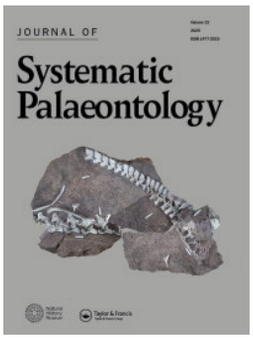

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A new hupehsuchian (Reptilia: Ichthyosauromorpha) with widely spaced autopodium from the marine Lower Triassic of South China

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Hupehsuchia is a group of marine reptiles from the uppermost Lower Triassic of South China, known for their segmented neural spines covered by dermal ossicles and polydactyl forelimbs. Although five genera and species are currently known for this group, our understanding of their true diversity is limited. In this study, we report a new hupehsuchian, *Lentamanusuchus hubeiensis* gen. et sp. nov., based on the combination of unique characters in the trunk region and forelimb. These include widely spaced autopodial elements, an extra distal carpal and metacarpal, and a two-layered dermal armour. Phylogenetic analysis recovered the new species as a sister taxon to Parahupehsuchinae within Hupehsuchidae, supporting the gradual addition of extra carpal and digital elements in hupehsuchians. The widely spaced autopodia of *Lentamanusuchus hubeiensis* represent previously unknown morphologies in hupehsuchians. The wide spacing of the proximal autopodia, along with hyperphalangy, may help smooth the paddle surface to reduce vortices during wrist and proximal digit flexion and extension while swimming. Alternatively, it could result from reduced ossification of manual elements due to diminished muscular control in the manus.

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Keywords: convergent evolution; marine reptiles; aquatic adaptation; cetaceans

Introduction

The Permian–Triassic mass extinction is the most devastating extinction in Earth's history (Chen, Z. Q. & Benton, 2012). Following the recovery from this extinction event in the Early Triassic, several groups of reptiles adapted to aquatic environments and diversified rapidly (Kelley & Pyenson, 2015; Liu & Sander, 2019; Motani, Jiang, Chen, et al., 2015; Scheyer et al., 2014; Stubbs & Benton, 2016). Among these groups are hupehsuchians with edentulous jaws and heavy armour, including *Nanchangosaurus suni* (Liu et al., 2025), *Hupehsuchus nanchangensis* (Carroll & Dong, 1991), *Parahupehsuchus longus* (Chen, X. H. et al., 2014a), *Eohupehsuchus brevicollis* (Chen, X. H. et al., 2014b), and *Eretmorhipis carrolldongi* (Chen, X. H. et al., 2015).

The appendicular skeleton of hupehsuchians is characterized by paddle- or flipper-like fore- and hind limbs, along with extra carpals and five to seven manual digits (polydactyly) in some species. Similar to the forelimb of cetaceans, where fused carpals and extra digits and phalanges enhance hydrodynamic performance and manoeuvrability in the aquatic environment (Cooper, Berta, et al., 2007; Muller, 2021; Watson et al., 2008), the convergent appendicular evolution in7 hupehsuchians likely represents a marine adaptation (Fish, 2023; Motani & Vermeij, 2021). However, the extent to which limb morphology reflects marine adaptation in hupehsuchians is still incompletely characterized (Chen, X. H. et al., 2014b; Qiao et al., 2023).

In this study, we describe a new species of hupehsuchian with widely spaced forelimb autopodial elements from Hubei Province, China, increasing the morphological diversity within Hupehsuchia. A new phylogenetic analysis indicates the stepwise evolution of extra distal carpals and digits in hupehsuchians. The widely spaced proximal autopodia in the new species are

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reminiscent of the forelimb of extant cetaceans, which may contribute to smoothing the paddle surface, thereby reducing vortices during wrist and digit flexion and extension while swimming. Alternatively, it could result from reduced ossification due to weakened muscular control in the manus (Cooper, Dawson, et al., 2007; DeBlois & Motani, 2019).

