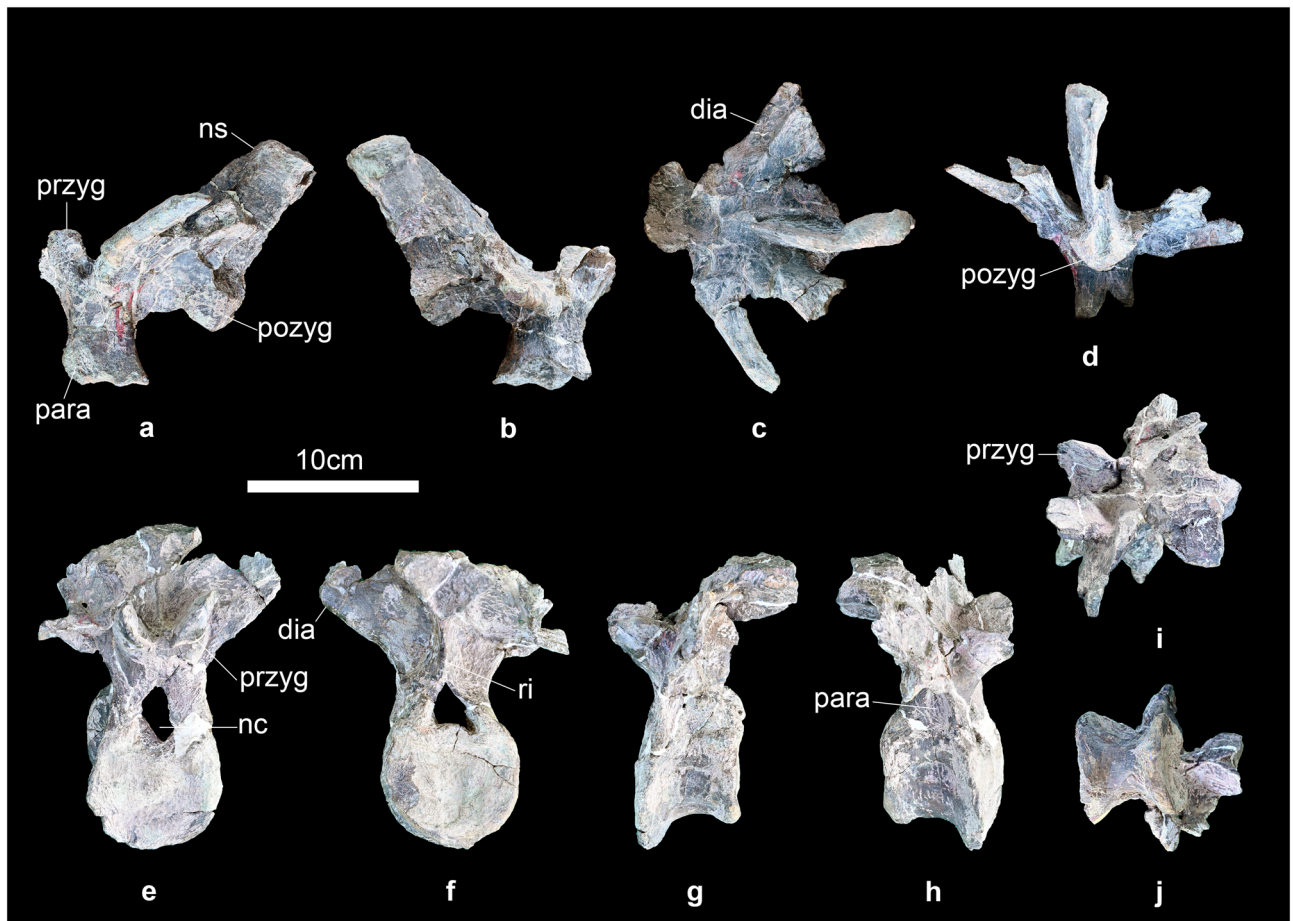


Figure 5. (a–j) anterior dorsal vertebrae of *Baiyinosaurus baojiensis* (IVPG-D021-08 and IVPG-D021-09). (a, g) left lateral, (b, h) right lateral, (c, i) dorsal view, (d, f) posterior, (e) anterior, (j) ventral view. *Dia* diapophysis, *nc* neural canal, *ns* neural spine, *para* parapophysis, *pozyg* postzygapophysis, *przyg* prezygapophysis, *ri* ridge.

