Ancestral body plan and adaptive radiation of sauropterygian marine reptiles

Highlights

- An Early Triassic complete skeleton related to sauropterygian is described
- Hanosaurus is the basal-most in sauropterygiforms that include saurosphargids
- Early sauropterygiform developed a slender body convergent to other marine reptiles
- High rate and diversity reflect the adaptive radiation of Triassic sauropterygiforms
SUMMARY
Sauropterygia is the most diversified and dominant clade among marine reptiles, but their early evolution is scarcely understood. Here we report the earliest known complete specimen related to sauropterygians from the Early Triassic. It is referred to *Hanosaurus hupehensis* by an exclusive combination of features and shows mosaic morphology integrating the characters of multiple sauropterygian sub-lineages. In phylogenetic results from both parsimony and Bayesian analyses employing our reconstructed dataset, *Hanosaurus* is stably resolved as the basal-most member of Sauropterygiformes, a clade comprising all sauropterygians and saurosphargids. This skeleton reveals an unexpected ancestral body plan for sauropterygiforms with an elongate trunk and four short limbs, differing from many of its immediate descendants but more similar to non-sauropterygiform marine reptiles at their early aquatic stage as axial swimmers. After this convergence on body plan, we quantitatively confirm the rapid divergence of sauropterygiform reptiles following the end-Permian mass extinction.

INTRODUCTION
The Mesozoic was the age of reptiles that not only occupied the land and sky but also adapted to the sea. Marine reptiles are great models for evolutionary study because they exhibit secondarily aquatic adaptations modified from their terrestrial ancestors, and multiple lineages have independently adapted to aquatic life involving both convergences and divergences.1 Sauropterygia,2 comprising turtle-like placodonts, lizard-like pachypleurosaurs, predatory nothosaurs, and long-necked pustosaurs including plesiosaurs, is the most predominant lineages among secondarily aquatic reptiles and is having been studied for about two hundred years. Contrary to the long study history, the origin and the very early evolution of sauropterygians remain largely unknown. It is because of the scarcity of complete fossils assigned to this clade from the Early Triassic shortly after its origin, and partially because the existing datasets are less applicable when more taxa are discovered. Based on abundant complete skeletons of sauropterygians and other important taxa,3,4 particularly those discovered during the recent two decades from southern China,5 we could have better glimpses of sauropterygian origin and early evolution.

We report a nearly complete skeleton referred to *Hanosaurus hupehensis*, an early Triassic marine reptile erected by Young6 and restudied in detail by Rieppel7 based on an incomplete specimen known as its holotype. In this research, we aim to resolve the relationship within sauropterygians and related marine reptiles such as saurosphargids, illuminate the very early history, and evaluate the adaptive radiation of sauropterygians and allied reptiles, whereas testing the clade consisting of sauropterygians, ichthyosaurs, and thalattosaurs is beyond our scope herein and will be part of our future work. Based on the previous studies, we reconstructed a morphologic dataset involving almost all the placodonts, cosauropterygians, and saurosphargids, as well as the basal members of turtles, huphsuchians, ichthyosaurs, and some thalattosaurs. Our result identifies a taxonomic clade, Saurop"t"erygiformes, comprising all the sauropterygian and saurosphargid taxa with *H. hupehensis* stably as the basal-most member, and it provides an updated framework for further studies such as the macro-evolution and the biotic recovery of this group of marine reptiles.
RESULTS
Systematic paleontology

Diapsida Osborn, 1903

Sauropterygiformes clade nov.

_Hanosaurus hupehensis_ Young, 1972

**Holotype**
Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) V 3231, a skull (Figure S1 [Skull of the holotype of _Hanosaurus hupehensis_(IVPP V 3231)], Related to Figure 1) in dorsal view and a partial postcranial skeleton (Figure S2 [Detailed comparisons between the referred specimen (IVPP V 15911) and the holotype of _H. hupehensis_ (IVPP V 3231)], Related to Figure 1) in ventral view.6,7

**Type locality and horizon**
Songshugou, Xunjian Village, Nanhang County, Hubei Province, China; dolomitic limestone (Member II) of the Jialingjiang Formation, Olenekian, Early Triassic.5

**Referred specimen**
IVPP V 15911, a nearly complete skeleton in ventral view (Figures 1 and S1 [Skull of the holotype of _H. hupehensis_ (IVPP V 3231)], Related to Figures 1 and S2 [Detailed comparisons between the referred specimen (IVPP V 15911) and the holotype of _H. hupehensis_ (IVPP V 3231)], Related to Figure 1).

**Locality and horizon**
Yingzishan, Yuanan County, Hubei Province, China; dolomitic limestone (Member II) of the Jialingjiang Formation, Olenekian, Early Triassic.

**Amended diagnosis**
A medium-sized sauropterygiform reptile with the exclusive combination of snout without constriction; supratemporal fenestrae smaller than orbits; nasals longer than frontals; mandibular articulation far posterior to the level of occiput, with retroarticular processes well-developed; anterior teeth short and conical; posterior teeth constricted at the base, with the lingual surface of tooth crown slightly concave; cervical ribs with evident anterior processes; dorsal ribs pachyostotic; coracoid not waisted; pubis extremely round; ischium kidney-shaped; no distinct thyroid fenestra between pubis and ischium; and minimally four carpals and three tarsals.

