

The first pan-trionychid turtle from the Upper Cretaceous of southern China, with a summary of the turtle succession in the Ganzhou Basin

YUZHENG KE, FENGLU HAN, and WALTER G. JOYCE



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Pan-trionychids are a group of aquatic turtles with a geological occurrence from the Early Cretaceous to the present. Here, we report a small pan-trionychid specimen from the Upper Cretaceous Zhoutian Formation of the Ganzhou Basin of Jiangxi Province, China, which consists of a nearly complete carapace and several associated fragments. The specimen is the first definitive pan-trionychid record from the Upper Cretaceous of southern China. Its general skeletal features are comparable with those of other pan-trionychids from the mid Cretaceous of Asia. However, because the specimen appears to be a juvenile and lacks sufficient anatomical details, we refrain from naming a new species or hypothesizing phylogenetic relationships. Upper Cretaceous sediments in the Ganzhou Basin document a succession of turtle faunas ranging from aquatic pan-trionychids to semi-aquatic lindholmemydids to possibly terrestrial nanhsiungchelyids, but the relationship between this succession and paleoclimate remains ambiguous.

Key words: Pan-Trionychidae, Ganzhou Basin, Cretaceous, Zhoutian Formation, China.

Yuzheng Ke [key1480@163.com; ORCID: <https://orcid.org/0000-0002-3728-898X>], School of Earth Sciences, China University of Geosciences (Wuhan), Wuhan 430074, China. Department of Geosciences, University of Fribourg, 1700 Fribourg, Switzerland.

Fenglu Han [hanfl@cug.edu.cn; ORCID: <https://orcid.org/0000-0003-3399-4008>] (corresponding author), School of Earth Sciences, China University of Geosciences (Wuhan), Wuhan 430074, China.

Walter G. Joyce [walter.joyce@unifr.ch; ORCID: <https://orcid.org/0000-0003-4726-2449>], Department of Geosciences, University of Fribourg, 1700 Fribourg, Switzerland.

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Introduction

Pan-Trionychidae is the total-clade of crown clade Trionychidae (Joyce et al. 2021). Its representatives are colloquially known as “soft-shell turtles”. This clade originated in Asia during the Early Cretaceous (Georgalis and Joyce 2017) and has an abundant, nearly world-wide fossil record consisting of at least 70 valid species in addition to countless fragmentary remains (Vitek and Joyce 2015; Georgalis and Joyce 2017). The 33 species of extant pan-trionychids (Turtle Taxonomy Working Group 2021) exhibit a number of unusual morphological characteristics: the nostrils are extended into a tube, the hard, keratinous scales (scutes) of the shell are replaced by leathery skin, and extensive webbing is developed between the digits (Zhou and Li 2013). In combination, these adaptations enable pan-trionychids to burrow themselves into the sediments at the bottom of freshwater ecosystems where they ambush their prey. Fossilized pan-tri-

onychids can readily be distinguished from other turtles in the reduction of their carapace and plastron, as well as their unique shell surface texture (Vitek and Joyce 2015).

Even though soft-shelled turtles originated in Asia (Georgalis and Joyce 2017), their fossil record is scarce in the Cretaceous of China. Only five species are currently recognized as valid: *Perochelys hengshanensis* Brinkman et al., 2017, from the Lower Cretaceous of Zhejiang Province (Brinkman et al. 2017), *Perochelys lamadongensis* Li et al., 2015, from the Lower Cretaceous of Liaoning Province (Li et al. 2015a), “*Trionyx*” *jixiensis* Li et al., 2015, from the Early Cretaceous of Heilongjiang Province (Li et al. 2015b), as well as *Kuhnemys maortuensis* (Yeh, 1965) and *Khunnuchelys erinhotsensis* Brinkman et al., 1993, from the Late Cretaceous of Inner Mongolia (Yeh 1965; Brinkman et al. 1993). Yeh (1965) also erected *Aspideretes alashanensis* Yeh, 1965, from the Upper Cretaceous of Inner Mongolia, but this species has been regarded as a junior synonym of *Kuhnemys maortuensis* (Georgalis and Joyce 2017). Another invalid spe-

cies is *Sinamyda fuchienensis* (Yeh, 1974) from the Lower Cretaceous of Fujian Province (Yeh 1974), which has been regarded as a nomen dubium due to its uncertain provenience, unusual morphology, and doubtful authenticity (Georgalis and Joyce 2017). No other pan-trionychid remains, even fragments, have been reported from the Cretaceous of China, which stands in sharp contrast to the rich record of other pan-trionychians, such as the continental Nanhsiungchelyidae (e.g., Tong et al. 2024). This scarcity thus limits our understanding of the early diversification and evolution of pan-trionychids in this part of the world during the Cretaceous.