Caudal vertebra

One anterior caudal vertebra is preserved but it is incomplete (Fig. 7a–f). Only the bases of the transverse processes are preserved, and the prezygapophyses, postzygapophyses and neural spine are missing. The anterior and posterior articular surfaces of the centrum are flat and round in outline. The anterior part of the ventral surface of the centrum has a chevron facet (Fig. 7e). The neural canal is round in outline.

Phylogenetic analysis

A single most parsimonious tree was recovered (Fig. 8). The MPT was 276.06 steps in length and had a consistency index of 0.598 and a retention index of 0.659. *Baiyinosaurus* is recovered in a clade with *Isaberrysaura* and *Gigantspinosaurus*, albeit with low Bremer supports and bootstrap frequencies. Although *Paranthodon* is generally considered to be a stegosaur, it was found in Ankylosauria in this study. This result may be due to its fragmentary state and highly labile phylogenetic position⁴⁵.

Discussion

The neurocentral sutures on the dorsal vertebrae are invisible, indicating *Baiyinosaurus* probably is adult⁵². Unfortunately, due to a paucity of other bones, we are not able to adequately assess the ontogenetic stage of *Baiyinosaurus*. Although *Baiyinosaurus* is clearly a stegosaur based on the elongate neural arch pedicel in dorsal vertebrae and the diapophyses of dorsal vertebrae projecting at a high angle to the horizontal, it has a significant difference from other stegosaurs in the morphology of the skull. The frontal of the *Baiyinosaurus* is wider than long, different to most stegosaurs except *Tuojiangosaurus*³⁸ (Fig. 9a–d). However, the frontal of the *Baiyinosaurus* not only contributes to the medial margin of the supratemporal fenestra but also makes up a much greater contribution to the anterior margin of the supratemporal fenestra than in other taxa, such as *Tuojiangosaurus*³⁸, *Huayangosaurus*³⁹ and *Stegosaurus*³⁴. Besides, *Baiyinosaurus* has some plesiomorphic characteristics in the vertebrae shared with early-diverging thyreophorans and early-diverging stegosaurs: its neural arch is not greatly expanded dorsally, similar to basally-branching thyreophorans and early-diverging stegosaurs such as *Bashanosaurus*⁶, *Gigantspinosaurus*⁴³ and *Huayangosaurus*⁵³. Its parapophysis is well developed and elevated on a short stalk, similar to the early-diverging stegosaur *Bashanosaurus*⁶ and the basally branching thyreophoran *Scelidosaurus*⁵⁴. It has broad, axially expanded neural spine in lateral view, similar to the condition in the early-diverging stegosaur