Material and methods

Phylogenetic analysis

The taxon–character matrix was updated from Liu et al. (2025) by incorporating the new taxon reported here and two new characters (see Supplemental material 1 for details) using Mesquite (Maddison & Maddison, 2023). Character states for *Nanchangosaurus suni* and HFUT YAV-10-001 were concatenated and coded as *Nanchangosaurus*, following Liu et al. (2025). Seven uninformative characters are inactive. Phylogenetic analysis was conducted with a matrix of 10 taxa and 45 characters using the implicit enumeration option in TNT 1.5 (Goloboff & Catalano, 2016). *Hovasaurus* was treated as an outgroup and all multistate characters were treated as unordered. Nodal support in TNT was measured through bootstrap sampling of 1000 dataset replicates. The taxon–character matrices are provided in Supplemental material 2 in NEXUS format.

Systematic palaeontology

Ichthyosauromorpha Motani, Jiang, Chen, Tintori, Rieppel, Ji, and Huang, 2015
Hupehsuchia Young, 1972
Hupehsuchidae Young, 1972
Genus ***Lentamanusuchus*** gen. nov.
Lentamanusuchus hubeiensis gen. et sp. nov.
(Figs 1, 2)

Holotype. The specimen HFUT YZSB-19-100 is housed at the Geological Museum of Hefei University of Technology (HFUT).

Horizon, age, and locality. Third Member, Jialingjiang Formation, Spathian, Olenekian, Lower Triassic (see Wolniewicz et al., 2023 for the discussion of stratigraphy). The specimen was collected from the Yingzishan Quarry (Gu et al., 2024; Wolniewicz et al., 2023), Yuan'an County, Hubei Province, China.

Diagnosis. A medium-sized (Benton et al., 2013) hupehsuchian with the following autapomorphies among hupehsuchians: two layers of dermal armour, with the osteoderms of the external layer filling the space between those of the internal layer without any gap; neural spines showing minimal variation in height; both the distal neural spines and the internal layer of dermal ossicles extending to the first sacral vertebra; first haemal spine and arch present from the fourth caudal vertebra; preaxial extra metacarpal small with crescent shape; manual elements widely spaced without contact.

Derivation of name. The genus name is a combination of lenta (Latin for 'pliant'), manus (Latin for 'hand') and suchus (Latin for 'crocodile' or 'crocodile-like reptile'). The species name is derived from Hubei province, the provenance of the new specimen.

Results

Description

HFUT YZSB-19-100 (Fig. 1) has a total length of approximately 1.3 m, which was estimated based on the relationship between the length of the largest centrum (8th preserved centrum: 17 mm) and total length (Qiao et al., 2019). The specimen includes most of the trunk, anterior tail, carpals, digits, pelvic girdle, and hind limb elements.

Vertebrae. Twenty-three vertebrae, including 16 dorsal, two sacral and five caudal vertebrae are articulated. Judging from the position of the forelimb, there would be no more than 30 dorsal vertebrae, similar to that of *Nanchangosaurus*, *Eretmorhipis* and *Hupehsuchus* (Chen, X. H. et al., 2014a, 2014c, 2015). The anterior and posterior zygapophyses are well preserved as in other hupehsuchians (Carroll & Dong, 1991; Chen, X. H. et al., 2014a, 2014b, 2014c, 2015). The centrum height exceeds its width, and the intercentral joint is concave based on the fourth centrum. Neurocentral sutures are observed in all vertebrae. The neural arch heights gradually decrease from dorsal to caudal vertebrae, leading to an increase in the ratio of neural spine to arch. The neural spines are segmented with distinct sutures. The distal neural spines are present throughout the dorsal vertebrae and extend to the first sacral vertebra. The heights and widths of the proximal neural spines are greater than those of the distal neural spines as in other hupehsuchians. Complete haemal spines and arches are present from the fourth caudal vertebra, with a 'V'-shape. The height of the haemal arches surpasses that of the haemal spines, which have rounded distal ends.

