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SPECIALTY SECTION This article was submitted to Paleontology, a section of the journal Frontiers in Earth Science

RECEIVED 20 December 2022 ACCEPTED 08 February 2023 PUBLISHED 20 February 2023

CITATION

Wang B, Zhang Z-Q, Wang Y-Q, Li Q, Bai B, Liu Y, Mao F-Y, Wang H-B, Wang J, Gong Y-X, Dong L-P, Wang L-H, Ma H-D, Xu R-C and Wang X-Y (2023), Lithostratigraphy of a long, fossiliferous Oligocene sequence: Revisiting Saint Jacques, Nei Mongol, China. *Front. Earth Sci.* 11:1127964. doi: 10.3389/feart.2023.1127964

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Lithostratigraphy of a long, fossiliferous Oligocene sequence: Revisiting Saint Jacques, Nei Mongol, China

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For a hundred years the Saint Jacques area has been known to produce rich Oligocene vertebrate fossils, yet only a handful of previous studies have focused on this area. Since 2010, we have conducted 12 field expeditions to Saint Jacques, and here we report findings from our paleontological excavations and stratigraphical investigations. Twenty-two fossiliferous blocks across the area are recognized and a chronostratigraphic framework has been established to aid fossil collection. Fossil-mammal materials have been recovered in situ from 1635 localities and additionally from surface sediments. Fossiliferous blocks in the area are correlated by lithological similarity and lateral tracing. Lithologically, the area is mainly composed of reddish silty mudstone and muddy siltstone, with three distinctive layers of grayish white sandstone. The measured composite stratigraphic column spans 239 meters and are divided into 12 lithostratigraphic units. Contrary to previous knowledge that Saint Jacques contains two Oligocene mammalian assemblages, our preliminary biostratigraphic analysis of small mammals shows that the area documents successive faunal transition from the Eocene to possibly the early Miocene. The hyracodontid perissodactyl Ardynia, the ctenodactyloid rodent Gobiomys, and the basal Glires Gomphos from the bottom litho-units imply the presence of the Eocene–Oligocene boundary, while small mammal assemblage of the top units is similar to Miocene faunas in northern China and Mongolia. Thus, rock strata in Saint Jacques likely span the Eocene through the early Miocene, bracketing an entire Oligocene sequence within. In sum, our re-exploration of Saint Jacques has greatly expanded the chronostratigraphic and taxonomic coverage of the mammalian fossil collection from this area. This long, successive Oligocene sequence makes an important record for studying the Eocene-Oligocene Transition. Further study in this area will contribute to a range of paleontological and paleoenvironmental questions.

KEYWORDS

Nei Mongol, lithostratigaphy, Saint Jacques, Eocene-Oligocene boundary, Oligocene-Miocene boundary, mammals

Introduction

The Oligocene epoch is a transitional time period marked by the most striking climate change in the Cenozoic from greenhouse to icehouse conditions, mainly evidenced by marine records (Zachos et al., 2001; Coxall et al., 2005; Eldrett et al., 2009; Westerhold et al., 2020) but less terrestrial records (Dupont-Nivet et al., 2007; Hren et al., 2013). This change in global climate is likely associated with the profound shifts observed in continental faunal and floral compositions (e.g., Zhang et al., 2012; Sun et al., 2014). The continental interior of Asia has been a focal region for studying faunal turnovers across the Eocene–Oligocene boundary (e.g., Meng and McKenna, 1998; Kraatz and Geisler, 2010). To better understand the response of land mammals to significant global and regional climatic changes, long sequences of terrestrial sediments with successive fossil records and precise stratigraphic calibration are pivotal.

Saint Jacques is one of the classic Oligocene fossil sites of Asia. Sitting on the right bank of the Yellow River near the town of Balagong, Hanggin Banner, Ordos City, Nei Mongol Autonomous Region, China, the namesake of the fossiliferous area is in fact a small town across the Yellow River in Dengkou County, Bayannur City (Figures 1A,B). Although known for its rich vertebrate fossils for nearly a century, detailed accounts on the lithology of the Saint Jacques area are still lacking, hindering finer divisions of the depositional sequence and fossil assemblages.

