



Freshwater gastropods across the Cretaceous–Paleogene boundary in the Songliao Basin, north-east China

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ABSTRACT

Gastropod faunas from the Cretaceous–Paleogene (K/Pg) boundary transition in the well-dated Songliao Basin (north-east China, East Asia) have been studied. In total, 673 specimens were counted, of which about 80% ($n = 538$) could be identified. In all, eight species, belonging to six genera, have been identified, including *Hydrobia? datangensis*, *Mesolanistes cf. nanxiogensis*, *Valvata jiaolaiensis*, *Valvata shakengensis*, *Tricula sp. 1*, *Tricula sp. 2*, *Zaptychius sp.*, Planorbidae gen. et sp. indet. and *Helisoma dongdawusuensis*. Combining data on species ranges in the Jiaolai and Pingyi basins of eastern China, it is shown that three out of 11 species went extinct during K/Pg boundary perturbations. Therefore, we conclude that freshwater gastropods in East Asia underwent minor extinction (c. 18% extinction rates; 72% survival rates). These snail faunas were not affected by short-lived detrimental conditions related to K/Pg boundary perturbations, such as darkness, cooling and starvation, because most of these genera are micro-herbivorous and/or micro-omnivorous grazers (including detritivores) that fed on bacterial films, algae and diatoms or ingested carrion and fine organic deposits. The global mass extinction event at the K/Pg boundary in freshwater environments has rarely been studied, meaning that the present study may help to understand patterns of selective extinction.

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1. Introduction

The Cretaceous–Paleogene (K/Pg) boundary is characterised by a worldwide ecological catastrophe with evident selectivity of extinction (Sheehan et al., 1996; Robertson et al., 2013). This extirpation event has been well documented in marine settings, whereas records for freshwater environments have only rarely been reported (Morgan et al., 2022). For instance, at the K/Pg boundary, freshwater charophytes (Characeae) underwent a minor extinction at middle latitudes, with a replacement of species within the family (Martín-Closas, 2003; Li et al., 2019). Vicente et al. (2019) documented that characeans experienced a step-wise extinction during the latest Cretaceous, with only a small number of species

going extinct at the K/Pg boundary. Likewise, previous studies based on the global vertebrate fossil record have shown freshwater species extinction levels of 10–22% (Robertson et al., 2013). Fish and amphibians display similar extinction patterns at this boundary, showing that freshwater biotas may somehow have been more resilient to catastrophic events during the extirpation event (Neubauer et al., 2022). However, estimates based on European freshwater gastropods show a species richness decline there, with 92.5% of all species and an average of 9.5% (3.5–15.8%) of all genera dying out (Neubauer et al., 2022). Here, we describe newly discovered continuous records of freshwater gastropods from Upper Cretaceous to lower Paleogene deposits of the Songliao Basin in north-east China. In the present study, gastropod fossils from the SK-1(North) borehole (Fig. 1) are described taxonomically and discussed in a palaeoecological context, with comparisons to extant relatives.

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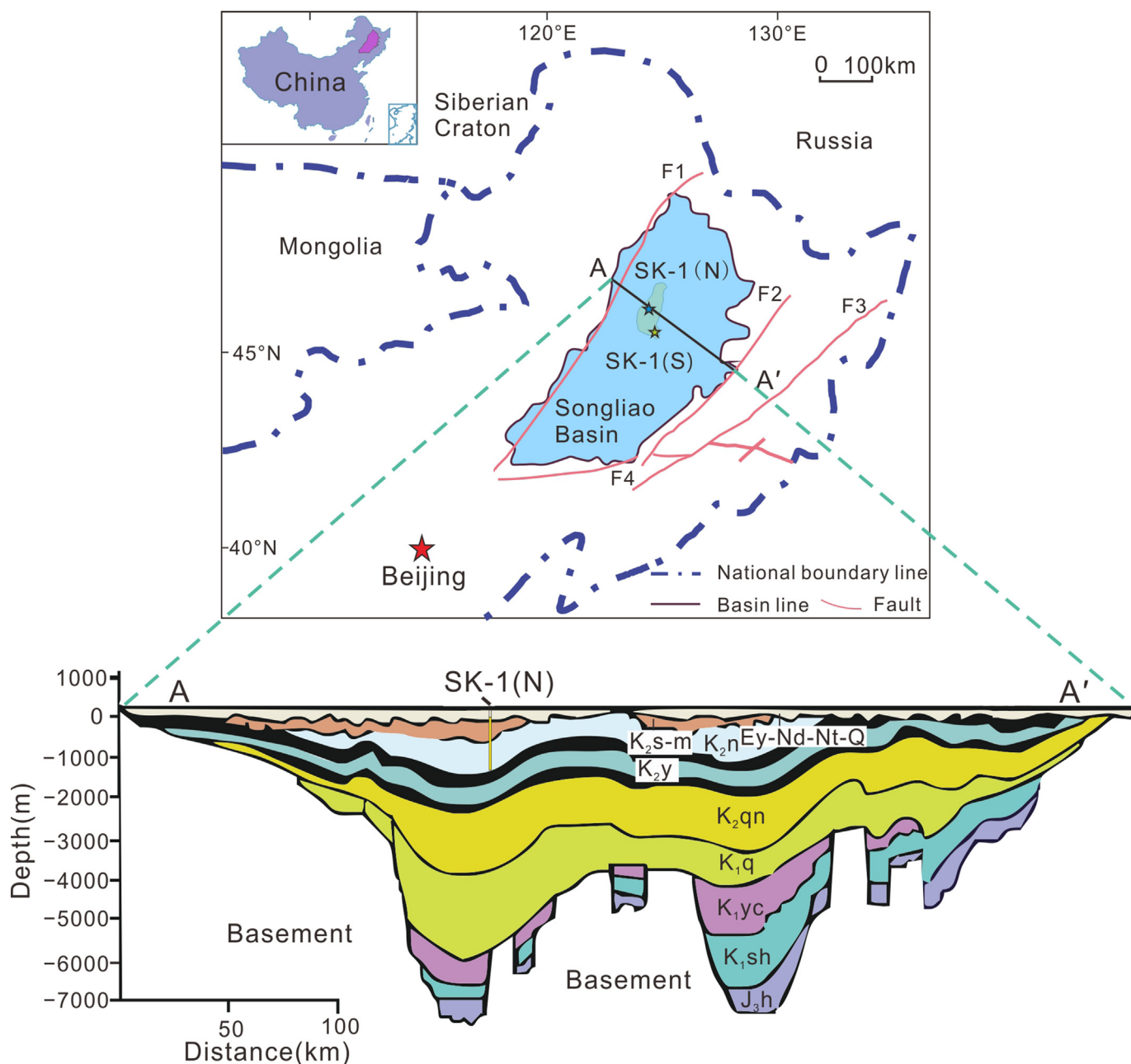


Fig. 1. Location of the SK-1(North) borehole in the Songliao Basin. F1, Nenjiang Fault; F2, Yilan-Yitong Fault; F3, Chifeng-Kaiyuan Fault. A–A', stratigraphical cross section through the Songliao Basin, modified from P.J. Wang et al. (2007) and Qu et al. (2014). J₃, Upper Jurassic; K₁, Lower Cretaceous; K₂, Upper Cretaceous; J₃h, Huoshiling Formation; K₁sh, Shahezi Formation; K₁yc, Yingcheng Formation; K₁d, Denglouku Formation; K₂q, Quantou Formation; K₂qn, Qingshankou Formation; K₂y, Yaojia Formation; K₂n, Nenjiang Formation; K₂s-m, Sifangtai and Mingshui formations; Ey-Nd-Nt-Q, Eocene Yi'an Formation to Neogene Da'an and Taikang formations, Quaternary deposits.