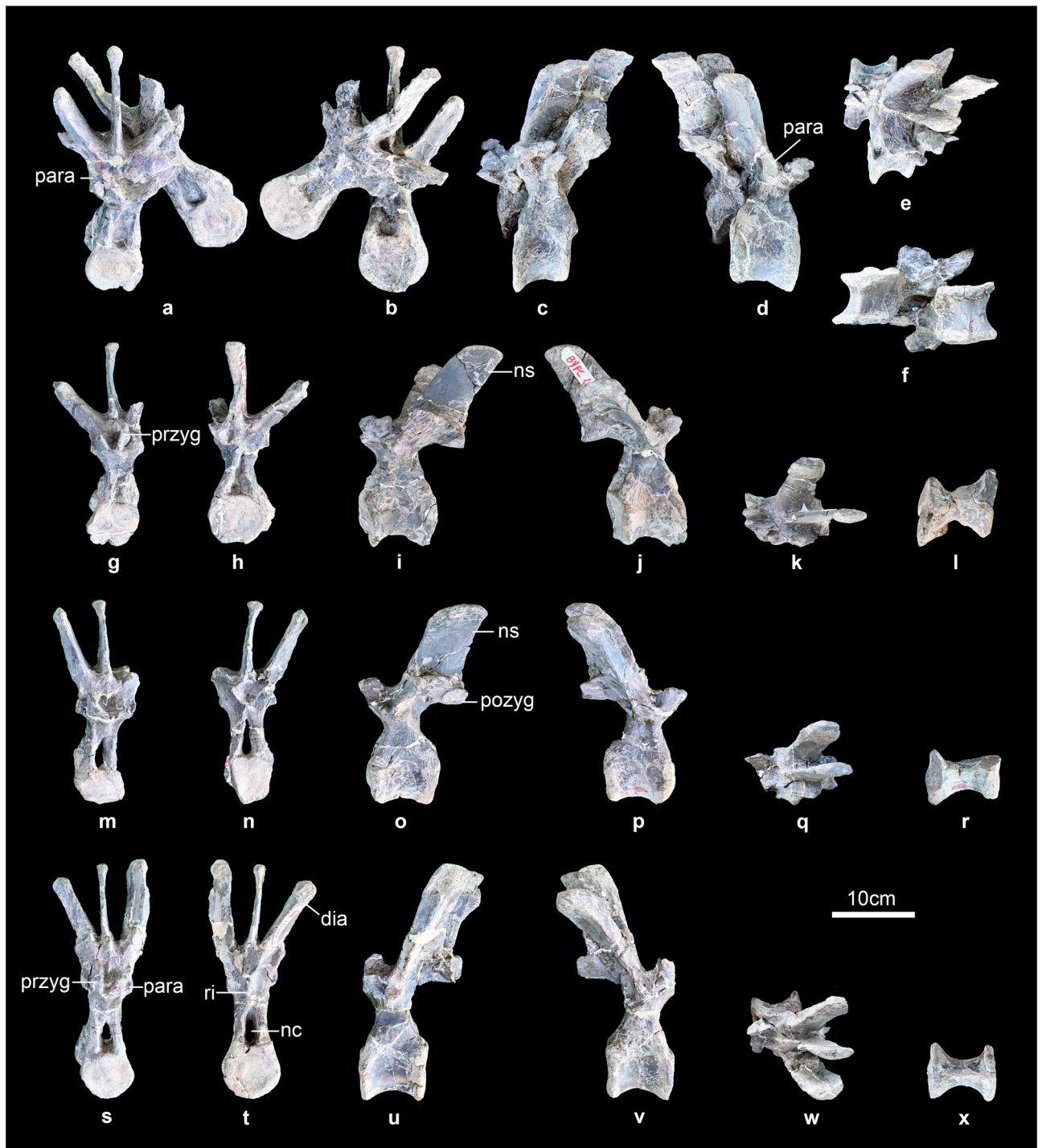


Figure 6. (a–x) middle or posterior dorsal vertebrae of *Baiyinosaurus baojiensis* (IVPG-D021-10 to IVPG-D021-14). (a, g, m, s) anterior, (b, h, n, t) posterior, (c, i, o, u) left lateral, (d, j, p, v) right lateral, (e, k, q, w) dorsal view, (f, l, r, x) ventral view. *Dia* diapophysis, *nc* neural canal, *ns* neural spine, *para* parapophysis, *pozyg* postzygapophysis, *przyg* prezygapophysis, *ri* ridge.

*Gigantospinosaurus*⁴³ and the basally branching thyreophorans *Scelidosaurus*⁵⁴, *Laquintasaura*⁵⁵ and *Lesothosaurus*⁵⁶. These character combinations of dorsal vertebrae of *Baiyinosaurus* are also different to other stegosaurs.