**Remark**
IVPP V 15911 and IVPP V 3231 (the type specimen of _H. hupehensis_6,7) are from the same horizon and adjacent quarries. As noted above in the amended diagnosis, this referred specimen can be readily assigned to _H. hupehensis_ by an exclusive combination of characters that is identical to the holotype. More comparative descriptions of IVPP V 3231 and IVPP V 15911 are provided in the supplemental information (Data S4 [supplemental information], Related to the STAR methods) with detailed figures (Figure S1 [Skull of the holotype of _H. hupehensis_(IVPP V 3231)], Related to Figures 1 and S2 [Detailed comparisons between the referred specimen (IVPP V 15911) and the holotype of _H. hupehensis_ (IVPP V 3231)], Related to Figure 1). In addition, when IVPP V 3231 and V 15911 are separately scored, the phylogenetic results obtained from the matrix of previous publication (Data S1 [Neenan matrix add _Hanosaurus_ V3231 V15911 for TNT], Related to the STAR methods) as well as our character matrix (Data S2 [Triassic marine diapsid matrix for TNT], Related to the STAR methods) both confirm their conspecific affinity (Figure S3 [Strict consensus tree based on the data matrix of Neenan et al. showing IVPP V 3231 and IVPP V 15911 as a single clade], Related to Figure 2 and S5 [Strict consensus tree based on our updated data matrix recovering IVPP V 3231 and IVPP V 15911 as a single clade], Related to Figure 2).

From the same horizon and neighboring localities, there are three specimens (YIGM V 0940, YIGM V 0941, and HFUT YZS-16-01) reported and identified as _Lariosaurus sanxiaensis_. According to the descriptions in previous studies, these specimens were distinguished from _H. hupehensis_ by the distinct count...
ossified tarsals and the different shapes of coracoids, when the ossification in tarsals can be varied in different ontogenetic stages and the coracid is poorly preserved in IVPP V 3231. However, in HFUT YZS-16-01, the same morphology of the coracid, the clavicle, the dorsal ribs, and the femur (possibly misinterpreted by Li and Liu as ‘ulna’) can be confirmed in the type specimen of *H. hupehensis* and this referred skeleton. Notably, in contrast to the aforementioned three specimens, all the other known *Lariosaurus* and *Nothosaurus* species exhibit supratemporal fenestrae much larger than orbits, higher counts of cervical vertebrae, obvious constrictions at the mid-points of coracoids and pubes, ulnae

Figure 1. A complete skeleton of *Hanosaurus hupehensis*, IVPP V 15911
(A–J) (A and B), referred specimen preserved in ventral view; (C and D), skull; (E and F), the medium region of cervical vertebrae; (G and H), the right side of the anterior region of the trunk with the pectoral girdle and the right forelimb, the line drawing is a mirror of the opposite side along the midline; (I and J), the left side of the sacral region and the anterior region of the tail, with the pelvic girdle and the left hindlimb, the line drawing is a mirror of the opposite side along the midline. (scale bar = 5 cm in A and B, = 1 cm in all the others; see abbreviations in Data S4 [supplemental information], Related to the STAR methods).
much broader than radii, humeri shorter than femurs and so on. Here we prefer not to consider *L. sanxiaensis* in our analyses and discussion, because the understanding of these three specimens are currently limited and their affiliation to *Lariosaurus* is questioned. In our separate future studies, more detailed comparisons and more unprepared fossil material will be involved to clarify the differences and the validity between these two taxa.

Figure 2. Dated cladogram of Sauropterygiformes based on the analyses of our updated dataset on Triassic marine reptiles

Taxonomic groups are marked by different colors. Topologies are combined with results from both maximum parsimony and model likelihood (Figure S5 [Strict consensus tree based on our updated data matrix (Data S2 [Triassic marine diapsid matrix for TNT], Related to the STAR methods) recovering IVPP V 3231 and IVPP V 15911 as a single clade], Related to Figures 2 and S10 [Majority-rule consensus (50%) Bayesian tree based on part of our updated data matrix recovering *Hanosaurus hupehensis* as the basal-most taxon of sauropterygiforms], Related to Figure 2). Colored bars of each taxon indicate the duration of discovered fossil remains. The ages of the nodes are obtained from the posterior median evaluations (Figure S11 [Tip-dating result of Triassic marine reptiles], Related to Figure 2). Geologic time follows the latest monographs (see the STAR methods).

much broader than radii, humeri shorter than femurs and so on. Here we prefer not to consider *L. sanxiaensis* in our analyses and discussion, because the understanding of these three specimens are currently limited and their affiliation to *Lariosaurus* is questioned. In our separate future studies, more detailed comparisons and more unprepared fossil material will be involved to clarify the differences and the validity between these two taxa.
Description

This referred specimen, IVPP V 15911, is entirely articulated and exposed in ventral view, with a total length of 79.4 cm (Figures 1A and 1B) being comparable in size to IVPP V 3231, the holotype of *H. hupehensis*. The cranial shape is an elongate triangle (Figures 1C and 1D). The snout is neither pointed nor blunt without lateral constriction. A pair of large pterygoids meet along the midline suture anteriorly and posteriorly leaving a narrow interpterygoid vacuity. In the holotype, the preorbital and postorbital regions of the skull are nearly equal in length, and the supratemporal fenestra is smaller than the orbit (Figure S1 [Skull of the holotype of *H. hupehensis*(IVPP V 3231)], Related to Figure 1), which is similar to saurosphargids, pachypleurosaur-like reptiles but contrasts with more derived eosauropterygians such as nothosaurs and pistosaurs. The same positions and proportions of orbits and supratemporal fenestrae can be tentatively identified in our referred specimen on the right side of the skull from the ventral view. The short mandibular symphysis is mainly contributed by the dentary. The retroarticular process is well developed as in the holotype, with a blunt termination.