2. Geological setting

The Songliao Basin covers roughly 260,000 square kilometres in the Heilongjiang, Jilin and Liaoning provinces of north-east China and is located between 119°40'E to 128°24'E and 42°25'N to 49°23'N (C. Wang et al., 2013). During the Cretaceous Period, the Songliao Basin was a large rift basin between the Siberian Craton and north China and hosted a long-lived, deep lake, although it also contains deposits of an alluvial plain and shore to the shallow lake (Chen, 1987; Ren et al., 2002; H.H. Wei et al., 2010). Terrestrial strata of the late Mesozoic to early Cenozoic age in the Songliao Basin include volcanic, volcanoclastic and sedimentary rocks; the basement consists of Palaeozoic strata and Middle Jurassic granites (Gao

et al., 1994; Wang et al., 2001). The Cretaceous strata consist of ten lithostratigraphical units (Fig. 1B), including the Lower Cretaceous Huoshiling (J₃h), Shahezi (K₁s) and Yingcheng (K₁y) formations, and the Upper Cretaceous to lower Paleocene Denglouku (K₁d), Quantou (K₂q), Qingshankou (K₂qn), Yaojia (K₂y), Nenjiang (K₂n), Sifangtai (K₂s) and Mingshui (K₂m) formations (P.J. Wang et al., 2001, 2007; Ren et al., 2002; Sha, 2007; H.H. Wei et al., 2010).

To date, the Cretaceous Continental Scientific Drilling (CCSD) project in Songliao Basin (SK1) has yielded 2485.89 m of continuous core (96.46% recovery), which has led to the recovery of a composite core representing almost the entire Upper Cretaceous to Paleocene succession (Wan et al., 2013). The SK1 was drilled separately in two boreholes: the upper 1636.72 m in the north core (SK1(N)), and the

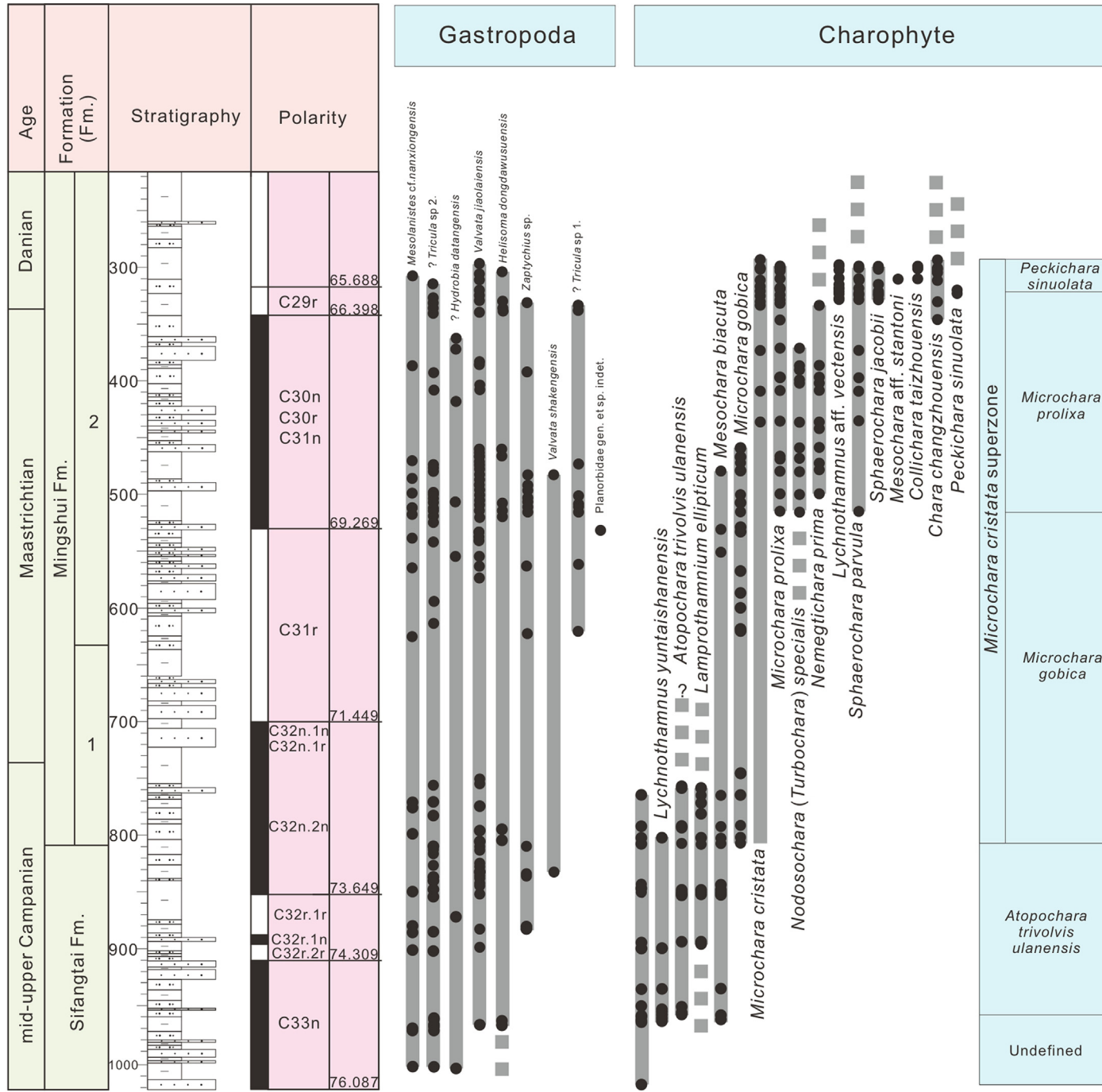
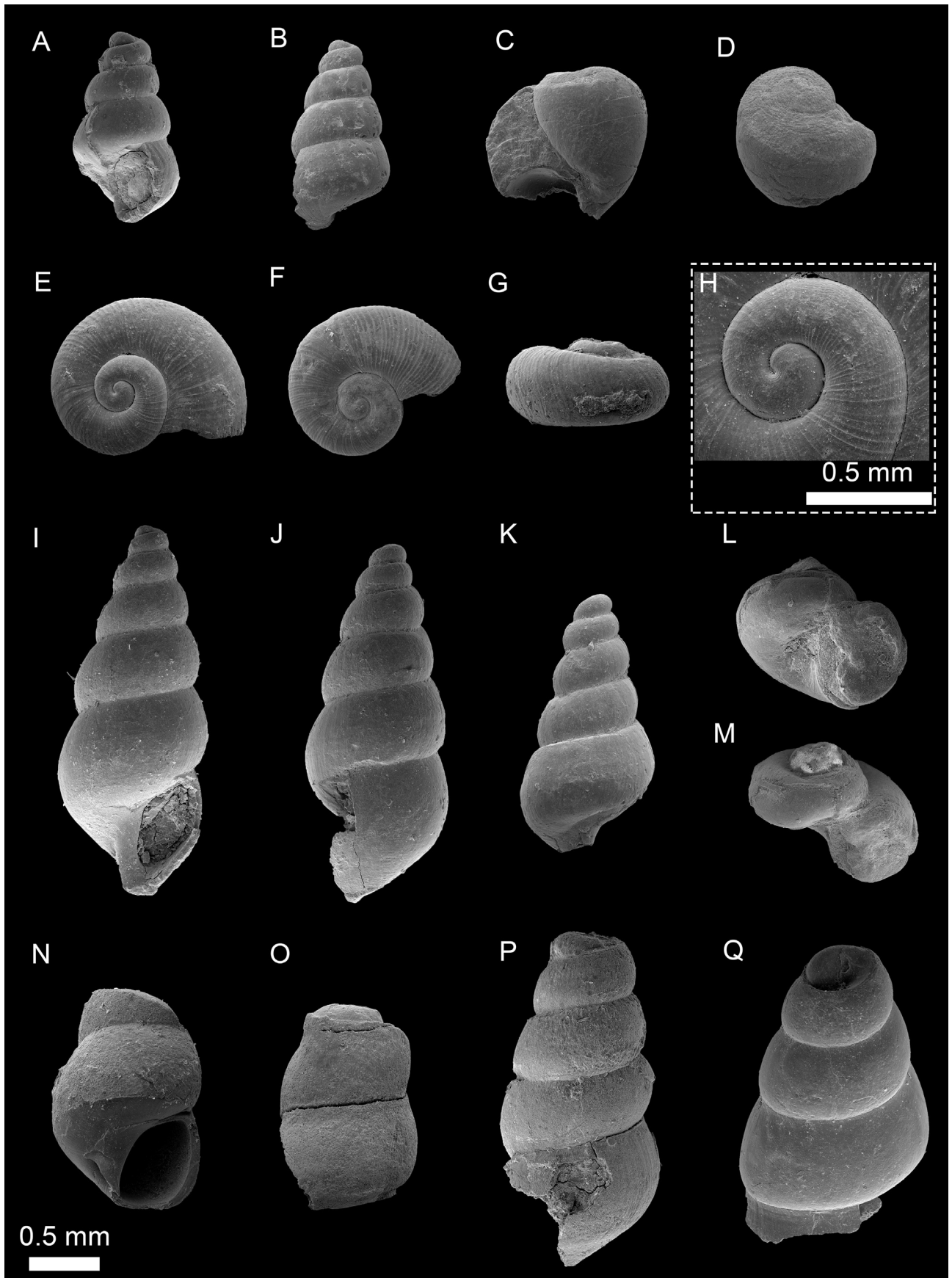