Here, we report a new pan-trionychid specimen (CUGW VH245) from the Upper Cretaceous Zhoutian Formation of Jiangxi Province, China. The specimen is too juvenile to allow diagnosing a new species, but shows intriguing similarities with other early pan-trionychids from across Asia and establishes the presence of pan-trionychids in south-eastern Asia as early as the early Late Cretaceous.

Institutional abbreviation.—CUGW, China University of Geosciences (Wuhan), Wuhan, China.

Geological setting

The Ganzhou Basin is a Mesozoic to Cenozoic fault basin situated in Jiangxi Province, China (Fig. 1A). The Upper Cretaceous, which forms the majority of the stratigraphic sequence (He et al. 2017), is comprised of five formations, namely the Maodian, Zhoutian, Hekou, Tangbian,

and Lianhe formations (Bureau of Geology and Mineral Exploration and Development of Jiangxi Province 2017). The new pan-trionychid specimen, CUGW VH245, was collected from the Zhoutian Formation in Shang Wu Zhu Village (25°55'N, 115°0'E, Fig. 1B). The Zhoutian Formation is locally comprised of purple-red calcareous mudstone and calcareous siltstone intercalated with gypsum and rock salt, suggesting deposition in a lacustrine basin under arid conditions (Bureau of Geology and Mineral Exploration and Development of Jiangxi Province 2017). The age of the Zhoutian Formation is unclear, but is believed to be early Late Cretaceous (Cenomanian–Turonian) based on the fossil assemblage, especially spores and pollen (Bureau of Geology and Mineral Exploration and Development of Jiangxi Province 2017). Several vertebrate fossils have been found from the Zhoutian Formation, such as the titanosaur *Gandititan cavocaudatus* Han et al., 2024 (Han et al. 2024), but no turtle fossil has been reported to date.

Material and methods

The new specimen, CUGW VH245, consists of a nearly complete carapace and associated fragments (Fig. 2). The specimen was taphonomically crushed along its anteroposterior axis. It is currently housed in the palaeontological collection room of China University of Geosciences (Wuhan). The skeleton was prepared using an Engraving Pen AT-310 and photographed with a Canon EOS 6D camera.

A map was created to show the distribution of pan-trionychid turtles in the Cretaceous of Asia (Fig. 3). Most data come from Georgalis and Joyce (2017), and three new fossil sites are also added, including Ganzhou (Jiangxi, China), Duntou (Zhejiang, China), and Ibaraki (Japan) (Brinkman et al. 2017; Kato et al. 2019; this article). ArcGIS 10.8 software was used to plot the map.

Systematic palaeontology

Testudines Batsch, 1788

Cryptodira Cope, 1868

Pan-Trionychidae Joyce et al., 2004

Pan-Trionychidae indet.

Material.—CUGW VH245, a nearly complete carapace and associated fragments from Shang Wu Zhu Village, Ganzhou City, Jiangxi Province, China; Zhoutian Formation, Cenomanian–Turonian (lower Upper Cretaceous).

Description.—*General aspects:* CUGW VH245 consists of a nearly complete carapace preserving eight neurals, eight pairs of costals, and associated postcranial fragments. As preserved, the midline length of the carapace is only 65 mm, but we estimate by comparison to *Perochelys lamadonensis* (Li et al. 2015a) that the total carapace length would

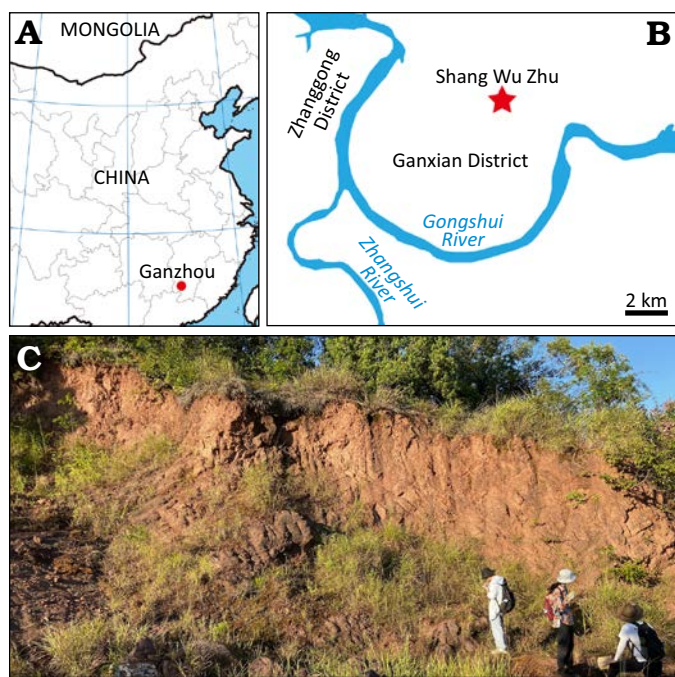


Fig. 1. Location and stratum of Ganzhou Basin, China. A. Map showing the location of Ganzhou Basin. B. Expanded map showing the location of Shang Wu Zhu Village, where Pan-Trionychidae indet. (CUGW VH245) was found. C. An outcrop of the Upper Cretaceous Zhoutian Formation near Shang Wu Zhu Village.