There are at least 6 dentary teeth exposed on the anterior portion of the right dentary and more than 10 maxillary teeth visible on the right side (Figures 1C and 1D). There is neither an obvious diastema between premaxillary and maxillary teeth nor prominently enlarged fangs. All the teeth are short, sharp, and thecodont. The anterior teeth are generally coniform, and slightly procumbent; they are relatively larger than the posterior teeth and possess longitudinal striations. The lateral teeth are smaller, mildly overbite, and show relatively smooth surfaces of the crowns with slight constrictions at the bases of the crowns (Figures 1C, 1D, and S2 [Detailed comparisons between the referred specimen (IVPP V 15911) and the holotype of *H. hupehensis* (IVPP V 3231)], Related to Figure 1). In addition, as in those in the type specimen (Figures S1 [Skull of the holotype of *H. hupehensis*(IVPP V 3231)], Related to Figure 1) and S2 [Detailed comparisons between the referred specimen (IVPP V 15911) and the holotype of *H. hupehensis* (IVPP V 3231)], Related to Figure 1), the crowns of the lateral teeth are slightly lingually concave showing leaf-shaped outlines, which resemble those in saurosphargids.

There are 15 cervical, 25 dorsal, and 3 sacral vertebrae, and at least 16 caudal vertebrae in IVPP V 15911. Based on this referred specimen, the number of cervical vertebrae in *Hanosaurus* (15 in total with 13 anterior to the pectoral girdle) is fewer than all Triassic eosauropterygians. We identify the last cervical vertebra according to the corresponding rib not articulated with the sternum instead of the position anterior to the pectoral girdle. Following the same approach, the previously reported cervical counts should be revised as about 20 in *Neusticosaurus* and 18 in *Serpianosaurus* based on our first-hand observation, which both have fewer cervical vertebrae than other Triassic eosauropterygians but more than *Hanosaurus*. The entire vertebral column is conspicuously pachyostotic by developing swollen ribs and neural arches, but whether the inner compactness of these bones is increased remains unknown. The centrum is wider than long and anteriorly narrow and posteriorly wide in ventral view (Figures 1A, 1B, 1G, and 1H). The cervical rib possesses a distinct anterior process in vertebrae 2 to 13 (Figures 1E–1H, and S2I–S2L [Detailed comparisons between the referred specimen (IVPP V 15911) and the holotype of *H. hupehensis* (IVPP V 3231)], Related to Figure 1). In addition, as in those in the type specimen (Figures S1 [Skull of the holotype of *H. hupehensis*(IVPP V 3231)], Related to Figure 1) and S2 [Detailed comparisons between the referred specimen (IVPP V 15911) and the holotype of *H. hupehensis* (IVPP V 3231)], Related to Figure 1), the crowns of the lateral teeth are slightly lingually concave showing leaf-shaped outlines, which resemble those in saurosphargids.

The clavicle is relatively broader than that of most pachypleurosaur-like sauropterygians and nothosaurids, and its expanded posterodorsal portion does not have an anterolateral process (Figures 1G and 1H). The clavicle anteriorly contacts the scapula (Figures 1G, 1H, S2A, and S2B [Detailed comparisons between the referred specimen (IVPP V 15911) and the holotype of *H. hupehensis* (IVPP V 3231)], Related to Figure 1). The scapula develops a distinct ridge along the midline of the ventral surface and a pit at the posterior end of this ridge. The coracoid is oval with a coracoid foramen open at the suture with the scapula, resembling that in saurosphargids, placodonts, and even hupehsuchians and thalattosaurs, but distinctly different from that in any eosauropterygian taxon. The ilium is not entirely exposed but it is evidently small, much smaller than other girdle elements (Figures 1I and 1J). In both the referred specimen and the
holotype, the pubis is plate-like and extremely round (Figures 1I, 1J, and S2M–S2P) and the ischium is recovered (Figure S4) being reminiscent of that in sauropshargids and placodonts but different from pachypleurosaur-like sauropterygians and nothosaurs. An open, drop-shaped obturator foramen is present in the pubis near its suture with the ischium as in the holotype (Figures 1I, 1J, and S2M–S2P) and the referred specimen (IVPP V 15911) and the holotype of H. hupehensis (IVPP V 3231), Related to Figures 1I, 1J, and S2M–S2P [Detailed comparisons between the referred specimen (IVPP V 15911) and the holotype of H. hupehensis (IVPP V 3231)], Related to Figure 1 being reminiscent of that in sauropshargids and placodonts but different from pachypleurosaur-like sauropterygians and nothosaurs. An open, drop-shaped obturator foramen is present in the pubis near its suture with the ischium as in the holotype (Figures 1I, 1J, and S2M–S2P) and the referred specimen (IVPP V 15911) and the holotype of H. hupehensis (IVPP V 3231), Related to Figure 1. The ischium is kidney-shaped, with an incurved lateral edge and a convex medial margin.

The humerus is nearly straight, with a slightly curved posteromedial margin (Figures 1G and 1H). It is almost uniform, column-like in outline. The ectepicondylar groove is absent, and an entepicondylar foramen is present. The radius and the ulna are equal in length and similar in width. The proximal end of the ulna is slightly expanded. There are at least four roundish carpal ossifications including two large elements, the ulnare and the intermedium. The femur is also straight and its posteromedial margin is concave; it is as long as but its shaft is thinner than that of the humerus (Figures 1I and 1J). The internal trochanter of the femur is weakly developed but evident, and the intertrochanteric fossa is distinct but reduced. Both the tibia and fibula are straight and nearly equal in length, whereas the former is slightly wider than the latter. At least three tarsals are present, which are identified as the astragalus, the calcaneum, and a distal tarsal abutting the metatarsals I. Both the manus and the pes are small relative to the body size and do not show a fin-like or a paddle-shaped modification.