Fig. 2. Stratigraphical log of the SK-1(North) borehole showing the position of samples of gastropods calibrated to the geomagnetic polarity time scale (Deng et al., 2013) and charophyte biozonation (Li et al., 2019).



lower 959.55 m in the south core (SK1(S)); SK1(N) penetrated the middle to upper Nenjiang, plus the Sifangtai and Mingshui formations and the lower part of the Taikang Formation (Qu et al., 2014). Great progress on sedimentological characteristics, age determinations and fossil contents has been achieved in recent research into the continental K/Pg boundary in the Songliao Basin (e.g., Wei et al., 2010; He et al., 2012; Deng et al., 2013; Wan et al., 2013; Wang et al., 2013). For biostratigraphy, major lacustrine microfossil groups such as ostracods, charophytes, and phytoplankton, as well as spores and pollen, have been studied (Zhang and Bao, 2009; Qu et al., 2014; Zhao et al., 2014; S. Li et al., 2019). On the basis of a detailed biostratigraphical study the sequence has been subdivided into high-precision biozones: twenty-one ostracod assemblages, ten phytoplankton assemblages, seven palynological zones and four charophyte biozones, plus one superzone.

3. Material and methods

The gastropods studied here stem from the Sifangtai and Mingshui formations of the SK-1 (North) borehole (co-ordinates: 46°12'44.22"N, 124°15'56.78"E) in the Songliao Basin (Fig. 2). The shells were recovered from siltstones and claystones, sampled at an average of 1-m-intervals, and more than 1100 samples were prepared. One to two hundred gr of sediment per sample dry weight were disaggregated in water for several weeks before sieving through two sieves of mesh widths of 63 and 1140 µm. Gastropods were handpicked under a stereomicroscope Stemi 508. The horizons in which gastropods were found were then resampled in order to obtain an adequate number of shells for taxonomic assessment.

Well-preserved gastropods were selected and measured (H = shell height; D = greatest shell width; h = apertural height; d = apertural width), and shell morphologies (general shape, apical features, number of whorls, sutures, aperture, and shell sculpture) were recorded. Species identifications rely on comparison with published literature on Chinese fossils, which occasionally present generic allocations that are provisional, as based on typically European or North American genera. In all likelihood, the Chinese fauna will warrant descriptions of new genera once the revisionary work is conducted in the future (Salvador and Yu, 2022). Selected specimens were imaged using a scanning electron microscope at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS); specimens illustrated are housed at NIGPAS under numbers NIGP180157 to 180173.

4. Systematic palaeontology

Class Gastropoda Cuvier, 1795.

Subclass Caenogastropoda Cox, 1960.

Superfamily Truncatelloidea Gray, 1840.

Family Hydrobiidae Stimpson, 1865.

Genus *Hydrobia* Hartmann, 1821.

Type species. *Cyclostoma acuta* Draparnaud, 1805.

Hydrobia? *datangensis* Yü, 1977.

Fig. 3A, B.

1977 *Hydrobia datangensis* Yü, p. 197, fig. 2.10–11.

2021 ?*Hydrobia datangensis*; T.T. Yu et al., p. 5, fig. 3J–L.

2022 ?*Hydrobia datangensis*; T.T. Yu et al., p. 3, fig. 3C–F.

Material.—Ten specimens, moderately to well preserved (Table 1). **Description.** Shell minute (H: 1.19–1.28 mm; D: 0.67–0.78 mm; h: 0.40–0.41 mm; d: 0.31–0.41 mm), conical in outline, consisting of about four whorls. Apex blunt and bulbous; no protoconch-teleoconch transition visible. Whorls convex, with maximum convexity at about mid-height; suture distinct. Body whorl broad, occupying more than half of shell height. Aperture broken, probably ovate in shape; columellar lip nearly straight and short. Shell imperforate. Surface ornament of fine and indistinct, weakly opisthocyrt growth lines.

Remarks. As argued by T.T. Yu et al. (2021, 2022), Chinese Cretaceous–Paleocene gastropods historically assigned to the genus *Hydrobia* are geographically and stratigraphically isolated from extant *Hydrobia* spp., their classification having been based solely on superficial similarity. We retain the usage of such classification here, but use a question mark; to date, no revision of Chinese fossil hydrobiids is available.

Distribution. *Hydrobia?* *datangensis* has previously been recorded from the Upper Cretaceous–Paleocene Shanghu Formation in the Nanxiong Basin of Guangdong Province in southern China (Yü, 1977), the uppermost Cretaceous Jiaozhou Formation in the Jiaolai Basin of eastern China (T.T. Yu et al., 2021), and K/Pg transition deposits in the Pingyi Basin of Shandong Province in eastern China (T.T. Yu et al., 2022).

Subclass Caenogastropoda Cox, 1960.

Superfamily Ampullarioidea Gray, 1824 Family Ampullariidae Gray, 1824.

Genus *Mesolanistes* Yen, 1945.

Type species. *Mesolanistes cretaceus* Yen, 1945.

Mesolanistes cf. *nanxiongensis* Yü, 1977.

Fig. 3C, D.

Material.—Twenty-five specimens, moderately preserved (Table 1).

Description. Shell of medium size (H: 1.22 mm; D: 1.28 mm), sinistral, oblique-ovate; apex blunt, first whorl very low and almost invisible in apertural view (many features remaining unscored due to fragmentary shell preservation); whorls seemingly dilating extensively with shell growth; whorl profile convex at upper/adapical part, rapidly tapering towards base; suture relatively shallow.

Remarks. This specimen is attributed to the genus *Mesolanistes* on account of its sinistral shell with a low spire and dilated whorls. Its seemingly low spire and relatively shallow suture differ from most other species of *Mesolanistes* from the Upper Cretaceous of Asia: *M. jilinensis* Yu and Lee, 1980; Zhu, 1980), *M. ziziformis* Yu and Lee, 1980, *M. dongtaiensis* Gu, 1989; Gu and Wang, 1989) and *M. yunnanensis* Yü, 1983 have deeper sutures, while *M. efremoni* Martinson, 1957, *M. bajanchongorensis* Barsbold, 1971 and *M. jingangkouensis* Pan, 1983 have higher spires. It also differs from *M. magnus* Perrilliat and Vega, in Perrilliat et al., 2008 and *M. murrayi* Perrilliat and Vega, in Perrilliat et al., 2008 from the Upper Cretaceous of Mexico in lacking shell sculpture (Perrilliat et al., 2008). The present fossil more closely resembles *M. nanxiongensis* Yü, 1977 from the Upper Cretaceous Nanxiong Formation of Guangdong

Fig. 3. Non-marine gastropods from the Sifangtai and Mingshui formations in the SK-1(North) borehole in the Songliao Basin. A, B, *Hydrobia?* *datangensis* Yü, 1977, NIGP180157; depth 321.76 m (Danian). A, apertural view, B, abapertural view. C, D, *Mesolanistes* cf. *nanxiongensis* Yü, 1977, NIGP180158; depth 517.71 m (Maastrichtian). C, apertural view, D, apical view. E–H, *Valvata jiaolaiensis* Yu et al., 2021, NIGP180159–NIGP180161, depth 504.2 m, 471.82 m and 816.58 m, respectively (Maastrichtian to mid-upper Campanian). E, F, apical views. G, lateral view. H, magnification of protoconch. I–K, ?*Tricula* sp. 1 [in text, this is sp. 1], NIGP180163–NIGP180164, depth 505.2 m and 336.04 m, respectively (Maastrichtian). I, apical view. J, lateral view. K, abapertural view. L, M, *Valvata shakengensis* Yü and Zhang, 1982, NIGP180162; depth 485.84 m (Maastrichtian). L, apertural view, M, apical view. N–Q, ?*Tricula* sp. 2 [in text, this is sp. 2], NIGP180165–NIGP180167, depth 504.20 m, 809.71 m and 1002.31 m, respectively (Maastrichtian to mid-upper Campanian). N, apertural view. O, P, lateral view. Q, apical view.