Osteoderms. The trunk displays two layers of closely arranged dermal armour (Fig. 2). The triangular inner dermal ossicles extend to the first sacral vertebra and

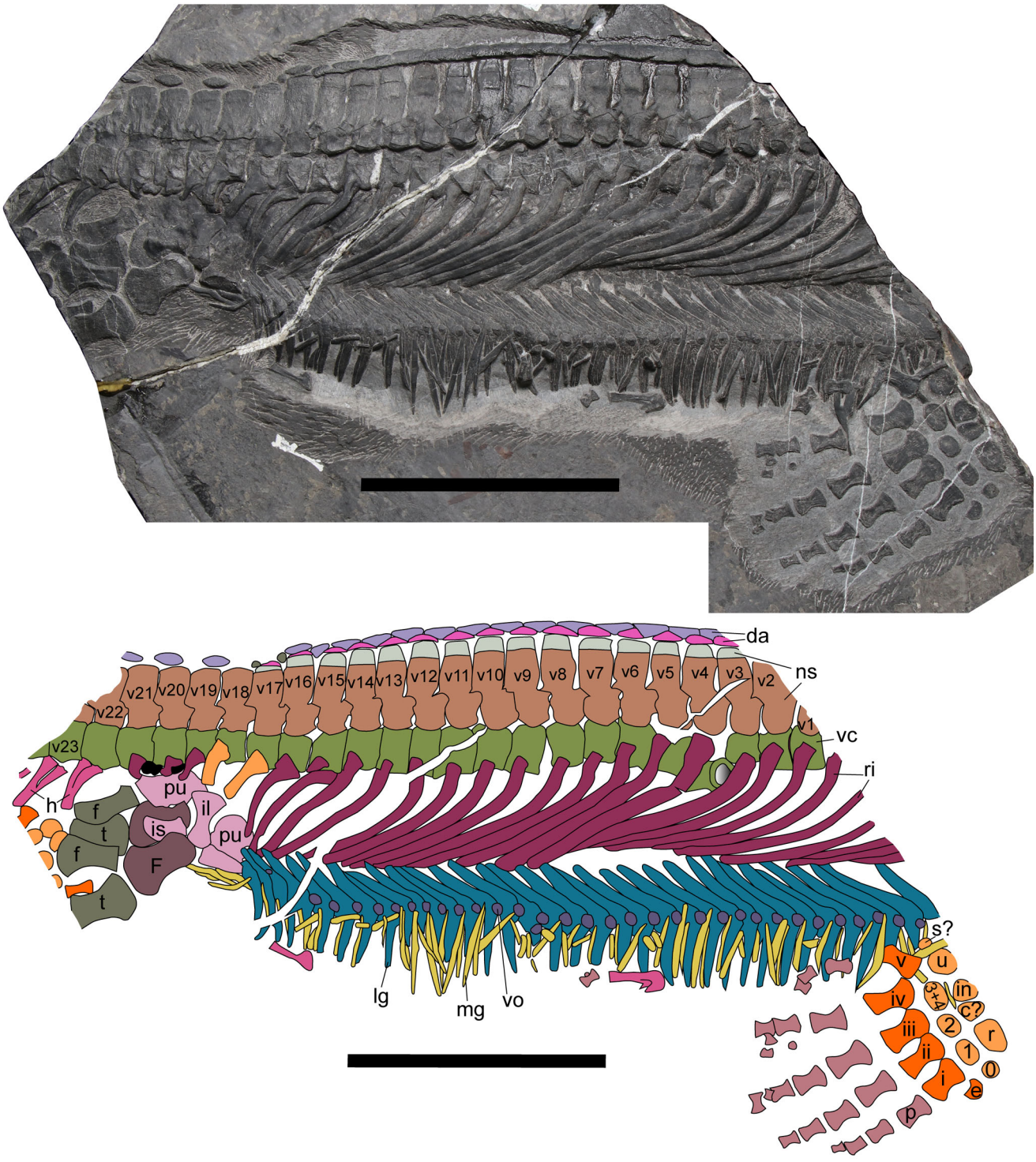

Figure 1. The holotype of *Lentamanusuchus hubeiensis* (HFUT YZSB-19-100). Scale bar = 10 cm. **Abbreviations: c**, centralia; **da**, dermal armour; **e**, extra preaxial metacarpal; **F**, femur; **f**, fibula; **h**, haemal spine; **il**, ilium; **in**, intermedium; **is**, ischium; **lg**, lateral gastralia; **mg**, median gastralia; **ns**, neural spine; **p**, phalanges; **pu**, pubis; **r**, radiale; **ri**, ribs; **s**, sesamoid; **t**, tibia; **u**, ulnare; **vc**, vertebral centrum; **vo**, ventral osteoderm; **i–v**, metacarpals; **0–4**, distal carpals; **v1–23**, vertebrae.

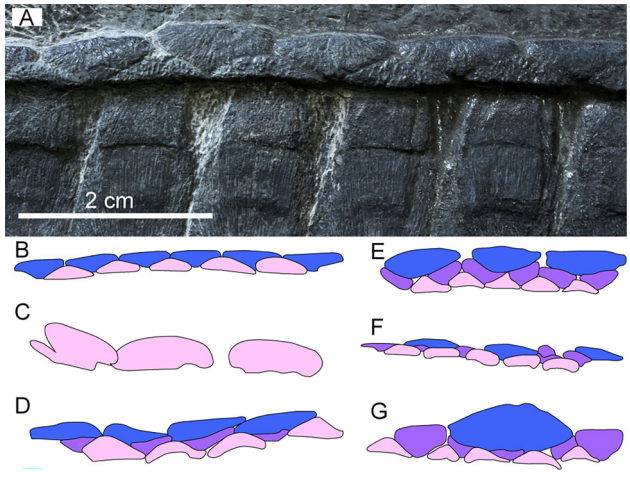

Figure 2. A, Photographic image of *Lentamanusuchus hubeiensis* (HFUT YZSB-19-100). **B–G**, Interpretive diagrams of **B,** *Lentamanusuchus hubeiensis* (HFUT YZSB-19-100); **C,** *Nanchangosaurus suni* (GMC V636, Chen, X. H. et al., 2014b); **D,** *Eohupehsuchus brevicollis* (WGSC V26003, Chen, X. H. et al., 2014a); **E,** *Hupehsuchus nanchangensis* (IVPP V3232, Carroll and Dong, 1991); **F,** *Parahupehsuchus longus* (WGSC 26005, Chen, X. H. et al., 2014c); **G,** *Eretmorhipis carrolldongi* (WGSC V26020, Chen, X. H. et al., 2015).