The diapophyses of the dorsal vertebrae of stegosaurs projecting dorsolaterally at a high angle to the horizontal is one of the most obvious differences compared to basally branching thyreophorans. *Baiyinosaurus* and other early-diverging stegosaurs such as *Bashanosaurus*⁶ and *Gigantospinosaurus*⁴³ show that features generally considered to be characteristic of stegosaurs, such as the elongated neural arch and parapophyses located at the base of the diapophyses as flattened, oval facets were acquired gradually during stegosaur evolution. First, there

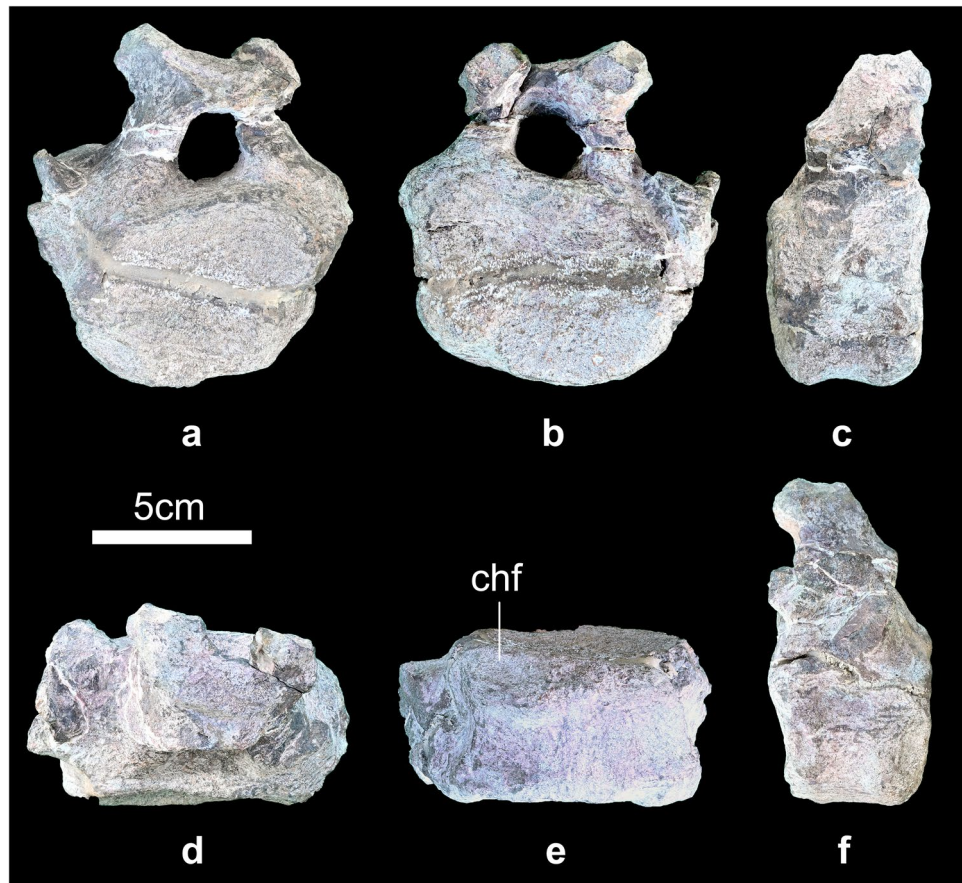


Figure 7. Anterior caudal vertebra of *Baiyinosaurus baojiensis* (IVPG-D021-15). (a) anterior, (b) posterior, (c) left lateral, (d) dorsal view, (e) ventral view, (f) right lateral. *chf* chevron facet.

was a gradual increase in the angle of projection of the diapophyses of the dorsal vertebrae: they project horizontally in basally branching thyreophorans such as *Scutellosaurus*⁵⁷ and *Laquintasaura*⁵⁵, slightly dorsolaterally in *Scelidosaurus*⁵⁴ and project dorsolaterally at a high angle in stegosaurs, even in the early-diverging stegosaurs *Baiyinosaurus* and *Bashanosaurus*⁶. The neural spine changed from anteroposteriorly broad to being narrower anteroposteriorly during thyreophoran evolution: the neural spine is axially expanded in basally-branching thyreophorans such as *Scelidosaurus*⁵⁴, *Laquintasaura*⁵⁵ and *Lesothosaurus*⁵⁶, and early-diverging stegosaurs such as *Baiyinosaurus*, but is narrower in the early-diverging stegosaur *Bashanosaurus*⁶ and other stegosaurs. Finally, the parapophysis was elevated on a short stalk in the basally branching thyreophoran *Scelidosaurus*⁵⁴, and early-diverging stegosaurs *Baiyinosaurus* and *Bashanosaurus*⁶, but is not elevated in later-diverging stegosaurs, and is instead present as a facet on the lateral surface of the neural arch ventral to the diapophysis.