Table 1
Number of gastropod specimens per sample from the Sifangtai and Mingshui formations in the Songliao Basin.

Depth (m)	? <i>Hydrobia</i> <i>datangensis</i>	<i>Mesolanistes</i> cf. <i>nanxiongensis</i>	<i>Zptychius</i> sp.	<i>Valvata</i> <i>jiaolaiensis</i>	<i>Valvata</i> <i>shakengensis</i>	? <i>Tricula</i> sp 1	? <i>Tricula</i> sp 2	<i>Helisoma</i> <i>dongdawusuensis</i>	Planorbidae gen. et sp. indet.	operculum	Number of specimens	Number of species
300				1							1	1
306		1									1	1
306.75								2		2	4	1
307.75				1							1	1
308.75				1							1	1
311.81							2				2	1
321.76	2			1							3	2
326											0	0
328.44							1				1	1
331.42				1							1	1
331.5				1							1	1
332			1	4				19			24	3
332.7								1			1	1
333.2	1										1	1
336							2	1			3	2
336.04						1					1	1
338						1					1	1
339.95				1				1			2	2
340								10	4		14	2
342									2		2	1
379.73	1										1	1
383				1							1	1
387.43		1		1							2	2
391			1				1				2	2
404.05				2							2	1
406.05				2							2	1
408.11							2				2	1
410.11							2				2	1
463.88				3				1			4	2
464.88				5							5	1
467.88	2			1							3	2
470.32		1		1				1			3	3
471.82				1							1	1
472.80				2				2			4	2
474				1							1	1
475				15							15	1
476				1		1	1				3	3
477				1							1	1
478				1							1	1
479				1							1	1
480.81								1			1	1
482.21				1							1	1
483.21				1							1	1
484.84				1							1	1
485.84		2	3	2	2						9	4
486.84				3							3	1
494.33			2	2							4	2
498.33		1		2				8			11	3
499.33			2	2				2			6	3
500.20				1				2			3	2
501.40			1	1				1			3	3
502.70			1	1				1			3	3
503.20			4	4				2			10	3
504.20			4	2		4	6				16	4
505.20			3	4		4	2				13	4
506.20								4			4	1
507.20		1		1				1			3	3
508.20		1	1					2			4	3
510.20						15	25				40	2
511.20						20	32				52	2
514.89	2			1				2			5	3
515.79				2				2			4	2
516.71			2	4		4		3			13	4
517.71		2		3		4					9	3
518.61				1							1	1
519.71				1				2			3	2
520.71				1							1	1
521.71				2				5			7	2
522.71							1	1			2	2
534.30				1							1	1
535.60				1							1	1
536.60				1							1	1
537.60		1							1		2	2

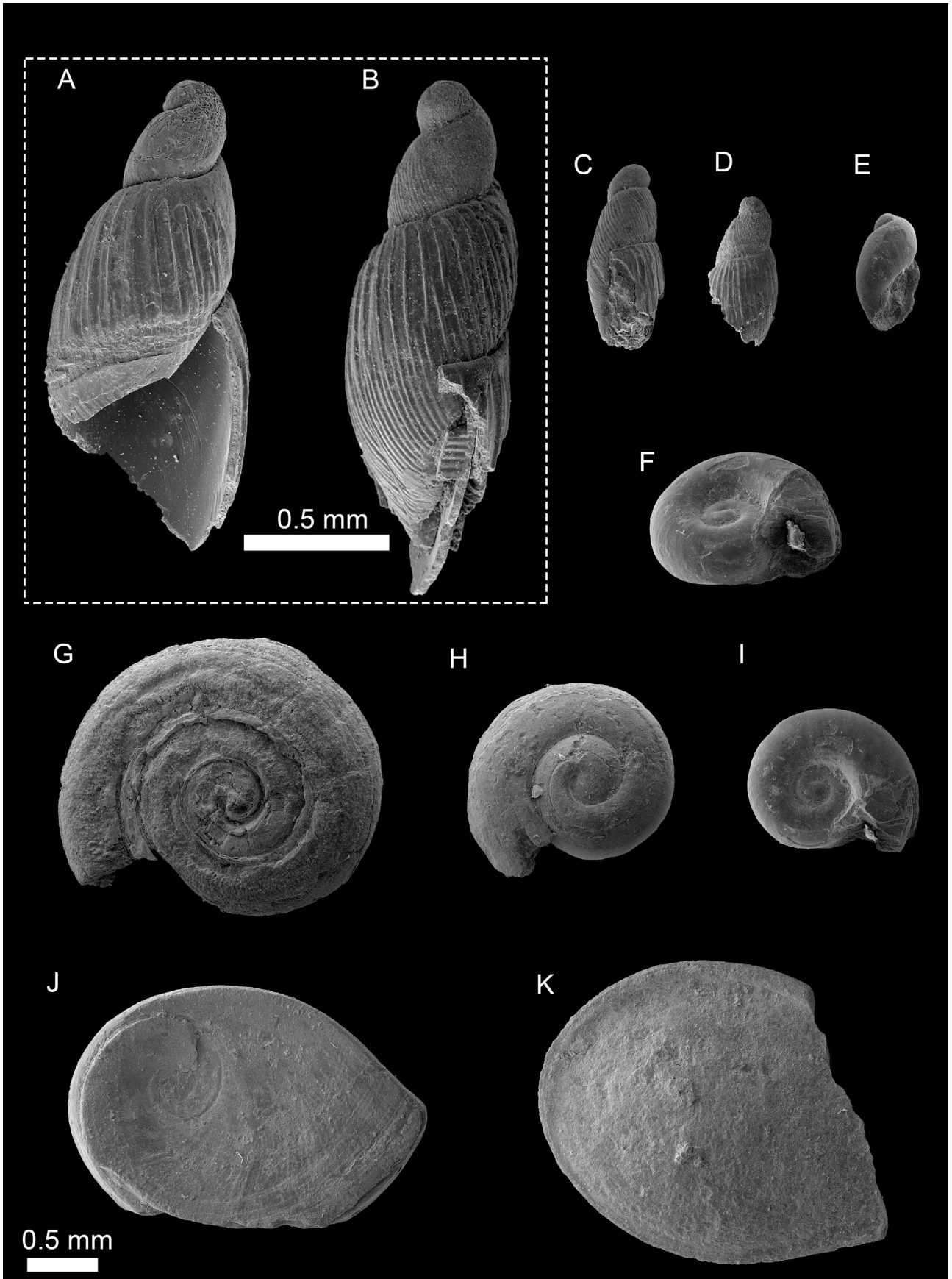
Table 1 (continued)