overlay the distal end of each neural spine. The outer dermal armour consists of inverted-triangle-shaped osteoderms positioned within each gap of the inner dermal armour, leaving no space, unlike *Hupehsuchus*, *Parahupehsuchus* and *Eretmorhipis*, which have distinct gaps (Fig. 2). Two small osteoderms are observed at the anterior and posterior ends of the first sacral neural spine. Fusiform osteoderms irregularly cover the caudal neural spines, with the space between them at least half the width of one element. A series of small osteoderms is present at the level of the convex angle of each lateral gastralia, similar to *H. nanchangensis* (Wu et al., 2016). The gastral osteoderms are dome-shaped, with pointed centres above the lateral gastralia.

Ribs. All ribs are thick, a feature shared with other hupehsuchians. The dorsal ribs maintain a uniform width from the head to the distal end and curve posteriorly. The intercostal spaces are relatively large, approximately the width of a single rib, and more widely arranged than in *Parahupehsuchus longus* (Chen, X. H. et al., 2014a). The two sacral ribs are short and robust, articulating with the ilium, a feature that aids in identifying the sacrum in *Lentamanusuchus* (Chen, X. H. et al., 2014b). The three anterior-most caudal vertebrae maintain single-headed ribs, which are notably smaller than the sacral ribs and have tapered ends.