Phylogeny
To investigate the relationship among early sauropterygians, we constructed an updated morphological character matrix, which is largely improved compared to previous studies16–18 (see the STAR methods and Data S4 [supplemental information], Related to the STAR methods), including 62 taxa (42 of those are sauropterygians) and 181 characters mostly observed by us personally on specific specimens. To further examine whether our referred specimen can be aligned to H. hupehensis, we coded the holotype specimen of H. hupehensis (IVPP V 3231) and the referred specimen (IVPP V 15911) respectively. Results from both the original matrix (Data S1 [Neenan matrix add Hanosaurus V3231 V15911 for TNT], Related to the STAR methods) of Neenan et al.16,17 and our updated matrix indicate that these two specimens stably form a single clade (Figure S3 [Strict consensus tree based on the data matrix of Neenan et al. showing IVPP V 3231 and IVPP V 15911 as a single clade], Related to Figures 2 and S5 [Strict consensus tree based on our updated data matrix (Data S2 [Triassic marine diapsid matrix for TNT], Related to the STAR methods) recovering IVPP V 3231 and IVPP V 15911 as a single clade], Related to Figure 2). Considering their diagnostic morphology and same locality, we referred this specimen to the same species and combined their scores into a single taxon as H. hupehensis to maximize the morphologic information in other analyses here. Using the original matrix from Neenan et al.16,17 the basal position of Hanosaurus is recovered (Figure S4 [Strict consensus tree based on the data matrix of Neenan et al. showing Hanosaurus as the basal-most taxon of sauropterygiforms], Related to Figure 2). Using the updated matrix (Data S2 [Triassic marine diapsid matrix for TNT], Related to the STAR methods), our phylogenetic analyses conduct both maximum parsimony and Bayesian methods, when this work includes a Bayesian analysis focused on sauropterygian phylogeny that was not used previously (see the STAR methods). The topology generated by the strict consensus of maximum parsimony trees (Figure S6 [Majority-rule consensus (50%) tree based on our updated data matrix recovering H. hupehensis as the basal-most taxon of sauropterygiforms], Related to Figures 2 and S8 [Strict consensus tree based on part of our updated data matrix recovering H. hupehensis as the basal-most taxon of sauropterygiforms], Related to Figure 2) is fairly comparable to the Bayesian results (Figure S9 [Majority-rule consensus (50%) Bayesian tree based on our updated data matrix recovering H. hupehensis as the basal-most taxon of sauropterygiforms], Related to Figures 2 and S10 [Majority-rule consensus (50%) Bayesian tree based on part of our updated data matrix recovering H. hupehensis as the basal-most taxon of sauropterygiforms], Related to Figure 2). Our phylogenetic results further confirm a clade including all the eosauropterygians, placodontiforms, sauropshargids, Helveticosaurus, and Atopodentatus. Here we identify this previously unnamed clade as Sauropterygiformes (Figure 2) and Hanosaurus is stably recognized as the basal-most taxon of this clade in all maximum parsimony trees and Bayesian results.

DISCUSSION

Hanosaurus as the basal-most sauropterygiform
Our work represents the most complete phylogenetic analysis of sauropterygian reptiles to date, including almost all known Triassic genera (Figures 2 and S11 [Tip-dating result of Triassic marine reptiles], Related to Figure 2). According to our analyses (see Data S4 [supplemental information], Related to the STAR
methods, for more synapomorphies of the main clades), Hanosaurus is recognized as a sauropterygiform reptile based on the possession of: an akinetic palate, a pectoral fenestration, gastralia segments with five elements, and the crown of marginal teeth with a concave lingual surface. Moreover, Hanosaurus is suggested to be the basal-most taxon of Sauropterygiformes in terms of the absence of: elongate transverse processes of dorsal vertebrae, radius longer than ulna, and curved humerus that all are shared by all other sauropterygiforms. In addition, Hanosaurus exhibits mosaic anatomical morphologies resembling saurosphargids, basal placodontiforms, and basal eosauropterygians. The general body size and shape, the cranial configuration, and the pachyostosis of the vertebral column, collectively reflect its close affinity to primitive eosauropterygians including the pachypleurosaur-like forms. However, compared to any of the known eosauropterygians, the neck of Hanosaurus is shorter and possesses fewer cervical vertebrae.

The monophyly of Sauropterygiformes, including Hanosaurus, saurosphargids, Helveticosaurus, Atopodentatus, placodontiforms, and eosauropterygians, is well supported. The internal relationships among these sauropterygiform reptiles are well resolved (Figures 2 and S5 [Strict consensus tree based on our updated data matrix recovering H. hupehensis as the basal-most taxon of sauropterygiforms], Related to Figure 2). Sauropsphargidae, a group composed of Eusaurosphargis, Largocephalosaurus, and Sinosaurosphargis, is confirmed to be the sister group of Sauropterygia, apart from the interpositions of the enigmatic and unstable taxa Helveticosaurus and Atopodentatus. Sauropsphargia bifurcates into Placodontiformes and Eosauropterygia. Placodonts are indubitable sauropterygians but do not diverge as early as previously considered within sauropterygians, and are gradually specialized through time after some conical-toothed and unarmored taxa. Placodontiformes is maintained and its intra-relationships are well resolved including the monophyletic Cyamodontoidea and more derived Placochelyida developing heavy armors and carapaces. Our topology of placodontiforms is well in accordance with other studies for placodonts, though there are a few minor differences such as here placing the highly specialized henodontids as the most derived taxa. Notably, the monophyletic ‘Pachypleurosauria’ is not conclusively recovered here, a result consistent with other recent analyses, despite the incomplete sampling of non-eusauropterygian eosauropterygians in these previous studies. In Eosauropterygia, Wumengosaurus and Qianxisaurus are the basal-most members, whereas the other Chinese pachypleurosaur-like taxa are more derived within eosauropterygians showing close affinities with each other, but whether these Chinese pachypleurosaur-like taxa form a monophyletic group is unsolved. European pachypleurosaurids form a monophyletic lineage as the family Pachypleurosauridae following the previous definition from Rieppel. Eusauropterygia is recovered including all the large eosauropterygians (adult length >1 m), in which Simosauridae, Nothosauridae, and Pistosauroidae are monophyletic as previously defined in other studies.