Depth (m)	? <i>Hydrobia</i> <i>datangensis</i>	<i>Mesolanistes</i> cf. <i>nanxiangensis</i>	<i>Zptychius</i> sp.	<i>Valvata</i> <i>jaolaiensis</i>	<i>Valvata</i> <i>shakengensis</i>	? <i>Tricula</i> sp 1	? <i>Tricula</i> sp 2	<i>Helisoma</i> <i>dongdawusuensis</i>	Planorbidae gen. et sp. indet.	operculum	Number of specimens	Number of species
538.70				8							8	1
540.17				1							1	1
541.17				4					1		5	2
541.92				2			2				4	2
557.96				2							2	1
565.46		1	2	2		2					7	4
577				1							1	1
593.90							1				1	1
606.20							1				1	1
625.81		1	1			1					3	3
753.09				1							1	1
754.09				1			1				2	2
762.99				1							1	1
763.99				1							1	1
764.99				1			1				2	2
770.30		1					1				2	2
772.63							6				6	1
775.13		1		3							4	2
783.94							2				2	1
799.93		1		2				1			4	3
808.27				1				1			2	2
808.97							1				1	1
809.77			1	1			2				4	3
811.97				5			10				15	2
814.97				3			4				7	2
815.58				2							2	1
816.58				4							4	1
827.31				1			3				4	2
829.11				4			2				6	2
830				1							1	1
834.13	1			2							3	2
836.23			2		1						3	2
837.23			1				2				3	2
838.73							2				2	1
840.59							4				4	1
843.59							2				2	1
849.34				1			2				3	2
849.84				2							2	2
850.84		1									1	1
855.34				2							2	2
856				2			2				4	2
856.34								2			2	1
880.14		1									1	1
882			1								1	1
883.94			1				2				3	2
884.44							8				8	1
886.14		1		2							3	2
900.60		1		2			5				8	3
901.40							1	1			2	2
963.67							1				1	1
964.87							1				1	1
966.57	1			2			2				5	3
967.67		1					2	1			4	3
969.67							2				2	2
970.17		1					1	2			4	3
1002.31		1					1	1			3	3
Total	10	25	34	163	3	57	213	31	2	2	540	223

Province in southern China (Yü, 1977; Yü et al., 1990), but apparently it has a wider whorl profile. In any event, the fragmentary preservation of the present specimen precludes certain identification.

Mesolanistes was widely distributed in Upper Cretaceous freshwater deposits worldwide, as the following enumeration illustrates: *Mesolanistes nanxiangensis* and *M. latericea* Yü, in Yü et al., 1990; upper and middle part of Zhenshui section of the Nanxiong Formation in the Nanxiong Basin (Yü et al., 1990); *Mesolanistes efremovi* Pan, in Pan and Zhu, 2007 from the Upper Cretaceous Majiacun Formation in the Xishan Basin and the Upper Cretaceous Honglishan Formation of Xinjiang (Pan and Zhu, 2007; J.M. Wei,

1989); *Mesolanistes jilinensis* and *M. ziziformis* Yü and Lee, 1983 from Upper Cretaceous Nenjiang Formation in Jilin and Heilongjiang provinces (Zhu, 1980; Yü, 1983); *Mesolanistes jingangkouensis* H.Z. Pan, 1983 from upper part of the Hongtuya Formation of the Wangshi Group at Laiyang City, Shandong Province (H.Z. Pan, 1983); *Mesolanistes yunnanensis* Yü, 1983 from the Upper Cretaceous Mankuanhe Formation in Yunnan Province (Yü, 1983); *Mesolanistes dongtaiensis* Gu, 1989 from the Upper Cretaceous second member of the Taizhou Formation at Taian City, Jiangsu Province (Gu and Wang, 1989); *Mesolanistes magnus* and *M. murrayi* from Cretaceous through Eocene sedimentary rocks in Mexico (Perrilliat et al., 2008).



Superfamily Truncatelloidea Gray, 1840.

Family Pomatiopsidae Stimpson, 1865.

Genus *Tricula* Benson, 1843.

Type species. *Tricula montana* Benson, 1843.

***Tricula?* sp. 1.**

Fig. 3I–K.

2022 ?Pomatiopsidae gen. et sp. indet.; Yu et al., p. 5, fig. 3J–O.

Material.—Fifty-seven specimens, moderately to well preserved (Table 1).

Description. Shell minute (H: 1.15–2.30 mm; D: 1.04–1.10 mm; h: 0.69–0.74 mm; d: 0.48–0.54 mm), with highly turreted spire and moderately dilated body whorl, c. 6–6.5 whorls. Apex preserved, papilliform; apical angle c. 75°. Protoconch seemingly smooth. Transition to teleoconch unclear. Teleoconch ornamented by fine indistinct opisthocyrt growth lines. Whorls slightly convex; suture deep. Shell imperforate. Aperture narrowly ovate to pyriform in outline; outer lip fragile and thin. In lateral view, outer lip straight, and columellar lip nearly so.

Remarks. This species from the Songliao Basin is probably conspecific with ‘?Pomatiopsidae gen. et sp. indet.’ from the K/Pg transition in the Pingyi Basin, sharing the elongate, smooth shell with a papilliform, intact apex (Yu et al., 2022). The present specimens are better preserved than the Pingyi Basin forms, showing a narrowly ovate to pyriform aperture. Its generalised pomatiopsid shell morphology (e.g., small size, elongated shell and lack of sculpture) indicates that this species is a conservative member of the subfamily Pomatiopsinae Stimpson, 1865. The present fossils are reminiscent of extant *Tricula* spp. from eastern Asia, which is why we tentatively assign them to this genus.

***Tricula?* sp. 2.**

Fig. 3N–Q.

2021 ?Pomatiopsidae gen. et sp. indet.; Yu et al., p. 5, fig. 3F–I.

Material.—Two hundred and thirteen specimens, moderately to well preserved (Table 1).

Description. Shell minute (H: 1.20–2.63 mm; D: 0.74–1.04 mm; h: 0.45–0.85 mm; d: 0.36–0.43 mm), slender ovate-turreted, with c. 5–6 whorls. Apex of most specimens eroded; apical angle c. 75°. Suture impressed and distinct. Shell imperforate. Body whorl long, not inflated, about half of shell height. Aperture narrowly ovate to cylindrical in outline, angular above; lower part widely rounded. Outer lip fragile and thin; inner view with outer lip thin and straight; inner lip adnate to body wall; columellar lip nearly straight. Teleoconch ornamented by fine and indistinct weakly opisthocyrt growth lines.

Remarks. A second morph attributable to the genus *Tricula* has been recognised in the present material and likely represents a second species. *Tricula?* sp. 2 has a larger shell than *T.?* sp. 1 (see above) and also lacks the apex (a decollated or complete apex is a variable feature among *Tricula* spp.; Davis et al., 1986) and has a potentially more circular aperture. It is probably conspecific with ‘?Pomatiopsidae gen. et sp. indet.’ from the Jiaolai Basin in sharing the elongated, smooth shell with a blunt apex (Yu et al., 2021).

Tricula? sp. 2 shares the closest similarity with the extant *Tricula cylindrica* Liu, Wang and Zhang, 1991 from the Sanxia Reservoir in central China; both have cylindrical shells with a long body whorl and obliquely-ovate aperture (Liu et al., 1991). Due to the incomplete

preservation of the shell aperture in material from the Songliao Basin and the difference in geological age, the specimens from the Songliao Basin are provisionally placed in this genus, as *T.?* sp. 2.

Distribution. Species of *Tricula* are widely distributed in the region of Sanxia Reservoir (upper Yangtze River), and are the dominant group of freshwater gastropods in this region. *Tricula* spp. are found mainly in the source areas of mountain streams, pools under waterfalls, spring water slope seepage and other places (Liu et al., 1991). Grego (2018) investigated several caves and karstic springs in Laos for the presence of underground freshwater gastropod species and reported eight new species assigned to the genus *Tricula*. *Tricula* is widely distributed from the Naga Hills and Arunachal-Pradesh in India through Myanmar, Thailand, Laos and Vietnam to south China (Yunnan and Guangxi) and likely also northwards into the central and east mainland of China and Korea.

Subclass Heterobranchia Burmeister, 1837.

Superfamily Valvatoidea Gray, 1840.

Family Valvatidae Gray, 1840.

Genus *Valvata* Müller, 1774.

Type species. *Valvata cristata* Müller, 1774.

Valvata jiaolaiensis T. Yu, Salvador, H. Wang, Y. Fang, Neubauer, S. Li, H. Zang & X. Wan, 2021.