Geological setting

Located in the northwestern margin of the Ordos block, the study area is bounded by the Jilantai Basin to the west, Hetao Basin to the north, and Yinchuan Basin to the south. Cenozoic strata are well exposed in the gullies along the Yellow River, from Balagong area in the north to Qianlishan area in the south (Wang, 1987). Our preliminary exploration in the region finds no exposure of Cenozoic strata superimposed with Mesozoic strata. In the Qianlishan area, the Cenozoic strata overlie the Cambrian strata by faults. The earliest Cenozoic strata in this area is possibly Early-Middle Eocene, as evidenced by our findings of Gomphos fossil from Saint Jacques. Late Eocene to Oligocene strata are superimposed by Neogene strata. Quaternary terrace sediments of the Yellow River cover most of the highland. Major faults in the Saint Jacques area cut through the Eocene, Oligocene, and Neogene strata, revealing that tectonic movements were active during late Cenozoic period, as studied by Shi et al. (2020) in their review of the neotectonics around the Ordos block.

History of research

Vertebrate fossils were first discovered in the Saint Jacques area by French paleontologists Pierre Teilhard de Chardin and Emile Licent while exploring along the Yellow River in 1923 (Teilhard de Chardin and Licent, 1924a, 1924b). They initially considered the site Pliocene in age, but soon revised it to the Oligocene based on the occurrence of *Paraceratherium* (Teilhard de Chardin and Licent, 1924c). Later, the mammalian fossils from Saint Jacques were reported in detail by Teilhard de Chardin, (1926). In the decades to follow, this area was rarely investigated except for a short visit by the Sino-Soviet Paleontological Expedition in 1959 (Chow and Rozhdestvensky, 1960). In 1977 and 1978, more extensive explorations by the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) were carried out, revealing a greater exposure of fossiliferous area than previously recognized (Wang, 1987). However, further work on its geology was hampered by its complicated structure. Wang (1987) noted that "it [was] difficult to define a formal lithostratigraphic unit based on beds exposed in Saint-Jacques area" (p.45). Based on similarity in lithology and assemblage of mammal fossils, the beds in Saint Jacques were thought to be equivalent to the lower member of the Wulanbulage Formation in Qianlishan district (Wang, 1987). Further investigation on the mammal fossil have led subsequent authors to recognize two local faunas from different horizons at Saint Jacques, one from early Oligocene and the other possibly late Oligocene (Wang, 1987; Wang and Emry, 1991; Wang and Qiu, 2003). The faunas in Saint Jacques are primarily composed of small mammals, especially ctenodactyloid rodents, although several species of ungulates and carnivores are also present (Meng and McKenna, 1998; Wang and Qiu, 2003).

For over a decade now, a new team of IVPP researchers have been conducting field explorations back in the Saint Jacques area and have collected abundant fossil-mammal materials from different blocks and stratigraphic levels. New specimens of the carnivore *Palaeogale sectoria*, the hyracodontid *Ardynia*, and the lagomorph *Ordolagus* have been recently reported (Wang and Zhang, 2015; Bai et al., 2018; Angelone and Zhang, 2021), and studies on other groups are still underway.

In this study, we present the first detailed description of the lithology of the Saint-Jacques depositional sequence, along with a preliminary list of identified small mammals based on discoveries accumulated over 12 field seasons. Stratigraphical correlation of sections across the area provides a means for age comparison between fossils collected from different fault blocks. Our fine lithological divisions of this long sequence, coupled with abundant fossil material from extensive field surveys, allow for an analysis of faunal succession with improved temporal resolution. Although Saint Jacques deposits have long been considered to be exclusively Oligocene, we show that the area has well exposed sections with rich fossils that document successive faunal turnover from the Eocene to the Miocene, bracketing the entire Oligocene sequence within.