Body plan of early sauropterygiforms

Although recovered as the basal-most sauropterygiform, Hanosaurus does not represent the terrestrial ancestor of sauropterygians. Apart from being preserved in marine sediments, Hanosaurus is certainly an aquatic animal based on its pachyostotic vertebral column serving as the ballast for buoyancy control underwater, and the reduced ilium with bar-shaped sacral ribs that could not support the body weight to walk on land. Besides these modifications, the slender and elongate trunk with the remarkably shortened limbs of Hanosaurus also featured aquatic adaptations as seen in other marine reptiles. We illustrate the body shape of marine reptiles by direct measurements and ratios of various body regions (Figure 3, see details in the STAR methods and Data S4 [supplemental information], Related to the STAR methods). Terrestrial reptiles (e.g., Araeoscelis and Vadassaurus) normally have modest trunk lengths with elongate limbs (Figures 3 and 4) for support and movement on land. Conversely, at the early stage of aquatic adaptation in many marine reptilian groups (e.g., Chaohusaurus, an ichthyopterygian; Nanchangosaurus, a
Hupehsuchian; Pleurosaurus, a marine rhynchocephalian), they consistently exhibit a body form combining an elongate trunk and shortened limbs, when the ratios of log-transformed trunk length to forelimb length and hindlimb length respectively are both more than 1.3 (Figure 4). The elongate trunk can be additionally reflected by the higher number of dorsal vertebrae more than 24 and a higher ratio of the body length to the width over 6 (Figure 3). Many marine reptiles also have a very long tail, but this long tail might be an ancestral feature inherited from their terrestrial ancestors like the early diapsids (Figure 3).

In multiple lineages of marine reptiles, this “long-trunk” convergence reflects the evolutionary constraints inheriting the axial undulatory movement from their terrestrial ancestors. Many primitive members such as the basal ichthyosauriforms are anguilliform swimmers, relying on axial undulatory locomotion involving the movement of the entire slender body. Sauropterygia used to be considered as an exception because many of them were usually known as paraxial swimmers having relatively short and rigid trunks and using the limbs as thrusters, in which nothosaurs and plesiosaurs are representatives. Axially manueverable body plans were briefly suggested in European pachypleurosaur bodies, but in the scope of the entire group of sauropterygiforms, they are relatively derived. Based on our result, Hanosaurus is resolved to be more primitive than all saurospherids, placodonts, and eosauropterygians, and of interest, it possesses a large number of dorsal vertebrae and evidently shortened fore- and hind-limbs compared to other sauropterygiforms including basal eosauropterygians, but resemble other aquatic reptiles like Nanchangosaurus and Chaohusaurus in this aspect (Figures 3, 4, and S13). With the discovery of this referred fossil of Hanosaurus, we, therefore, propose that the basal sauropterygiform marine reptiles are also dominated by the evolutionary constraint to evolve an elongate trunk and short limbs.
at their early stage of secondarily aquatic adaptation. A long trunk is easily caused by the mutation of dorsal vertebra duplication, and then this convergent body plan in marine reptiles (Figures 3 and 4) probably has some selective advantages on movement and ambush in the coastal marine environment full of rocks and reefs (Figure S13 [Marine reptiles of the shallow marine habitat in the Early Triassic, Hubei, China], Related to Figures 3 and 4). Although the pachyostotic dorsal ribs and the dense gastric basket potentially limit the flexion of the trunk, the marine reptiles developing pachyostosis could be anguilliform swimmers. We speculate that Hanosaurus was capable of axial undulatory movement at least better than most other sauropterygiforms such as placodonts, nothosaurs, and plesiosaurs, if not comparable with basal ichthyosauriforms like Chaohusaurus. Therefore, before evolving the underwater-flying stroke of pistosaurs, the elongate neck in eosauropterygians, and the turtle-like appearance in placodonts and saurosphargids (Figure 2), Hanosaurus, as the basal-most sauropterygiform, shows an unexpected long-trunk body plan as an anguilliform swimmer at the beginning of sauropterygiform evolution.

Adaptive radiation of early sauropterygiforms

After the “long-trunk” stage, sauropterygiforms show a divergent evolution to generate Saurosphargidae with laterally expanded flat trunks, Placodontia with a shortened body covered with heavy armors superficially resembling turtles, and Eosauropterygia including abundant pachypleurosaur-like small members and large plesiosaurs developing long necks and broad fins (Figure 2). These different sauropterygiform clades evolved manifold phenotypes occupying a large region in the morphospace resulted from our principal component analyses (Figures S5 and S12 [Morphospace based on principal components PC1 and PC2], Related to Figure 5). In comparison, ichthyopterygians have less change from anguilliform Chaohusaurus to dolphin-like derived ichthyosaurs, which are thunniform swimmers propelled mainly by tails but retaining axial undulation, and thalattosaurs show little bauplan modification besides the changes of head shape and neck length (Figure 5). Based on our latest dataset and phylogenetic results of Sauropterygiformes, our tip-dating result indicates that Sauropterygiform marine reptiles radiated rapidly (Figure S11 [Tip-dating result of Triassic marine reptiles], Related to Figure 2) possibly from the latest Permian to the earliest Triassic (Figure 2). High rates are estimated at the beginning of sauropterygiform evolution, and the three main subclades (Saurosphargidae, Placodontiformes, and Eosauropterygia) arose within less than 10 Ma hypothetically from the latest Permian. When more taxa of early sauropterygiforms were added, the high evolution rates among placodonts are not recovered. Another episode of rapid evolution is at the early stage of eusauropterygian clades leading to the large-sized nothosaurs and pistosaurs (Figure S11 [Tip-dating result of Triassic marine reptiles], Related to Figure 2). Apart from the taxon diversity with more...
than 40 genera discovered from Triassic, under our updated phylogenetic framework, sauropterygiform reptiles took advantage of the emerged marine ecological opportunities by evolving innovative morphologies with associated changes in locomotion,37 habitats, and diets. Sauropterygiforms soon rose from the aftermath of the end-Permian mass extinction to become a predominant reptilian group conquering the sea.