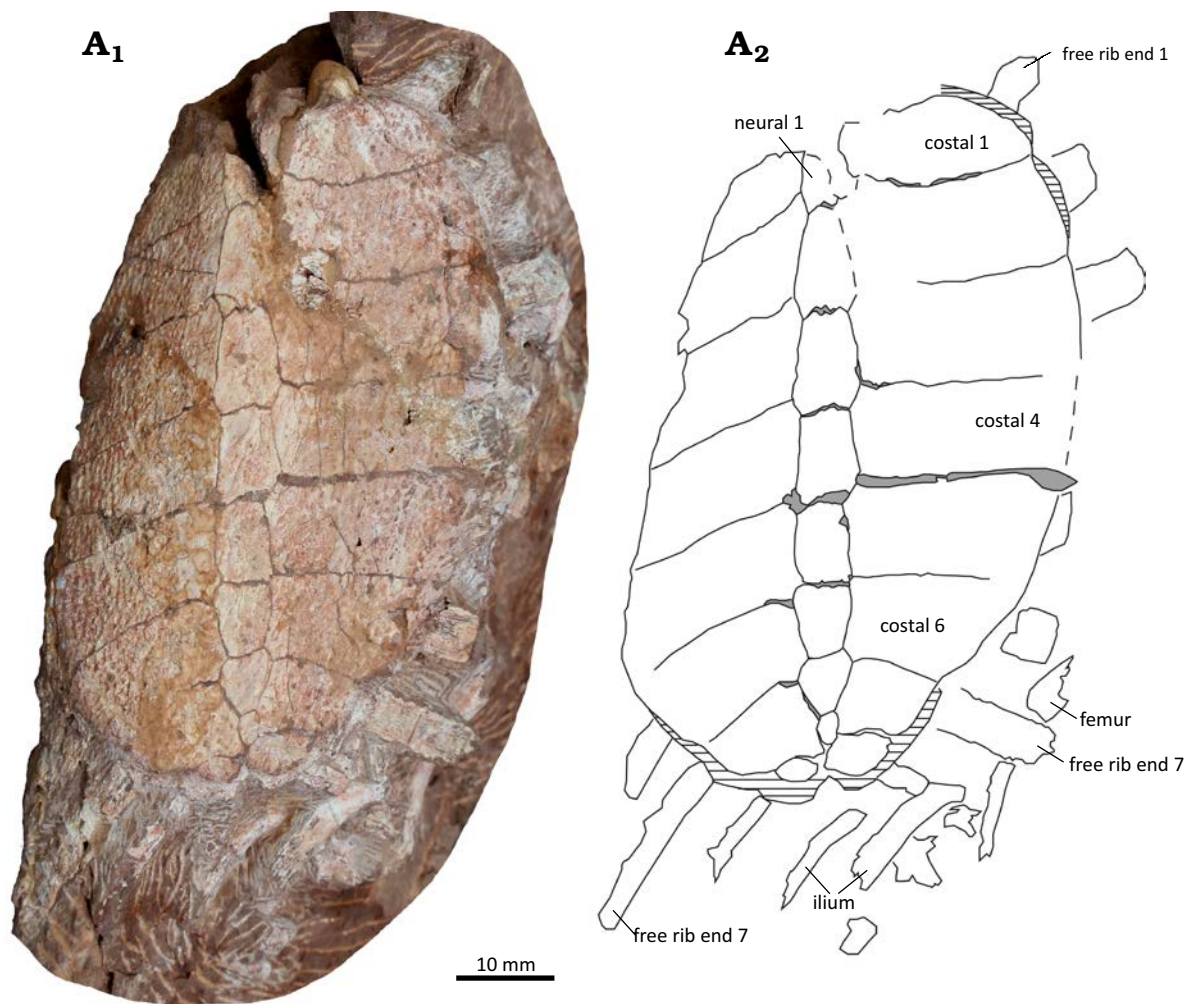


Fig. 2. Photograph (A₁) and interpretive drawing (A₂) of Pan-Trionychidae indet. (CUGW VH245, in dorsal view) from the Upper Cretaceous of Ganzhou Basin, China. Grey parts denote gaps between bones and hatched areas exposed internal bone.

have been about 72 mm. The other parts of the skeleton, such as the skull, the nuchal, and the plastron, have not been found. Due to poor preservation, it is unclear if a preneural or suprascapular fontanelles were present. The specimen was severely deformed taphonomically in the stratum, thus showing a pronounced inverted U-shape. The surface of the carapace is covered with the typical netlike pattern of most pan-trionychids (Joyce 2025) consisting of pits and ridges (“type A” of Danilov et al. 2014). There is no evidence of scute sulci.