Methods

We carried out annual field expeditions to Saint Jacques in 2010 through 2022, with a gap year in 2016. Major faults in the area have previously hampered precise lithostratigraphical and biostratigraphical correlation in the past. Therefore, for the convenience of stratigraphical investigations and to avoid mixing faunal compositions across the faulted area, we divided the area into 22 fossiliferous blocks. Each block contains geographically and stratigraphically continuous exposure of beds bounded either by major faults or by topographic features. Blocks are divided into varied numbers of stratigraphic layers. Divisions are based on

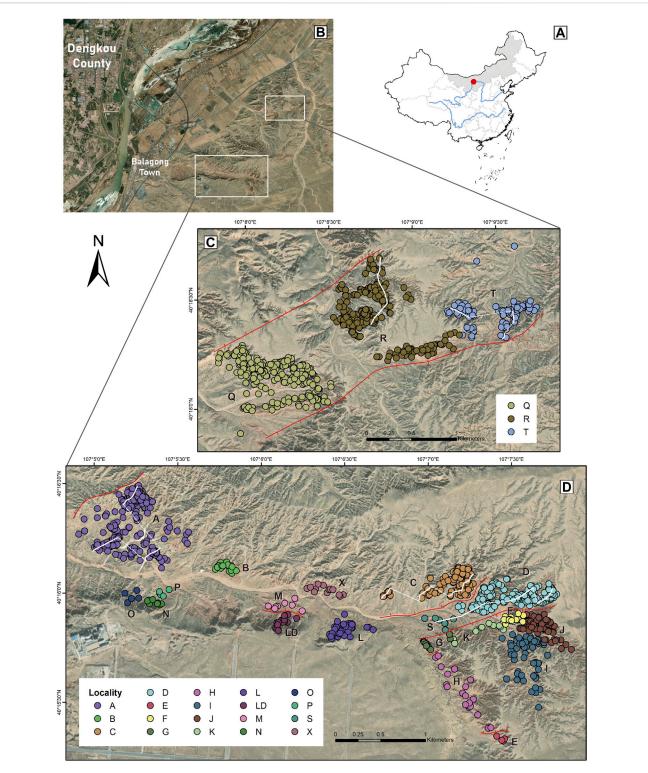


FIGURE 1

Location of Saint Jacques and its fossil localities. (A) Map of China, showing the location of Saint Jacques (red circle) in Nei Mongol (gray area). (B) The Saint Jacques fossiliferous area is near the town of Balagong, across the Yellow River from Dengkou County. Fossil localities are densely distributed in (C) Sanshenggongbei and (D) Langhaogou. White lines in (C) and (D): measured stratigraphic sections. Red lines: faults.

changes in particle size and sediment color, and they are ordered from bottom to top. For example, the strata exposed in block A are divided into eight layers, referred to as A1 (bottom) through A8 (top). We recorded fossil occurrences by their stratigraphic layers in their respective blocks, then we correlated facies across blocks by similarity in lithology.

10.3389/feart.2023.1127964

TABLE 1 Stratigraphic levels of selected small mammals identified from Saint Jacques.

	Taxon	Eocene			Oligocene								ne
		L1 S1 LD1	L2 S2 LD2	D1 Q1 T1	R2 Q2 H1 D3 T2+3	R3 Q3 J2 D4 T4	A3 R4 Q4 J5 D5 T5	A4 D6 Q5+6+7 R5+6+7	A5 C5 Q8 R8	A6 C6 R9	A7 C7 R10	C8+9	C10
Erinaceidae	Amphechinus								\checkmark				
	Palaeoscaptor						\checkmark	\checkmark	\checkmark				
Changlelestidae	Zaraalestes			\checkmark			\checkmark						
Ochotonidae	Sinolagomys												\checkmark
	Sinolagomys ulunguensis										\checkmark	\checkmark	
	Sinolagomys cf. major										\checkmark	\checkmark	
	Sinolagomys cf. kansuensis										\checkmark	\checkmark	
	Sinolagomys cf. pachygnathus										\checkmark	\checkmark	
	Sinolagomys pachygnathus										\checkmark		
	Sinolagomys major										\checkmark		
	Sinolagomys kansuensis									\checkmark	\checkmark	\checkmark	
	cf. Sinolagomys								\checkmark				
	cf. Desmatolagus							\checkmark	\checkmark				
	Desmatolagus cf. pusillus							\checkmark	\checkmark				
	Desmatolagus pusillus						\checkmark	\checkmark	\checkmark				
	Desmatolagus gobiensis				\checkmark	\checkmark	\checkmark	\checkmark					
	Desmatolagus cf. vetustus				\checkmark	\checkmark	\checkmark						
	Desmatolagus vetustus				\checkmark								
	Desmatolagus cf. gobiensis			\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark				
	Desmatolagus	\checkmark	\checkmark		\checkmark		\checkmark	\checkmark	\checkmark	\checkmark			
Leporidae	Ordolagus teilhardi						\checkmark		\checkmark				