Limitation of the study

The objective descriptions in this research are limited to the preservation of fossil specimens, and better-exposed skulls of Hanosaurus could supply the cranial anatomical information of this taxon. The convergence in body plan of Hanosaurus and other marine reptiles is currently only suggested by the similar occupation in morphospace, and functional morphologic methods and experiments can better demonstrate their locomotions.

STAR METHODS

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

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2022.105635.

ACKNOWLEDGMENTS

We thank J.Z. Ding for specimen preparation; W. Gao for photographing; G. Ugueto for fauna reconstruction; C. Zhang, Y.L. Yu, and H.B. Wang for assistance on Bayesian analyses; Z.H. Zhou, X. Xu, and X.J. Ni for
discussion; R.X. Zhu, C.L. Deng, and H.Y. He for support. We especially thank the editor, A. Bolognesi, and the four anonymous referees for their careful review and helpful comments. W.W. thanks T.M. Scheyer, O.W.M. Rauhut, E.E. Maxwell, R.R. Schoch, I. Werneburg, S. Nosotti, L.J. Zhao, and D.Y. Jiang for their hospitality and access to the collections. The study was supported by the Strategic Priority Research Program (B) of the Chinese Academy of Sciences (XDB26000000), the Youth Innovation Promotion Association of Chinese Academy of Sciences, the National Natural Science Foundation of China (42002019 and 41972014), State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (20203119), Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences (IVPP, CAS) (LVEH020001).

AUTHOR CONTRIBUTIONS
C.L. and W.W. conceived the research; C.L., Q.S., L.C., and W.W. participated in the fieldwork; W.W. undertook the morphological comparisons, data collection, figure preparation, and phylogenetic and statistical analyses. W.W., X.W., and C.L. interpreted the fossil and wrote the manuscript with feedback from Q.S. and L.C.

DECLARATION OF INTERESTS
The authors declare no competing interests.

Received: January 10, 2022
Revised: July 8, 2022
Accepted: November 16, 2022
Published: December 22, 2022

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STAR METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---------------------|--------|------------|
| Biological samples  |        |            |
| Referred specimen of Hanosaurus hupehensis | Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science | IVPP V 15911 |

| Deposited data       |        |            |
|----------------------|--------|------------|
| Character matrix of Triassic marine reptiles | This paper | N/A |

| Software and algorithms |        |            |
|-------------------------|--------|------------|
| TNT version 1.5          | Goloboff and Catalano | https://www.lillo.org.ar/phylogeny/tnt/ |
| MrBayes version 3.2.7    | Ronquist et al. | https://www.softpedia.com/get/Science-CAD/MrBayes.shtml |
| paleontological statistics software package (PAST) version 4.0 | Hammer et al., 2001 | https://past.en.lo4d.com |

RESOURCES AVAILABILITY

Lead contact
Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Chun Li (lichun@ivpp.ac.cn).

Materials availability
The fossil skeleton studied here is accessioned and accessible at the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, with an accession number of IVPP V 15911.

Data and code availability
All data used in the study are included in this publication with the supplemental data and are publicly available as of the date of publication. The present research did not use any updated codes.

METHOD DETAILS

Fossil material
The referred to specimen (IVPP V 15911) and the holotype (IVPP V 3231) of *H. hupehensis* are permanently deposited at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, China. As for the other 174 listed specimens (Table S1 [Specimen list of sampled Triassic marine diapsids], Related to Figures 2 and 3), we have physically examined the specimens as many as possible, especially from the richest collections of Triassic marine reptiles in China and European countries. We (at least one of the authors) personally examined 142 specimens, and the leading author (WW) personally observed 120 specimens when other 54 taxa were scored from the literature by him (Table S1 [Specimen list of sampled Triassic marine diapsids], Related to Figures 2 and 3). One or more of the authors have conducted detailed studies on 28 taxa (about half of the total 62 taxa) used in this study. To avoid bias due to the observation and interpretations of different authors, the state codes for all characters were carefully scored by the leading author (WW) with consultation with other authors. As for the genera including several species, if possible, we chose a species that is represented by complete, well-preserved adult specimens (Table S1 [Specimen list of sampled Triassic marine diapsids], Related to Figures 2 and 3).