Neurals: A total of eight neurals are developed in CUGW VH245. The anterior part of the first neural is damaged, but it is apparent that this element was hexagonal with short sides facing posteriorly. The second to the fourth neurals are hexagonal with short sides facing posteriorly, too. The neural reversal (i.e., the transition from hexagonal neurals with short sides oriented posteriorly versus hexagonal neurals with short sides facing anteriorly) is spread between the fifth and sixth neurals, a common anomaly found across pan-trionychids (Joyce 2025). The seventh neural is hexagonal with short sides facing anteriorly. Its posterior contact with the eighth neural is much narrower than all more anteriorly lo-

cated interneural contacts. The eighth neural is developed asymmetrically, as it contacts the right eighth costal posteriorly, but not the left eighth costal. It is much smaller than all further anteriorly located neurals. As in *Perochelys lamadongensis* (Li et al. 2015a), the neurals are relatively broad, but not as broad as in many extant chittrines (Joyce 2025).

Costals: CUGW VH245 exhibits eight pairs of costals, most of which are damaged along their lateral margins. The first costal is incompletely preserved, which further hinders our understanding of its full shape and size, but its anteriorly convex margin is reminiscent of *Perochelys lamadongensis* (Li et al. 2015a) and somewhat suggestive of medially confluent suprascapular fontanelles. The second to the fifth costals are rectangular elements of similar size and with nearly parallel margins. The sixth costal is much shorter mediolaterally than the previous costals, expands distally, and is somewhat oriented posteriorly. The seventh costal is even shorter mediolaterally and further oriented towards the posterior. The eighth costal is greatly reduced in size but developed asymmetrically, the right element between twice as large as the left element. While the neural column medially separates all more anteriorly located costals, a short midline