The basally-branching thyreophorans, the ancestors of the stegosaurs, are all from the Early Jurassic, including *Scelidosaurus*⁵⁴ from England, *Emausaurus*³³ from Germany, *Lesothosaurus*^{56,58,59} from South Africa, *Scutellosaurus*^{57,60,61} from the United States, *Laquintasaura*⁵⁵ from Venezuela and the poorly known *Tatisaurus*^{62,63} and *Bienosaurus*^{64,65} from China. Although the earliest tracks of possible stegosaurs are from the Early Jurassic¹, the earliest bones of stegosaurs are found in the Middle Jurassic⁴. *Baiyinosaurus* has some character states that indicate it was transitional in morphology between the basally branching thyreophorans and the stegosaurs, and is also from the Middle Jurassic, indicating a Middle Jurassic (or much earlier) origin for the split between Stegosauria and its sister taxon Ankylosauria is likely.

Conclusions

Baiyinosaurus is a new taxon and represents one of the earliest records of Stegosauria. Systematic analysis shows that *Baiyinosaurus* is an early-diverging stegosaur closed to *Isaberrysaura*, *Alcovasaurus*, *Jiangjunosaurus* and *Gigantspinosauros*. *Baiyinosaurus* has some plesiomorphic characteristics and is transitional in morphology between early thyreophorans and early-diverging stegosaurs. The increasing diversity of Middle Jurassic stegosaurs that also occupy early-diverging positions indicates that it is likely that the stegosaurs split from their sister taxon, the ankylosaurs, early in the Middle Jurassic (or much earlier).