Fig. 3E–H.

2021 *Valvata jiaolaiensis* Yu et al., p. 5, fig. 3M–P.

Material.—one hundred and sixty-three specimens, moderately to well preserved (Table 1).

Description. Shell minute (diameter: 0.90–1.44 mm), nearly planispiral, consisting of up to c. 2.5 whorls. Whorls strongly convex, increasing in diameter fairly rapidly with shell growth. Suture distinct and deeply impressed. Apex flattened. Umbilicus broad and deep. Aperture broadly elliptical in outline. Protoconch (c. 0.5 whorls; initial cap measuring 0.22 mm in width, maximum diameter c. 0.55 mm), ornament of numerous parallel spiral cordlets. Transition to teleoconch marked by appearance of axial ornament: thin, orthocone and closely spaced axial ribs (more prominent on apical side). For initial c. 0.75 whorls of teleoconch, continuation of protoconch’s spiral cordlets seen on adapical area of whorl, close to suture; spiral ornamentation intermingling with axial ribs forming light, reticulated pattern.

Remarks. The protoconch of the present specimens is slightly better preserved than that in specimens from the Jiaolai Basin, enabling the observation of the fine sculpture described above.

Distribution. *Valvata jiaolaiensis* was originally recorded from the uppermost Cretaceous Jiaozhou Formation of the Jiaolai Basin (Yu et al., 2021), which remained the sole record of this species up to now.

Valvata shakengensis Yü and Zhang, 1982.

Fig. 3L, M.

1982 *Valvata (Cincinna) shakengensis* Yü and Zhang, p. 45, pl. 1, figs 13–15.

Material.—Three specimens, moderately to well preserved (Table 1).

Description. Shell minute, low conical, consisting of about 2.5–3 convex whorls. Spire protruding, apex blunt. Whorls slightly shouldered; first two whorls regularly increasing in size with shell

Fig. 4. Non-marine gastropods from the Sifangtai and Mingshui formations in the SK-1(North) borehole in the Songliao Basin. A–E, *Zaptychius* sp., NIGP180167–NIGP180171; depth 836.23 m, 503.2 m and 504.20 m, respectively (Maastrichtian, mid-upper Campanian). A, C and E, apertural view; B, D, lateral view. F, I, *Helisoma dongdawusuensis* Zhu, 1976, NIGP180172; depth 506.20 m (Maastrichtian). F, apertural view. I, apical view. G, H, Planorbidae gen. et sp. indet., NIGP180173–NIGP180174; depth 537.60 m (Maastrichtian). apical view. J, K, opercula, depth 306.75 m (Danian).

Table 2

The distribution of non-marine gastropod species in this paper.

Species	Localities and Formations		
? <i>Hydrobia datangensis</i>	Shanghu Formation, Nanxiong Basin (south China)	Jiaozhou Formation, Jiaolai Basin (east China)	Bianqiao Formation, Pingyi Basin (east China)
<i>Mesolanistes</i> cf. <i>nanxiongensis</i>	Nanxiong Formation, Nanxiong Basin (south China)	Sifangtai and Mingshui Formations, Songliao Basin (northeast China)	
<i>Valvata jiaolaiensis</i>	Jiaozhou Formation, Jiaolai Basin (east China)	Sifangtai and Mingshui Formations, Songliao Basin (northeast China)	
<i>Valvata shakengensis</i>	Sanshui Formation, Sanshui Basin (south China)	Sifangtai and Mingshui Formations, Songliao Basin (northeast China)	
? <i>Tricula</i> sp. 1	Bianqiao Formation, Pingyi Basin (east China)	Sifangtai and Mingshui Formations, Songliao Basin (northeast China)	
? <i>Tricula</i> sp. 2	Jiaozhou Formation, Jiaolai Basin (east China)	Mingshui Formation, Songliao Basin (northeast China)	
<i>Helisoma dongdawusuensis</i>	Banlashan Formation (northeast China)	Nenjiang and Sifangtai Formations, Songliao Basin (northeast China)	Sifangtai and Mingshui Formations, Songliao Basin (northeast China)

growth; body whorl expanding more rapidly. Suture distinct and deeply impressed. Abapical region of shell rounded and convex, with narrow and deep umbilicus. Shell sculpture not preserved. Aperture large and circular.

Remarks. The present specimens attain slightly larger shell sizes than those from the Sanshui Formation.

Distribution. *Valvata shakengensis* was originally recorded from the Upper Cretaceous Sanshui Formation in the Sanshui Basin, Guangdong Province, south-east China (Yü and Zhang, 1982).

Superfamily Ellobioidea L. Pfeiffer, 1854

Family Ellobiidae L. Pfeiffer, 1854

Genus *Zaptychius* Walcott, 1883.

Type species. *Zaptychius carbonarius* Walcott, 1883.

***Zaptychius* sp.**

Fig. 4A–E.

Material.—Thirty-four specimens, moderately to well preserved (Table 1).

Description. Small (H: 0.81–1.91 mm; D: 0.44–0.74 mm), fusiform shell with protruded spire. Protoconch sinistral and heterostrophic, comprising more than one smooth whorl, separated from teleoconch by demarcation and beginning of sculpture. Whorls regularly increasing in dimensions. Suture deep; in later whorls, subsutural region of whorl becoming cord-like structure. Teleoconch surface covered by collabral costae; costae more numerous (seemingly twice as many) on abapical region of whorl. Aperture not preserved, but in juvenile and incomplete specimens, aperture narrow and elongated. Shell seemingly imperforate.

Remarks: Despite the incomplete preservation of these specimens, the characteristic protoconch, fusiform shell and axial sculpture allow them to be assigned to *Zaptychius*. In particular, the present fossils resemble *Z. costatus* Pan and Zhu, 2007 (Lower Cretaceous Xiaozhuang Formation, Beijing) and *Z. kuwajimaensis* Isaji, 2010 (Lower Cretaceous Kuwajima Formation, Japan), but differ from these in having a lower spire and unshouldered whorls. Likely, the present material represents a still undescribed species, although additional and better-preserved specimens are needed to assess its status fully.

Distribution. Species of *Zaptychius* range from the Upper Jurassic to Upper Cretaceous in nonmarine formations and are distributed widely in North America and northern China. The North American species include the following: *Zaptychius carbonaria* Walcott, 1883 from the Lower Cretaceous of Nevada (Walcott, 1883); *Zaptychius* aff. *haldemani* White, 1878 from the Upper Jurassic Morrison Formation of Wyoming (Yen and Reeside, 1946; Yen, 1952); *Zaptychius tetonensis* Yen, 1951 and *Z. cylindricus* Yen, 1951 from the Lower Cretaceous Cloverly Formation of Montana (Yen, 1951); *Zaptychius*

wyomingensis (Henderson, 1920) from the Upper Cretaceous Bear River Formation of Wyoming (Yen, 1951).

These species are characterised by cylindrical shells, which is the major difference separating them from *Z. kuwajimaensis* and Early Cretaceous Chinese species.

Subclass Heterobranchia Burmeister, 1837.

Superfamily Lymnaeoidea Rafinesque, 1815.

Family Planorbidae Rafinesque, 1815.

Planorbidae gen. et sp. indet.

Fig. 4G, H.

Material.—Two specimens, poorly preserved (Table 1).

Description. Shell of medium size; sinistral (pseudodextral), planispiral; apex depressed. Suture deeply impressed. Whorls slightly rapidly growing in size.

Remarks: The sole shell available is incomplete. The sinistral planispiral shell allows placement in the Planorbidae. The size of the preserved whorls and their rapid expansion is indicative of affinity with Late Cretaceous and early Cenozoic forms from China (e.g., Yü, 1977; Y.T. Li, 1984) that have been referred to genera such as *Planorbarius* Duméril, 1805, *Sinoplanorbis* W. Yü, 1965 and, mistakenly, *Australorbis* Pilsbry, 1934 (a junior synonym of *Biomphalaria* Preston, 1910).

Genus *Helisoma* Swainson, 1840.

Type species. *Planorbis anceps* Menke, 1830.