Gastralia. Three sets of gastralia are observed throughout the presacral region, similar to other hupehsuchians (Carroll & Dong, 1991; Chen, X. H. et al., 2014a, 2014b, 2014c, 2015): a median set and a pair of lateral sets. The lateral rami are boomerang-shaped with the posterior rami overlapping the anterior ones. The convex angle of the lateral rami face anteriorly, and the curvature of the shaft gradually increases towards the posterior ones. The lateral rami are slightly longer than the medial one, unlike *Hupehsuchus nanchangensis* and *Parahupehsuchus longus*, which have a greater length difference between the two rami (Chen, X. H. et al., 2014a; Wu et al., 2016). Both rami gradually taper towards the ends and the shaft of the lateral gastralia is sculptured and furrowed longitudinally. The median gastralia in the trunk region are nearly rod-shaped with pointed ends, in contrast to boomerang- or 'V'-shaped gastralia in other hupehsuchians (Chen, X. H. et al., 2014a; 2014b; Liu et al., 2025; Wu et al., 2016). Median gastralia near the pelvic girdle show weakly curved shafts.

Forelimb. The forelimb of *Lentamanusuchus* differs from that of other hupehsuchians due to the large space between each element (Table S1, Supplemental material 1). The digits form a large paddle, radiating distally as in *Hupehsuchus nanchangensis* (Carroll & Dong, 1991). Among autopodial elements, four proximal carpals, a sesamoid, four distal carpals, six metacarpals and five digits are preserved. The radiale is the largest of the four proximal carpals, while the centralia and intermedium are the smallest. The median edges of the centralia and intermedium are straight and fit together, similar to other parahupehsuchines (Qiao et al., 2023). *Lentamanusuchus* displays a fused distal carpal, a feature only seen in seven-digit hupehsuchians (Qiao et al., 2023). The fusion of distal carpals 3 and 4 results in metacarpals 3, 4, and 5 sharing the single distal carpal, while metacarpals 1 and 2 contact distal carpals 1 and 2 separately. The space between the proximal and distal digits decreases toward the distal end of the digits. The crescent-shaped extra metacarpal distinguishes it from other parahupehsuchines (Qiao et al., 2023) and more closely resembles the second metacarpal in *Sclerocormus* (Qiao et al., 2022). The remaining metacarpals have a slightly larger proximal end than distal end, with a constricted shaft. *Lentamanusuchus* has no additional phalanx, like *Eretmorhipis carrolldongi* (Chen, X. H. et al., 2015). Only digit 4 completely preserves all phalanges including the small and round last phalanx. The digital formula is (1)-5?-5?-6?-7-4?, with digits 3 and 4 showing slight hyperphalangy.

Pelvic girdle and hind limb. The ilium, ischium, pubis, femur, tibia and fibula are preserved. The ilium has an hourglass shape with its distal end wider than the

proximal end, similar to *Eretmorhipis carrolldongi* (Chen, X. H. et al., 2015). The length of the ilium is about 1.5 times its width. The pubis is wide and plate-like. The ischium is rod-like with a slight constriction at its midshaft, and its distal end is slightly wider than the proximal end, resembling that of *Eohupehsuchus brevicollis* (Chen, X. H. et al., 2014b). The proximal end of the femur is well preserved in three dimensions, featuring a large and rounded articular surface that contacts the pelvic girdle. The femur is a short bone with a significantly enlarged distal articular surface. Both the tibia and fibula are slightly shorter than the femur. The tibia shows proximal expansion, while the fibula displays distal expansion, as in other hupehsuchians.

Phylogenetic analysis

The data matrix was analysed using implicit enumeration in TNT, resulting in one most parsimonious tree (tree length = 53, consistency index = 0.736, retention index = 0.818). Fig. 3 shows the most parsimonious tree with bootstrap nodal support values (>50%). *Lentamanusuchus* (HFUT YZSB-19-100) was recovered as a sister taxon to Parahupehsuchinae, within Hupehsuchidae.