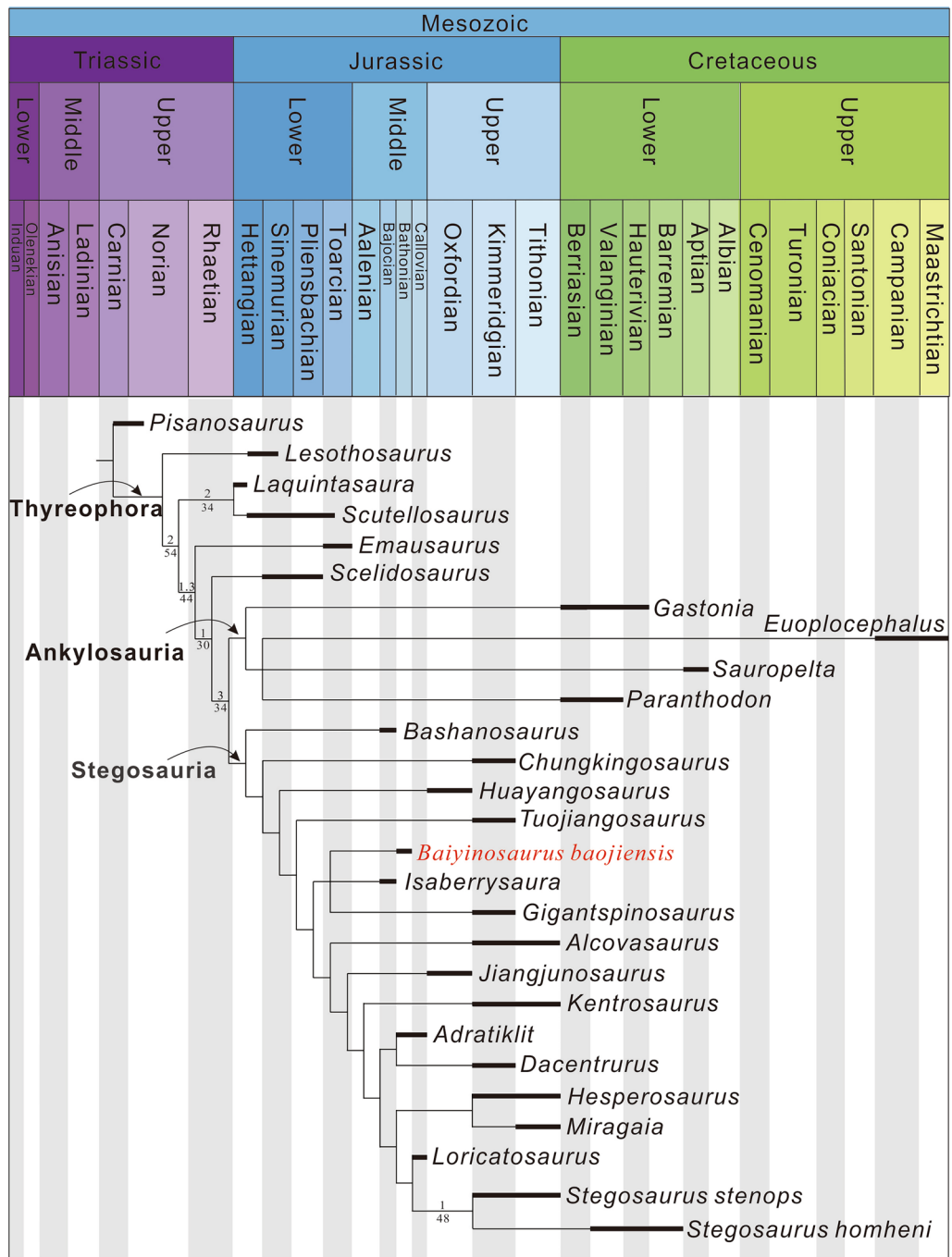


Figure 8. A single most parsimonious tree recovered by the phylogenetic analysis. Bremer supports no less than 1 and bootstrap support percentages are indicated above and below the line. Modified from Dai⁶.

Methods

Phylogenetic analysis. To assess the phylogenetic position of *Baiyinosaurus*, it is added to the character-taxon matrix of Dai et al.⁶. The matrix (updated from Maidment et al.⁴) is based on Raven and Maidment⁶⁶ which originally comprised 23 taxa scored for 115 characters. We added two new characters to the dataset: 9. Dorsal vertebrae: neural spines length (measured at the base) to centrum length ratio coded continuously. 64. Dorsal vertebrae: parapophyses are well developed that held on stalks at the base of the diapophyses; (0); poorly developed (1). The data matrix consists of 27 taxa scored for 117 morphological characters. The character list and data matrix can be found in supplementary A and B. The matrix was analyzed in TNT v1.5⁶⁷. *Pisanosaurus*⁶⁸ was set as the outgroup. All continuous characters (1–25) and characters 108 and 109 were ordered. A New Technology search was performed using sectorial, ratchet, drift and tree fusing options and 10 random addition sequences. The most parsimonious trees (MPTs) recovered from the New Technology search were used as the starting