***Helisoma dongdawusuensis* Zhu, 1976**

Fig. 4F, I.

1976 *Gyraulus dongdawusuensis* Zhu, p. 56, figs 14/20–23; 17/41–44.

1987 *Helisoma dongdawusuensis*; Yu, p. 87, figs 8, 15, 16.

Material.—Thirty-one specimens, moderately to well preserved (Table 1).

Description. Shell small, sinistral (pseudodextral), planispiral, with depressed apex submerged and rounded whorls. Suture moderately incised. Protoconch apparently of 1.5 whorls; transition to teleoconch marked by slight bulge.

Remarks: These shells are incomplete and apertures are not preserved. However, these small planispiral shells with a rounded whorl profile, deeply sunken spire, and no fine spiral striae on the protoconch could be assigned to *Helisoma* (Zilch, 1959 [in 1959–1960]). The state of preservation of the shells from SK-1 was better than congeners recorded by Zhu (1976). *Helisoma sheyangensis* Wang, 1977 (in Yü and Wang, 1977) from the Upper

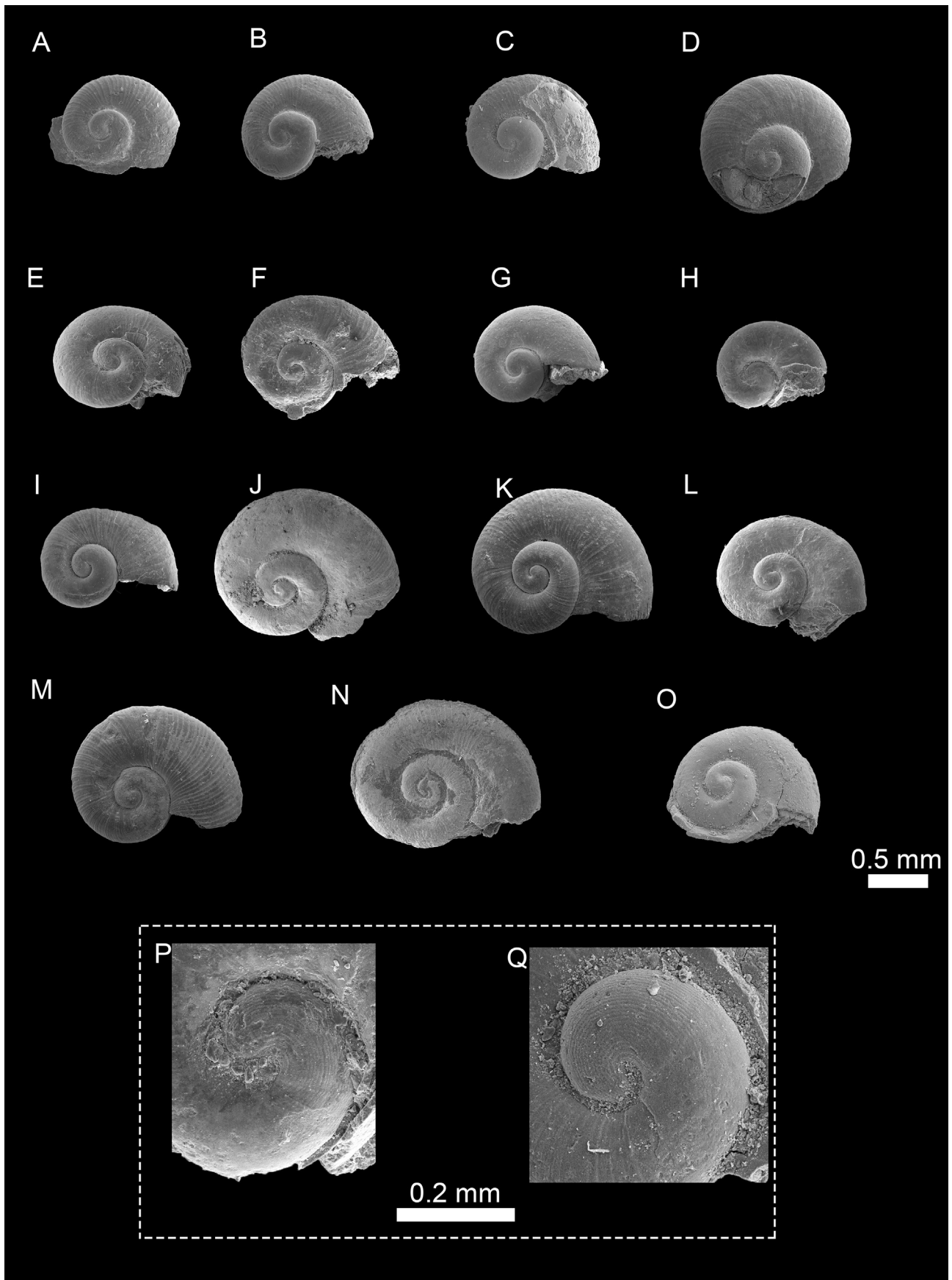


Fig. 5. *Valvata jiaolaiensis* Yu et al., 2021, NIGP180159–NIGP180161 and NIGP202774–NIGP202785, from the Sifangtai and Mingshui formations in the SK-1(North) borehole of the Songliao Basin. A, depth 966.57 m; B, depth 856.34 m; C, depth 839.11 m; D, depth 814.97 m; E, depth 809.77 m; F, depth 541.92 m; G, depth 516.71 m; H, depth 515.79 m; I, depth 507.20 m; K, J, depth 504.2 m; L, depth 485.84 m; M, depth 471.82 m; N, depth 408.11; O, depth 332 m. P, Q, magnifications of protoconch, depths 515.79 m and 839.11 m, respectively.