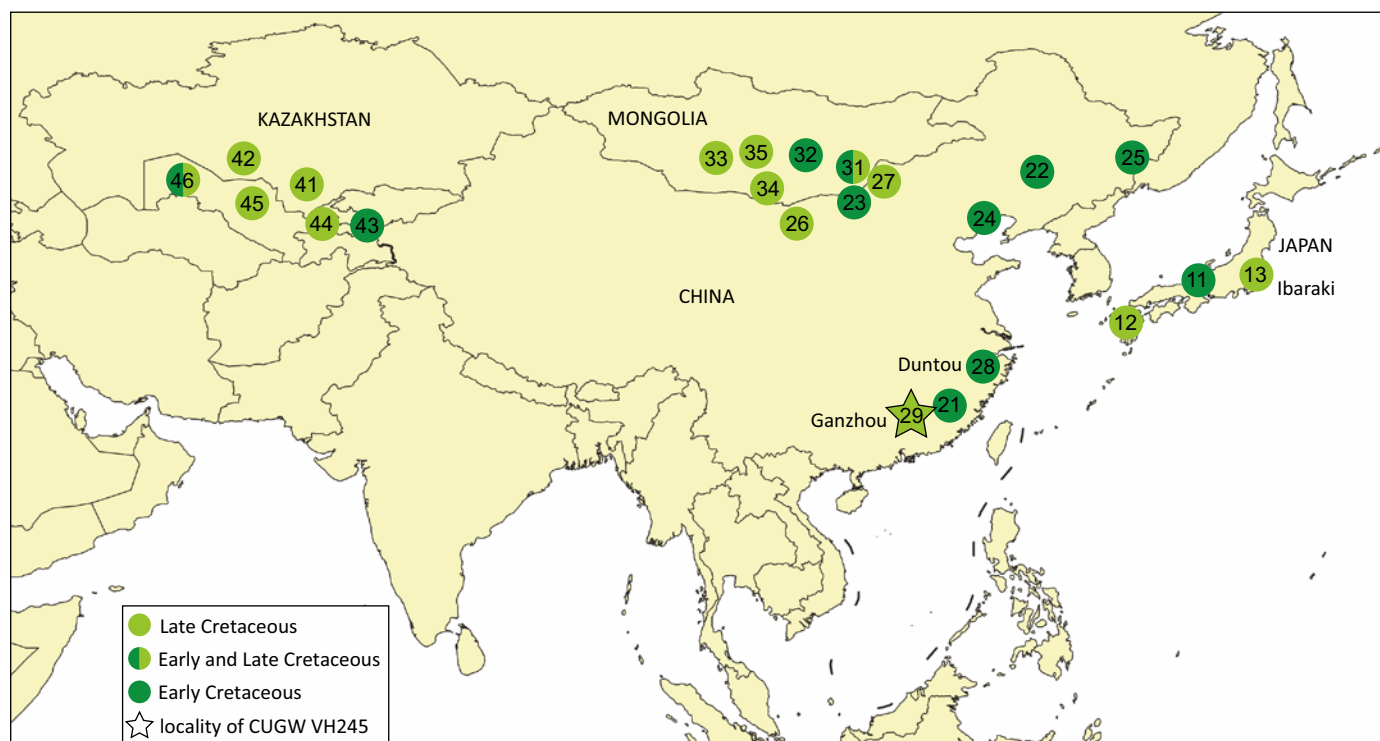


Fig. 3. Pan-trionychid distribution in the Cretaceous of Asia. Numbers represent fossil sites: 11, Fukui; 12, Kumamoto; 13, Ibaraki; 21, Fujian Province; 22, Jilin Province; 23 Inner Mongolia; 24, Liaoning Province; 25, Heilongjiang Province; 26, Inner Mongolia (Maoertu); 27, Inner Mongolia (Erenhot); 28, Zhejiang Province; 29, Jiangxi Province; 31, Dornogovi Aimag; 32, Dundgovi Aimag; 33, Bayankhongor Aimag; 34, Ömnögovi Aimag; 35, Övörkhangaï Aimag; 41, South Kazakhstan Region; 42, Kyzylorda Region; 43, Osh Province; 44, Khodzhen Province; 45, Navoiy Region; 46, Karakalpakstan. Fossil sites from Georgalis and Joyce (2017), Brinkman et al. (2017), Kato et al. (2019), and this article.

contact is present between the eighth costals. Most rib ends are poorly preserved, but their length relative to the costal callosities combined with the overall small size of CUGW VH245 suggests that it is a juvenile (Danilov and Vitek 2013; Brinkman et al. 2017; Joyce 2025). The eighth costal rib is only half as wide as of all more anteriorly located costal ribs.

Femur: The long bone located under the right seventh rib is identified as the femur, whose size relative to the shell is similar to that of extant juvenile *Pelochelys cantorii* Gray, 1864 (Xie et al. 2022). The ends of the femur are incompletely ossified, which is comparable with the juvenile *Pelochelys cantorii* as well (Xie et al. 2022). This also suggests that CUGW VH245 represents a juvenile.

Ilium: We interpret two recurved bones behind the eighth costals as the ilia. The dorsal ends are striated, as in extant trionychids.

Discussion

Alpha taxonomy and systematics.—CUGW VH245 can readily be attributed into Pan-Trionychidae based on the absence of carapacial scutes, presence of a netted surface texture, and the apparent absence of peripherals and suprapygals (Vitek and Joyce 2015). The general carapace morphology of CUGW VH245 is consistent with that of other Asian pan-trionychid turtles from the Cretaceous by exhibiting eight neu-

erals (Yeh 1965; Danilov et al. 2014; Li et al. 2015a, b), but that characteristic does not have particularly strong taxonomic value as it occurs broadly across the tree (Joyce 2025). The position of the neural reversal and the distribution of the reversal across two neurals are highly variable among extant trionychids (Joyce 2025). The neural reversal in CUGW VH245 across the fifth and sixth neurals is thus highly consistent with other Cretaceous pan-trionychids, where the reversal typically occurs at the fifth or sixth neural (Yeh 1965; Danilov et al. 2014; Li et al. 2015a, b). Among Cretaceous Asian pan-trionychids, CUGW VH245 resembles *Kuhnemys maortuensis*, *Perochelys lamadongensis*, and *Gobiapalone* spp. (Yeh 1965; Danilov et al. 2014; Li et al. 2015a) by exhibiting notably reduced eighth costals. This character is of significance among these named taxa, as they are otherwise known from specimens suggesting skeletal maturity. CUGW VH245 is isolated from all other named Late Cretaceous pan-trionychids by being the only known specimen from the southern China, indeed all of southeastern Asia (Fig. 3). Pan-trionychids were also found in the Cretaceous of Japan (e.g., Kato et al. 2019), providing more evidence that the Japanese archipelago was still connected to Asian continent during the Cretaceous. Yet, as CUGW VH245 lacks sufficient anatomical details, we refrain from naming a new species.