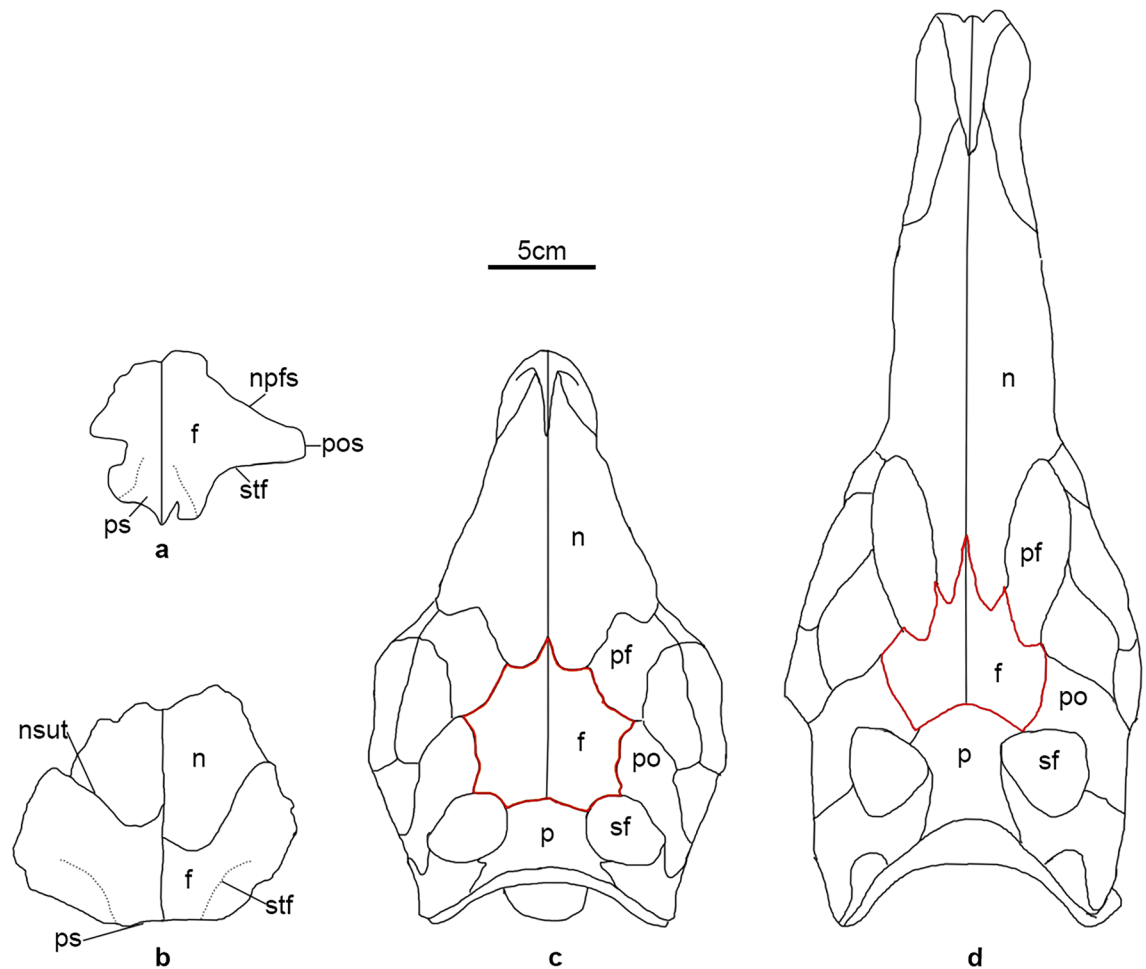


Figure 9. Outline of the frontal and other skull elements in dorsal view. (a) *Baiyinosaurus*, (b) *Tuojiangosaurus* (modified from Maidment and Wei³⁸), (c) *Hauyangosaurus* (modified from Sereno and Dong³⁹), (d) *Stegosaurus* (modified from Galton and Upchurch¹). *F* frontal, *n* nasal, *npfs* nasal and prefrontal suture, *nsut* nasal suture; *p* parietal, *pf* prefrontal, *po* postorbital, *pos* postorbital suture, *ps* parietal suture, *sf* supratemporal fossae, *sq* squamosal, *stf* margin of supratemporal fenestra.

point for a round of tree bisection-reconnection (TBR) using the Traditional Search option with one random addition seed and 1000 replicates. Support for the relationships obtained was evaluated using Bremer support and bootstrap analysis (1000 replicates, traditional search). Nomenclatural acts: The nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix '<http://zoobank.org/>'. The LSID for this publication is: urn:lsid:zoobank.org:pub:5A2665F4-F3D0-4519-808C-E4CEC8E07E00.

Data availability

All data generated or analysed during this study are included in this published article and its supplementary information files.

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Author contributions

L.N., L.D., Y.H. and P.G. wrote the main manuscript text. S.M. provided comparative data and helped with English language editing. L.N. and P.G. prepared all the figures and measured the specimens. L.D. and Y.H. oversaw the project. All authors reviewed the manuscript.

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Competing interests

The authors declare no competing interests.

Additional information

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