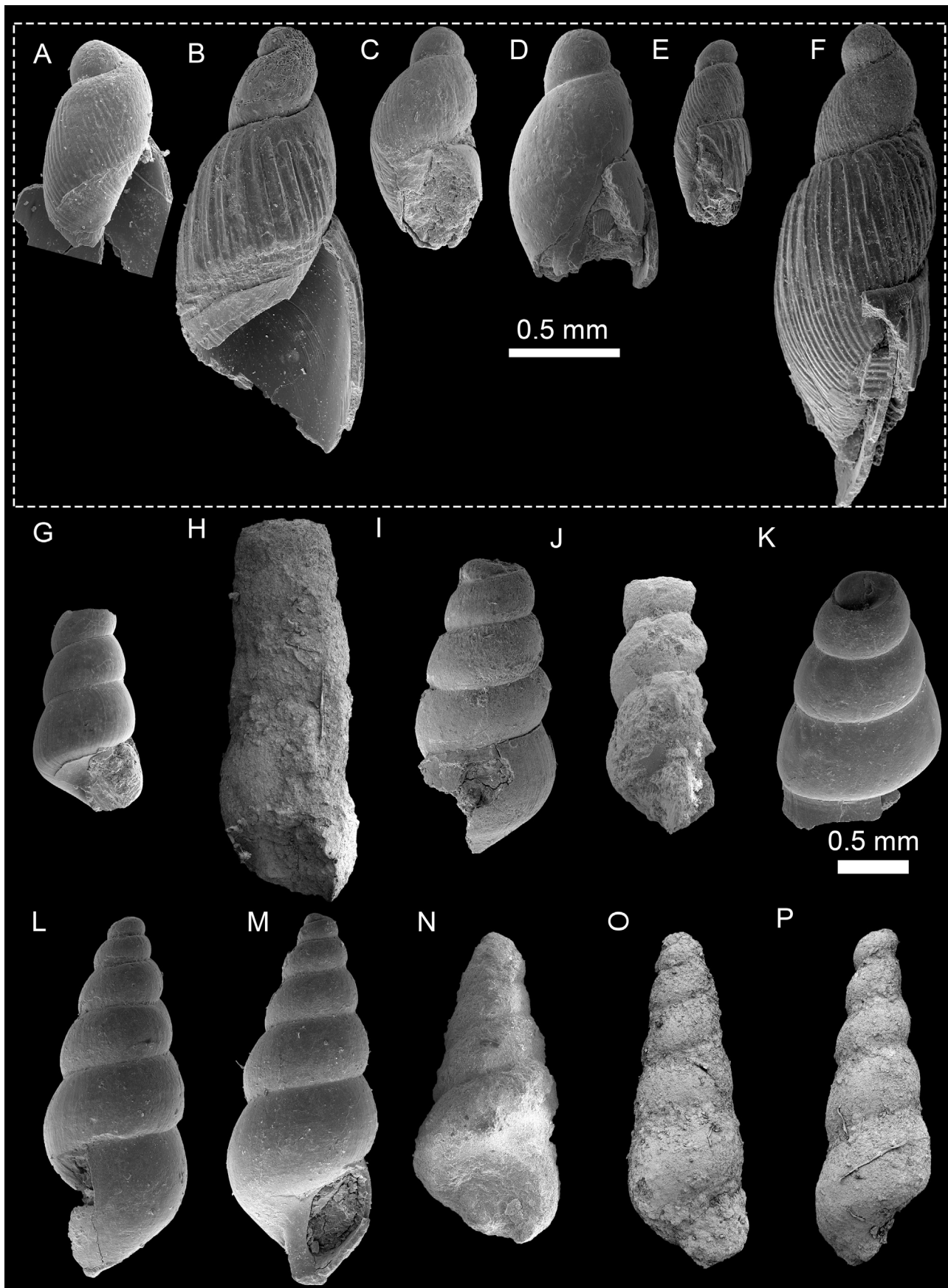


Fig. 6. *Zptychius* sp., *Tricula?* sp. 1 and *Tricula?* sp. 2, from the Sifangtai and Mingshui formations in the SK-1(North) borehole of the Songliao Basin. A–F, *Zptychius* sp., NIGP180167–NIGP180169 and NIGP202786–NIGP202788. A, depth 838.73 m; B, depth 836.23 m; C, depth 809.77 m; D, depth 516.71 m; E, depth 504.2 m; F, depth 503.2 m. G–K, *Tricula?* sp. 1, NIGP180165–NIGP180166, NIGP202792–NIGP202794. G, depth 1002.31 m; H, depth 838.73; I, depth 809.71 m; J, depth 511.2 m; K, depth 505.2 m. L–P, *Tricula?* sp. 2, NIGP180163, NIGP202789–NIGP202791. L, M, depth 511.2 m; N, depth 510.2 m; O, depth 505.2 m; P, depth 336.04 m.

Cretaceous to Paleocene of Jiangsu Province shows a similar deeply sunken spire and smooth protoconch. However, the latter has spiral ribs on the body whorl (Yü and Wang, 1977). *Helisoma dongdawusuensis* also differs from *H. brevispira* Yen, 1946 from Pliocene deposits of southeastern Idaho (USA); this has strongly angulated whorls. *Helisoma dongdawusuensis* has also been recorded from the Lower Cretaceous Banlashan Formation of western Liaoning Province, and *H. cf. dongdawusuensis* from the Upper Cretaceous Nenjiang and Sifangtai formations (in Zhu, 1976).

Distribution. Fossil *Helisoma* spp. are known mainly from Cenozoic deposits such as the Neogene of the United States and Venezuela, and potentially the Miocene of Peru (Yen, 1946; Wesselingh et al., 2006; Salvador and Simone, 2013; Salvador et al., 2018).

5. Discussion

The gastropod fauna from the upper Campanian to lower Paleocene Sifangtai and Mingshui formations in the Songliao Basin comprise nine species, namely *H.? datangensis*, *M. cf. nanxiongensis*, *V. jiaolaiensis*, *V. shakengensis*, *T.? sp. 1*, *T.? sp. 2*, *Z. sp.*, Planorbidae gen. et sp. indet., *H. dongdawusuensis* and opercula. Among these, *V. shakengensis* and Planorbidae gen. et sp. indet. disappear ~150–200 m below the K/Pg boundary, making their disappearance unrelated to the mass extinction event. *Hydrobia datangensis* did survive the K/Pg boundary extinction event in the Nanxiong and Pingyi basins (Yü, 1977; Yu et al., 2021, 2022). *Hydrobia? datangensis*, *M. cf. nanxiongensis*, *V. jiaolaiensis*, *T.? sp. 2* and *H. dongdawusuensis* survived K/Pg perturbations on the basis of range-through data from the Jiaolai, Pingyi, Songliao and Nanxiong basins (Table 2); *Z. sp.* and *T.? sp. 1* went extinct at the end-Cretaceous crisis in the Songliao Basin. Besides, *Physa dongtaiensis* Gu, 1989 died out in the Pingyi Basin (Yu et al., 2022). According to combined data on the range of species, three out of 11 species disappeared during the K/Pg boundary extinction in the Songliao and Pingyi basins (Table 2). Therefore, freshwater gastropods underwent a minor extinction rate in east and north-east China, with c. 18% extinction and 72% survival rates.

However, in marine environments, extinction rates among gastropods at the genus level are about 30–43% on Seymour Island (Antarctica), 21.7–32.1% in Patagonia (Argentina) in the Southern Hemisphere (Aberhan and Kiessling, 2014; Witts et al., 2016). Freshwater gastropods revealed a lower proportion of extinction than that observed in marine environments, probably because of differences in lifestyle, such as the type of reproduction and life cycle (Neubauer and Georgopoulou, 2021). For example, *H. dongdawusuensis* survived the extinction event in the Songliao Basin; it is a member of the Hygrophila, a usually annual freshwater species with a 1-year life cycle (Pyron and Brown, 2015). Their higher reproductive rates and shorter life cycles, alongside some ability to survive desiccation, help them survive in ephemeral environments (e.g., Brown et al., 1998). On the basis of an analysis of a data set of European freshwater gastropods over the last 23 million years, Neubauer and Georgopoulou (2021) showed that Hygrophila were more likely to survive extinction events. Feeding habits may also have been linked to survival likelihood. Detrital feeders appear to experience low extinction rates, both in marine and freshwater environments. Ampullariids (related to *M. cf. nanxiongensis* from the Songliao Basin) are herbivores and detritivores, mostly feeding on aquatic vegetation, algae and detritus, whereas planorbids (related to Planorbidae gen. et sp. indet. and *H. dongdawusuensis* at Songliao) generally ingest detritus (Dillon, 2000). Therefore, polyphagous and detrital feeders in freshwater settings had a greater potential for survival across K/Pg boundary perturbations.

Ancient lakes have existed continuously for over 100,000 years and have long been recognised as evolutionary theatres and hot

spots of endemism. Evolution of morphologically often highly diverse species flocks makes fossils of special importance in extant and fossil lakes (Gorthner and Meier-Brook, 1985; Gorthner, 1992; Albrecht et al., 2006). Gorthner (1992) indicated that high selective pressure was common in ephemeral habitats, resulting in stable morphologies, while low selective pressure prevailed in long-lived settings, resulting in unstable morphologies. The evolution of gastropod species, including such long-ranging species as *V. jiaolaiensis*, *T.? sp. 1*, *T.? sp. 2* and *Z. sp.* (Figs 5, 6) from the mid-upper Campanian and Maastrichtian in the Songliao Basin, was relatively steady as far as morphology is concerned, probably suggesting high selective pressure in habitats of the Songliao Basin.

6. Conclusions

The gastropod fauna comprises nine species, including four indeterminate ones and one unidentified genus and species. *Hydrobia? datangensis*, *V. jiaolaiensis*, *T.? sp. 1*, *T.? sp. 2*, *V. shakengensis*, *M. cf. nanxiongensis* and *Helisoma dongdawusuensis* are widely distributed in lacustrine basins in China and can be used for intracontinental correlations. Some species found in the Songliao Basin had a more extensive stratigraphical range. For instance, *Hydrobia? datangensis* is also known from the mid-upper Campanian, and *V. jiaolaiensis* and *T.? sp. 2* are known to extend upwards into the Danian in the Songliao Basin. The gastropod fauna experienced a minor extinction across the K/Pg boundary in east and north-east China, probably because of their higher reproductive rates, shorter life cycles and detritus feeding habits.

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