Discussion

One notable feature in *Lentamanusuchus* is the widely spaced autopodia (including mesopodia, metapodia and phalanges). Specifically, there are larger spaces for cartilages between the metacarpal and the first phalanx, as well as between the first and second phalanges for each digit (Table 1, Supplemental material 1). This differs from other hupehsuchians, such as *Hupehsuchus nanchangensis* (WGSC V26000), *Eretmorhipis carrolldongi* (YAGM V1401), and Parahupehsuchinae sp. (HFUT YZSB-19-141), which exhibit much smaller cartilaginous spaces at the metacarpophalangeal and interphalangeal joints (Table 1). The widely spaced autopodia in *Lentamanusuchus* is similar to those observed in some ichthyosauriforms, including *Chaohusaurus* and extant cetaceans (Caldwell, 2002; Cooper, Berta, et al., 2007; Huang et al., 2019; Motani, Jiang, Tintori, et al. 2015; Motani et al., 2018).

The excellent *in situ* preservation of the specimen suggests that taphonomic effects had minimal influence on the manus arrangement. In another basal ichthyosauromorph *Chaohusaurus*, the spacing between manus elements remains consistent throughout ontogeny (Motani & You, 1998), making it unlikely that the manus arrangement in *Lentamanusuchus* results from an early ontogenetic stage. Furthermore, ossification sequences

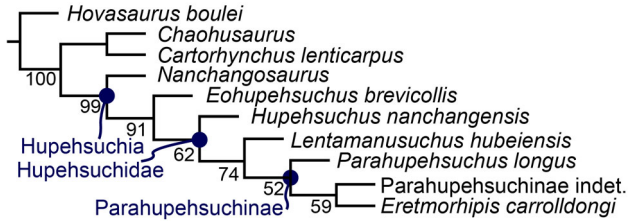

Figure 3. Phylogeny of hupehsuchians including *Lentamanusuchus hubeiensis* (HFUT YZSB-19-100). Bootstrap support values (>50%) are shown below the nodes.

in aquatic tetrapods generally follow a pattern in which the metacarpals ossify first, with delayed ossification of the proximal phalanges relative to the distal phalanges being common, while the carpals ossify significantly later than the rest of the autopodial elements in most tetrapods (Fröbisch, 2008). Given that the entire skeleton, including the autopodial elements, is well ossified in *Lentamanusuchus*, this further supports the conclusion that *Lentamanusuchus* is not in an early ontogenetic stage.

The widely spaced autopodia in *Lentamanusuchus* also do not appear to be a result of sexual dimorphism. Although Early Triassic ichthyosauriform *Chaohusaurus chaoxianensis* exhibits sexual dimorphism, with longer forelimbs and thicker phalanges in alleged males (Motani et al., 2018), the sexual variation in the phalangeal spacing appears to be minimal. Further sampling of hupehsuchians will allow for morphometric comparisons to determine whether sexual dimorphism is present in hupehsuchians and if its pattern aligns with that observed in *Chaohusaurus*.

The presence of large cartilages, particularly at the proximal manus in *Lentamanusuchus*, may smooth the paddle surface during the wrist and digit flexion and extension, potentially reducing vortex intensity while swimming (Cooper, Berta, et al., 2007). Additionally, its moderate hyperphalangy (increased numbers of phalanges), similar to the contemporaneous *Lariosaurus sanxiaensis* (Li & Liu, 2020), would further improve steering, balance and possibly lift generation during aquatic locomotion (Maxwell, 2012; Richardson & Chipman, 2003). Alternatively, the increased joint space at the proximal manus in *Lentamanusuchus* might be attributed to reduced ossification caused by diminished muscular control, potentially limiting the range of motion at metacarpophalangeal and proximal interphalangeal joints (Cooper, Dawson, et al., 2007; Cooper, 2009; DeBlois & Motani, 2019).