Population succession of turtles in Ganzhou Basin.—Turtle fossils are abundant in the Ganzhou Basin, but only nanhsiungchelyids have been formally published to date

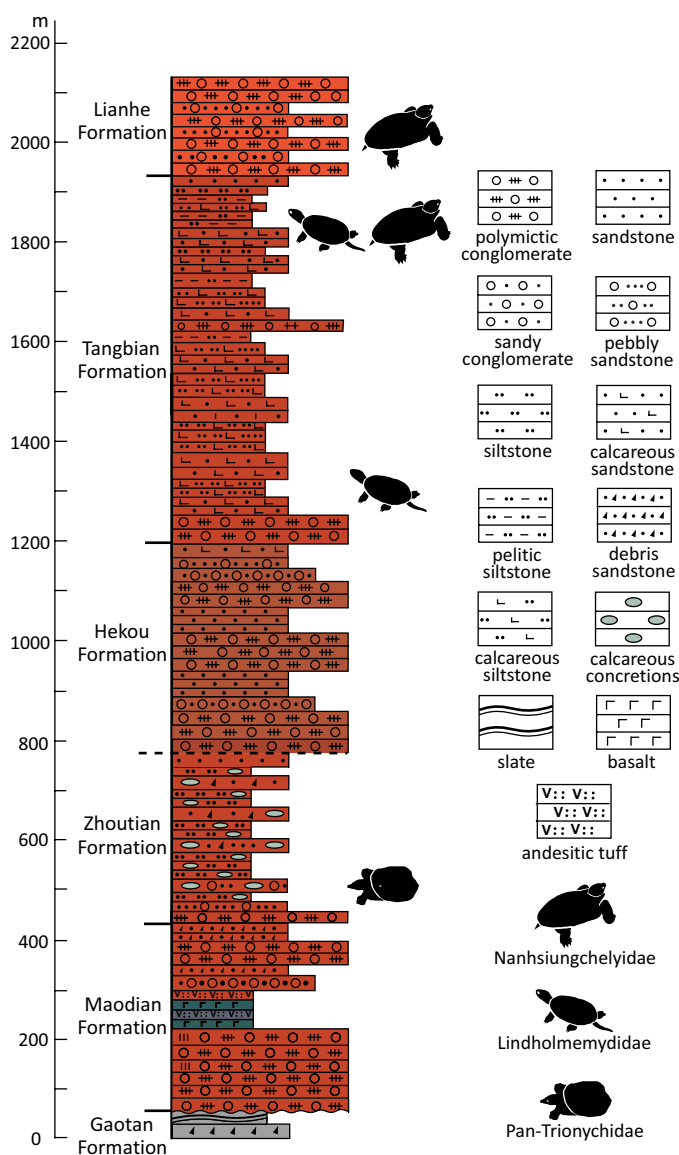


Fig. 4. The stratigraphic column of Ganzhou Basin, China, as revised by Han et al. (2024).

(Tong and Mo 2010; Ke et al. 2024a, b; Tong et al. 2024). He et al. (2017) reported many turtle skeletons from the Ganzhou Basin, but did not provide any photographs or taxonomic assessments. From 2021 to 2024, the corresponding author (FH) organized four field expeditions in Ganzhou Basin and collected a wealth of turtle fossils. Here, we briefly summarize these specimens and discuss the population succession of turtles among different strata.

With a lacustrine sedimentary face, the Zhoutian Formation only yielded Pan-Trionychidae indet. (CUGW VH245, this article) to date. Extant pan-trionychid turtles usually have a benthic lifestyle in rivers and lakes (Zhou and Li 2013), and given their broad correspondence in morphology, it is plausible to assert that Cretaceous pan-trionychids, including CUGW VH245, had a similar lifestyle. The Tangbian Formation also represents a fluvial and lacustrine environment (Ling 1996), and Lindholmemydidae indet. (CUGW VH146 and CUGW VH171, yet unpublished)

were found in this formation. Lindholmemydids likely had a freshwater lifestyle (Danilov 2003), but their hard shells and scutes also allowed them to move across land, much as their living descendants, turtles of the clade Testudinoidea, do today. At the upper end of the Cretaceous succession, the upper member of the Tangbian Formation and the Lianhe Formation have yielded abundant nanhsiungchelyid materials, in particular *Xianyuechelys yingliangi* Ke et al., 2024, and *Nanhsiungchelys* sp. (Ke et al. 2024a, b). The lifestyle adaptation of nanhsiungchelyids has been debated for a long time, but most evidence supports a terrestrial lifestyle (see the summary in Mallon and Brinkman 2018). Although the sample is certainly limited, it is interesting to note that a gradation is apparent from fully aquatic pan-trionychids, to plausibly semiaquatic lindholmemydids, to terrestrial nanhsiungchelyids in the Late Cretaceous of the Ganzhou Basin (Fig. 4). Hutchison (1992) utilized a similar trend in the turtle fauna to support a climatological drying trend from the Eocene to the Oligocene of western North America, which is broadly supported by other data. Yet, while the turtles of the Ganzhou Basin perhaps suggests a trend towards increasing aridity over the course of the Late Cretaceous, the sedimentological record suggests a trend towards increasing humidity (Xiao et al. 2013). Although recent turtles are known to be more diverse in humid environments (Iverson 1992), numerous highly aquatic species are known to inhabit arid environments (e.g., the trionychid *Trionyx triunguis* Forskål, 1775, which inhabits the Nile river of northern Africa) while numerous terrestrial species occur in humid environments (e.g., the tortoise *Manouria emys* [Schlegel & Müller, 1840], which inhabits tropical rain forests) (Turtle Taxonomy Working Group 2021). There is thus no real conflict in the two opposing trends noted herein, as the single available trionychid retrieved from the arid Zhoutian Formation may have inhabited a rare desert lake, while the common nanhsiungchelyids of the Lianhe Formation may have walked upon the flood plains of a humid landscape. We thus conclude that turtle faunal successions may yield compelling trends, but that these should not be interpreted verbatim.