Character matrix construction
To investigate the phylogenetic relationships of *Hanosaurus* among marine reptiles, we constructed an updated morphological dataset (62 taxa, 181 characters) focusing on Triassic sauropterygians and relevant reptiles. Compared to the previous most comprehensive dataset of sauropterygians, we added 26 additional taxa to include all the known placodontiforms, eosauropterygians, and saurosphargids as the
ingroups or the target groups herein, and sampled the taxa more adequately and representatively than previous datasets to avoid involving multiple species of one genus. Youngina capensis was used to root the cladogram because it could represent the morphology of primitive diapsids. According to the latest studies from multiple independent research groups and our phylogenetic results using the previous matrix (Figure S3 [Strict consensus tree based on the data matrix of Neenan et al. showing IVPP V 3231 and IVPP V 15,911 as a single clade]), we used specific species of the basal-most and well-documented Tethyan fauna, instead of using Ichthyopterygia and Thalattosauria as two operational taxonomic units on any level are added in a future study. Therefore, with more primitive members of Ichthyosauriformes discovered from eastern Tethyan fauna, instead of using Ichthyopterygia and Thalattosauria as two operational taxonomic units (OTUs) as in the previous studies, we used specific species of the basal-most and well-documented members of ichthyosauriforms (hupehsuchians included) and thalattosaurians as the outgroups to investigate the relationship among sauropterygian and saurosphargid taxa. Although the monophyly of the marine reptile group combining Ichthyopterygia, Thalattosauria, and Sauropterygia is controversial, it is beyond our scope here focusing on the inner relationship within sauropterygians and their relationship with unsolved taxa such as saurosphargids and Apatospondylus. A larger matrix involving the basal members of Archosauromorpha and Lepidosauromorpha will be considered in our future work when their inner relationships are better resolved respectively and more specimens are personally checked by us. The taxa of stem turtles (or pantestudines) were possibly related to sauropterygians in a few recent studies, and we first-hand observed some specimens and tentatively added them to our matrix to double test. We added 40 additional characters according to the homology principle and tried to avoid adding more features dominantly affected by their aquatic lifestyle. We adopted the characters, which are generally applicable to all of our OTUs, from the datasets on specific lineages like Placodontiformes, Pachypleurosauria, Nothosauria, Thalattosauria, and Ichthyopterygia. The added characters mainly include the counts in different vertebral regions, dentition on palatal elements, and the morphology of ribs, gastralia, and dermal armors (see the character list in Data S4 [supplemental information], Related to the STAR methods), for more information). When possible, we scored the character states based on the best-preserved adult specimens to decrease the ontogenetic, sexual, and individual variations. Under these criteria, our character matrix can be considered on the genus level and the species level for all the taxa, and even the specimen level for some taxa scored by a specific single specimen (Table S1 [Specimen list of sampled Triassic marine diapsids], Related to Figures 2 and 3), being available when extra operational taxonomic units on any level are added in a future study.

Phylogenetic analyses and tip-dating

To obtain the phylogeny of sauropterygian and allied marine reptiles such as saurosphargids, we conducted the maximum parsimony inference using TNT version 1.5. All the characters were equally weighted and unordered. The general RAM in the memory was adjusted to 500 MBytes. Because the number of taxa was fewer than 100 and the new technology search was unnecessary, herein we conducted the traditional search with random additional sequence and tree bisection-reconnection (TBR). The heuristic search ran 1000 replications of Wagner trees with one random seed and 10 trees saved per run. We conducted six rounds of maximum parsimony analyses. In the first round of analyses, we employed the data matrix (Data S1 [Neenan matrix add Hanosaurus V3231 V15911 for TNT], Related to the STAR methods), of Neenan and colleagues and coded the character states of the holotype (IVPP V 3231) and the referred to specimen (IVPP V 15911) separately, when more informative scores from the skull were obtained in the holotype but more from the postcranal skeleton were coded in the referred to specimen respectively. In the second round, considering the result (Figure S3 [Strict consensus tree based on the data matrix of Neenan et al. showing IVPP V 3231 and IVPP V 15,911 as a single clade], Related to Figure 2) when two specimens were coded separately in the previous data matrix, we combined the information into one OTU as Hanosaurus hupehensis (Data S1 [Neenan matrix add Hanosaurus V3231 V15911 for TNT], Related to the STAR methods), used with the OTU H. hupehensis excluded. In the third round, we coded IVPP V 3231 and IVPP V 15,911 separately again in our updated data matrix (Data S2 [Triassic marine diapsid matrix for TNT], Related to Figure 2), used with the OTU H. hupehensis excluded) to further test the affiliation of these two specimens (Figure S5 [Strict consensus tree based on our updated data matrix recovering IVPP V
3231 and IVPP V 15,911 as a single clade), Related to Figure 2. In the fourth round, the scores were combined as one OTU H. hupehensis (Data S2 [Triassic marine diapsid matrix for TNT], Related to Figure 2, used when V 3231 and V 15911 were excluded) with all 62 taxa involved (Figure S6 [Majority-rule consensus (50%) tree based on our updated data matrix recovering H. hupehensis as the basal-most taxon of sauropterygiforms], Related to Figure 2). Based on the result of the fourth round, we conducted the reduced consensus tree analysis to find the wildcard OTUs, which came to be the stem pantestudines and hupehsuchians. Therefore, we excluded the stem pantestudines in our fifth round (Figure S7 [Strict consensus tree based on part of our updated data matrix recovering H. hupehensis as the basal-most taxon of sauropterygiforms], Related to Figure 2), and removed both pantestudines and hupehsuchians in the sixth round of analyses (Figure S8 [Strict consensus tree based on part of our updated data matrix recovering H. hupehensis as the basal-most taxon of sauropterygiforms], Related to Figure 2).

To further examine the phylogeny of sauropterygians and saurosphargids, we employed Bayesian phylogenetic inference using MrBayes version 3.2.7.48 Sauropetergians were all extinct without extant descendants, and our character matrix (Data S3 [Triassic marine diapsid matrix for Bayes], Related to the STAR methods) included only morphological data, therefore, we used the Mk model49 with variable ascertainment bias, equal state frequencies, and gamma rate variation across characters and the prior for the gamma shape parameter was exponential (1.0). For the Markov chain Monte Carlo (MCMC), two independent runs and four chains, including a cold chain and three hot chains, were used per run for 10 million generations and sampled every 1000 generations. The average SD of split frequencies (ASDF) was less than 0.01, and the effective sample size (ESS) was larger than 100 both indicating an adequate result. We conducted two rounds of Bayesian analyses when H. hupehensis was scored based on both two specimens. All 62 OTUs were involved in the first round (Figure S9 [Majority-rule consensus (50%) Bayesian tree based on our updated data matrix recovering H. hupehensis as the basal-most taxon of sauropterygiforms], Related to Figure 2), and 54 OTUs with pantestudines and hupehsuchians removed in the second round (Figure S10 [Majority-rule consensus (50%) Bayesian tree based on part of our updated data matrix recovering H. hupehensis as the basal-most taxon of sauropterygiforms], Related to Figure 2).