Lentamanusuchus exhibits a set of preaxial extra distal carpals and metacarpals, similar to the digital pattern of *Eretmorhipis carrolldongi* (Chen, X. H. et al., 2015).

Table 1. Ratios of metacarpal-to-phalanx or interphalangeal distance to metacarpal length for digits 1–4. R1–4 represent the ratios of the metacarpal-to-first-phalanx distance relative to the metacarpal length for each digit (digits 1–4). RR1–4 represent the ratios of the distance between the first and second phalanges relative to the metacarpal length for each digit (digits 1–4).

Species	Specimen no.	R1	R2	R3	R4	RR1	RR2	RR3	RR4	Reference
Hupehsuchus sp.	WGSC V26000	0.15	0.21	0.21	0.19	0.07	0.13	0.16	0.11	Motani, Chen, et al., 2015
Hupehsuchus nanchangensis	IVPP V3232	∼0	∼0	∼0	∼0	∼0	∼0	∼0	∼0	Carroll and Dong, 1991
Hupehsuchus nanchangensis	WGSC 26004	∼0	∼0	∼0	–	∼0	∼0	∼0	–	Chen, X. H. et al., 2014a
Parahupehsuchus longus	WGSC 26005	∼0	∼0	∼0	∼0	∼0	∼0	∼0	–	Chen, X. H. et al., 2014a
Eohupehsuchus brevicollis	WGSC V26003	∼0	∼0	∼0	–	∼0	∼0	∼0	∼0	Chen, X. H. et al., 2014b
Eretmorhipis carrolldongi	YAGM V1401	0.04	0.09	0.07	0.09	0.12	0.06	∼0	0.05	Chen, X. H. et al., 2015
Parahupehsuchinae sp.	SSTM 5025	∼0	∼0	∼0	0.09	0.05	∼0	∼0	0.10	Qiao et al., 2023
Parahupehsuchinae sp.	HFUT YZSB-19-141	0.04	0.08	0.11	0.16	∼0	0.04	0.07	0.07	Qiao et al., 2023
Lentamanusuchus hubeiensis	HFUT YZSB-19-100	0.19	0.32	0.36	0.51	0.24	0.17	0.15	0.21	Current study

In the current phylogenetic hypothesis, *Hupehsuchus* and *Lentamanusuchus* are successive sister groups to Parahupehsuchinae (Fig. 3). Both *Hupehsuchus* and *Lentamanusuchus* have an extra distal carpal, and *Lentamanusuchus* has an extra metacarpal, while parahupehsuchines have extra carpals, metacarpals and digits. This supports a stepwise addition of extra carpals, metacarpals and digits in the evolution of hupehsuchians (Qiao et al., 2023). The *Lentamanusuchus* manus is also unique in the fusion of neighbouring distal carpals, similar to the seven-digit hupehsuchian (HFUT YZSB-19-141), likely due to tightly packed digits (Qiao et al., 2023). This contrasts with the fusion between the metacarpal and phalanges within a single digital ray in cetaceans (Cooper & Dawson, 2009), suggesting different underlying mechanisms of autopodial fusion in hupehsuchians and cetaceans.

The combination of forelimb characters observed in *Lentamanusuchus*, including the manual element spacing, extra carpals and metacarpals, and carpal fusion contributes to our understanding of the appendicular locomotor morphologies in hupehsuchians and reveals diverse aquatic locomotion and ecology within this group (Bininda-Emonds et al., 2007; Pardo et al., 2017).

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Disclosure statement

No potential conflict of interest was reported by the authors.

Supplemental material

Supplemental material for this article can be accessed online here: https://doi.org/10.1080/14772019.2025.2560884.

Data availability statement

The data that support the findings of this study are openly available from MorphoBank at https://doi.org/10.7934/P6012 (Qiao et al., 2025).

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