Conclusions

A small pan-trionychid specimen (CUGW VH245) is reported from the Upper Cretaceous Zhoutian Formation of Ganzhou Basin, southern China. The specimen includes a nearly complete carapace and several postcranial fragments. It not only represents the first pan-trionychid record from the Upper Cretaceous of southern China, but of all of southeastern Asia. As the specimen appears to be a juvenile that lacks sufficient anatomical details, we here identify it as Pan-Trionychidae indet. only. The Late Cretaceous turtle faunas of the Ganzhou Basin show a succession from aquatic pan-trionychids to semi-terrestrial lindholmemydids to terrestrial nanhsiungchelyids, but this likely does not reflect a climatological drying trend.

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References

- Batsch, A.J.G.C. 1788. *Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien*. 528 pp. Akademische Buchhandlung, Jena.
- Brinkman, D.B., Nessov, L.A., and Peng, J. 1993. *Khunnuchelys* gen. nov., a new trionychid (Testudines: Trionychidae) from the Late Cretaceous of Inner Mongolia and Uzbekistan. *Canadian Journal of Earth Science* 30: 2214–2223.
- Brinkman, D.B., Rabi, M., and Zhao, L. 2017. Lower Cretaceous fossils from China shed light on the ancestral body plan of crown softshell turtles (Trionychidae, Cryptodira). *Scientific Reports* 7: 6719.
- Bureau of Geology and Mineral Exploration and Development of Jiangxi Province 2017. *Regional Geology of China, Jiangxi Province* [in Chinese with English abstract]. 1069 pp. Geological Publishing House, Beijing.
- Cope, E.D. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* 20: 242–300.
- Danilov, I. 2003. *Gravemys* Sukhanov and Narmandakh, 1983 (Testudinoidae: Lindholmemydidae) from the Late Cretaceous of Asia: new data. *Paleobios* 23: 9–19.
- Danilov, I.G. and Vitek, N.S. 2013. Soft-shelled turtles (Trionychidae) from the Bissekty Formation (Late Cretaceous: late Turonian) of Uzbekistan: Shell-based taxa. *Cretaceous Research* 41: 55–64.
- Danilov, I.G., Hirayama, R., Sukhanov, V.B., Suzuki, S., Watabe, M., and Vitek, N.S. 2014. Cretaceous soft-shelled turtles (Trionychidae) of Mongolia: new diversity, records and a revision. *Journal of Systematic Palaeontology* 12: 799–832.
- Forskål, P. 1775. *Descriptiones Animalium. Avium, Amphibiorum, Piscium, Insectorum, Vermium. Quae in Itinere Orientali Observavit*. 12 pp. Mölleri, Haunia.
- Georgalis, G.L. and Joyce, W.G. 2017. A review of the fossil record of Old World turtles of the clade Pan-Trionychidae. *Bulletin of the Peabody Museum of Natural History* 58: 115–208.
- Gray, J.E. 1864. Revision of the species of Trionychidae found in Asia and Africa, with the descriptions of some new species. *Proceedings of the Zoological Society of London* 1864: 76–98.
- Han, F., Yang, L., Lou, F., Sullivan, C., Xu, X., Qiu, W., Liu, H., Yu, J., Wu, R., Ke, Y., Xu, M., Hu, J., and Lu, P. 2024. A new titanosaurian sauropod, *Gandititan cavocaudatus* gen. et sp. nov., from the Late Cretaceous of southern China. *Journal of Systematic Palaeontology* 22: 2293038.
- He, F., Huang, X., and Li, X. 2017. Occurrence rule and buried characteristics of dinosaur fossils in the Ganzhou Basin, Jiangxi Province [in Chinese with English abstract]. *East China Geology* 38: 250–254.
- Hutchison, J.H. 1992. Western North American reptile and amphibian record across the Eocene/Oligocene boundary and its climatic implications. In: D.R. Prothero and W.A. Berggren (eds.), *Eocene–Oligocene Climatic and Biotic Evolution*, 451–463. Princeton University Press, Princeton.
- Iverson, J.B. 1992. Global correlates of species richness in turtles. *Herpetological Journal* 2: 77–81.
- Joyce, W.G. 2025. Overcoming polymorphism: a revised list of shell characters for the phylogenetic analysis of soft-shelled turtles (Pan-Trionychidae). *Swiss Journal of Palaeontology* 144: art. 25.