To investigate the evolutionary rates and the divergence times among all sauropterygiform clades, we performed a Bayesian tip-dating (Figure S11 [Tip-dating result of Triassic marine reptiles], Related to Figure 2) using the updated data matrix (Data S3 [Triassic marine diapsid matrix for Bayes], Related to the STAR methods) with an unpartitioned model and the constrained parsimony tree topology in Mrbayes.3.2.7.48 We used an independent lognormal50 relaxed clock model and the Mk model49 with a gamma rate variation51 across all characters for likelihood calculation. The parameters of the MCMC process were the same as the above undated Bayesian phylogenetic analyses. The time tree was assigned a uniform prior,52 and the root age had an offset exponential prior with a mean of 256.3 Ma and a minimum of 251.9 Ma. The ages of all marine reptile genera/species in the matrix were assigned uniform priors respectively with their lower and upper bounds of the corresponding geologic time stages53 and stratigraphic ranges (Table S2 [Ages of Triassic marine reptiles], Related to Figure 2), except for Psephoderma alpinum being fixed at its last appearance date (201.4 Ma) because of having the youngest last appearance date among all taxa we considered.

**Specimen measurements and body shape analyses**

We assembled a series of linear measurements from representative marine reptiles (Table S3 [Measurements of representative marine reptiles], Related to Figures 3, 4, and 5). Our dataset includes all sauropterygiform subgroups and other major lineages of Mesozoic marine reptiles such as Hupehsuchia, Ichthyopterygia, Thalattosauria, marine lepidosaurs including marine sphenodontians and mosasauras. We sampled and measured 40 nearly complete skeletons of 40 species/genera representing basal to crown taxa of each group (Table S3 [Measurements of representative marine reptiles], Related to Figures 3, 4, and 5). According to our phylogenetic results and literature, we reconstructed a cladogram of all these sampled marine reptilian taxa (Figure 3). Measurements of the dataset were made either using a vernier caliper and flexible rule directly from the specimens or using the ImageJ program from the published photos and corresponding scale bars in literature. Our dataset included nine discrete and unrelated linear values (Table S3 [Measurements of representative marine reptiles], Related to Figures 3, 4, and 5): the skull length (SL) from the anterior margin of the snout to the posterior end of the occiput, the skull width (SW) as the maximum width of the dermal cranium, the neck length (NL), the body length (BL) (same as the trunk length in this study) from the first dorsal to the last sacral vertebra, the body width (BW) (same as the trunk width in this study) measured from the maximum width of the rib cage.
when the specimen was preserved strictly in dorsal view or doubled the radius of the longest rib in lateral view when the curved rib can be roughly regarded as the margin of a semicircle, the tail length (TL), the tail width (TW) as the maximum width of the proximal region of the tail strictly in dorsal view or the width of the largest caudal centrum including the length of the associated transverse process, the forelimb length (FL) from the proximal end of the humerus to the distal tip of the fingers, and the hindlimb length (HL) from the proximal end of the femur to the distal tip of the toes.

Our analyses were conducted using the paleontological statistics software package (PAST) version 4.0. To test the convergence of long trunk and short limbs, we conjunctively considered these two features and made a binary plot using the dimensionless ratios of BL/FL and BL/HL as the coordinates with all original measurements (BL, FL, and HL) already log10-transformed (Figure 4). Secondly, we made a bar graph based on the ratio of BL/BW to show the elongation of the trunk itself (Figure 3). Thirdly, we made a stacked bar chart of NL/BL/TL to compare the percentages of these three parts in different taxa (Figure 3). These results should be comprehensively considered, because some features might be ignored due to others, such as that the BL of *Henodus* (a highly specialized placodont) occupied a large percentage in the entire length but its trunk was not actually elongated, while the body of *Pleurosaurus* (a marine sphenodontian) was extremely long but not that notable with a tail even longer. These nine measurements could outline the body shapes, therefore, we collectively used the aforementioned nine linear measurements being log10-transformed and employed principal component analysis (PCA) to demonstrate the shape variances of the sampled marine reptiles. We also conducted principal coordinate analysis (PCoA), which showed almost the same results as PCA herein. The principal component 1 axis (PC1) reflected about 86% of the variance showing positive eigenvector coefficients with all the nine measurements, hence PC1 seemed mainly related to the size with large marine reptiles on one side and small ones on the other (Figure S12 [Morphospace based on principal components PC1 and PC2], Related to Figure 5). PC2 described more than 7% of the variance being evidently negative (~81%) with the neck length, which explained the elongation or the shortening of the cervical region with *Plesiosaurus* and *Cartorhynchus* (an ichthyosauriform) at the two opposite ends. PC3 explained over 3% of the variance, and its eigenvector coefficients were mostly negative (~64%) with the body width and mostly positive (61%) with the tail length when *Henodus* and *Anshunsaurus* (a thalattosaurian) were at the two extremes respectively. We preferred the binary morphospace using PC2 and PC3 to demonstrate the shape disparities of multiple marine reptilian lineages (Figure 4).

**QUANTIFICATION AND STATISTICAL ANALYSIS**

This study used no statistical analysis.

**ADDITIONAL RESOURCES**

There is no additional resource to report besides that in the above resource availability section.