- Joyce, W.G., Anquetin, J., Cadena, E., Claude, J., Danilov, I.G., Evers, S.W., Ferreira, G.S., Gentry, A.D., Georgalis, G.L., Lyson, T.R., Pérez-García, A., Rabi, M., Sterli, J., Vitek, N.S., and Parham, J.F. 2021. A nomenclature for fossil and living turtles using phylogenetically defined clade names. *Swiss Journal of Palaeontology* 140: art. 5.
- Joyce, W.G., Parham, J.F., and Gauthier, J.A. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology* 78: 989–1013.
- Kato, T., Sonoda, T., Miyata, S., Kawano, S., and Ando, H. 2019. Large soft-shelled turtle fossils from the Upper Cretaceous Nakaminato Group in Ibaraki Prefecture and their significance [in Japanese with English abstract]. *Bulletin of Ibaraki Nature Museum* 22: 31–36.
- Ke, Y., Niu, K., Rummy, P., Tong, H., Hu, J., and Han, F. 2024a. *Xianyu-chelys yingliangi*: a new nanhsiungchelyid turtle from the Late Cretaceous of Ganzhou Basin, China. *Journal of Systematic Palaeontology* 22: 2346838.
- Ke, Y., Tong, H., Qiu, W., Shi, Z., and Han, F. 2024b. A partial plastron of *Nanhsiungchelys* (Testudines: Cryptodira: Nanhsiungchelyidae) from the Upper Cretaceous of Ganzhou Basin, China. *Historical Biology*: 1–6.
- Li, L., Joyce, W.G., and Liu, J. 2015a. The first soft-shelled turtle from the Jehol Biota of China. *Journal of Vertebrate Paleontology* 35: e090450.
- Li, L., Tong, H., Gu, W., and Liu, J. 2015b. A new trionychid turtle from the Early Cretaceous of Heilongjiang Province, Northeastern China. *Cretaceous Research* 56: 155–160.
- Ling, L. 1996. Establishment of the Maodian, Hekou and Tangbian formations in the Cretaceous of Jiangxi Province [in Chinese]. *Geological Science and Technology of Jiangxi* 23: 55–59.
- Mallon, J.C. and Brinkman, D.B. 2018. *Basilemys morrinensis*, a new species of nanhsiungchelyid turtle from the Horseshoe Canyon Formation (Upper Cretaceous) of Alberta, Canada. *Journal of Vertebrate Paleontology* 38: e1431922.
- Schlegel, H. and Müller, S. 1840. Over de Schildpadden van den Indischen Archipel, en beschrijving eener nieuwe soort van Sumatra. In: C.J. Temminck (ed.), *Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche overzeesche bezittingen, 1839–44. Part 3. Zoologie*, 29–36. Luchtmans and van der Hoek, Leiden.
- Tong, H., Li, L., Ke, Y., Wang, Y., Jie, G., and Yi, L. 2024. Remarkable carapace morphology of *Nanhsiungchelys* (Testudines: Nanhsiungchelyidae) revealed by new material from Ganzhou Basin, Jiangxi Province, China. *Geosciences* 14: art. 184.
- Tong, H. and Mo, J. 2010. *Jiangxichelys*, a new nanhsiungchelyid turtle from the Late Cretaceous of Ganzhou, Jiangxi Province, China. *Geological Magazine* 147: 981–986.
- Turtle Taxonomy Working Group 2021. Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status (9th ed.). *Chelonian Research Monographs* 8: 1–472.
- Vitek, N.S. and Joyce, W.G. 2015. A review of the fossil record of New World turtles of the clade Pan-Trionychidae. *Bulletin of the Peabody Museum of Natural History* 56: 185–244.
- Xiao, G., Yao, Q., and Fan, A. 2013. Research on sequence stratigraphy of late Cretaceous in Jiangxi Province [in Chinese with English abstract]. *Resources Survey & Environment* 34: 141–149.
- Xie, M., Hong, X., Li, W., Liu, X., Chen, C., and Zhu, X. 2022. Skeletal system analysis of Asian giant soft-shelled turtles and comparison with Chinese soft-shell turtle [in Chinese with English abstract]. *Acta Hydrobiologica Sinica* 46: 1–10.
- Yeh, H. 1965. New materials of fossil turtles of Inner Mongolia. *Vertebrata Palasiatica* 9: 47–69.
- Yeh, H. 1974. A new fossil *Trionyx* from Fuchien [in Chinese with English abstract]. *Vertebrata Palasiatica* 12: 190–191.
- Zhou, T. and Li, P. 2013. *Primary Color Illustrated Handbook of Classification of Chinese Turtles* [in Chinese]. 285 pp. China Agriculture Press, Beijing.