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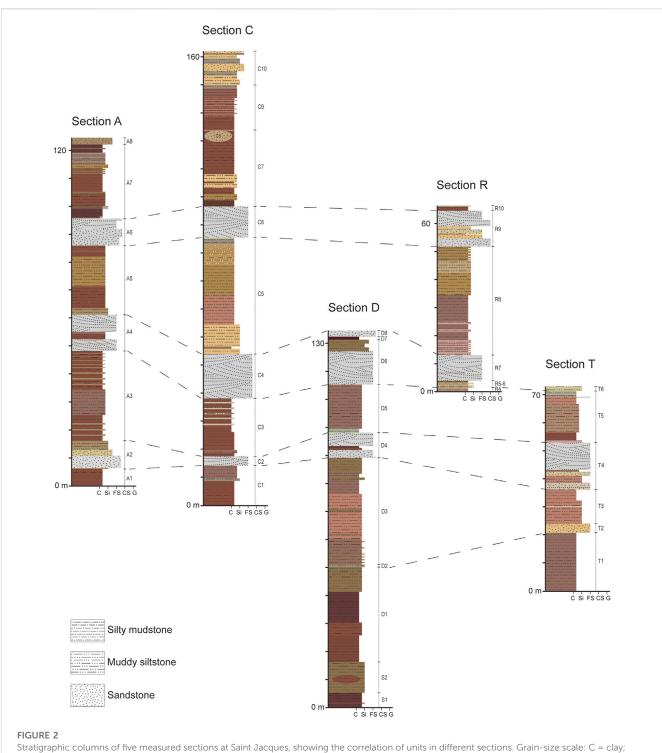
TABLE 1 (Continued) Stratigraphic levels of selected small mammals identified from Saint Jacques.

	Taxon	Eocene			Oligocene								Miocene	
		L1 S1 LD1	L2 S2 LD2	D1 Q1 T1	R2 Q2 H1 D3 T2+3	R3 Q3 J2 D4 T4	A3 R4 Q4 J5 D5 T5	A4 D6 Q5+6+7 R5+6+7	A5 C5 Q8 R8	A6 C6 R9	A7 C7 R10	C8+9	C10	
	Ordolagus			\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark					
	Leporidae indet.		\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark						
Cricetidae	Ayakozomys													
	Tachyoryctoides											\checkmark		
	Tachyoryctoides (small)									\checkmark				
	Tachyoryctoides kokonorensis									\checkmark				
	Eucricetodon youngi										\checkmark			
	Eucricetodon jilantaiensis							\checkmark	\checkmark				_	
	Eucricetodon asiaticus							\checkmark	\checkmark					
	Eucricetodon				\checkmark	\checkmark	\checkmark	\checkmark	\checkmark		\checkmark			
	Cricetops dormitor				\checkmark	\checkmark	\checkmark	\checkmark						
	Cricetops minor				\checkmark									
	Selenomys mimicus				\checkmark	\checkmark	\checkmark							
Ctenodactylidae	Prodistylomys												\checkmark	
	Yindirtemys suni													
	Yindirtemys cf. deflexus									\checkmark				
	Yindirtemys deflexus								\checkmark					
	Yindirtemys grangeri								\checkmark					
	Yindirtemys cf. grangeri								\checkmark					
	Yindirtemys							\checkmark	\checkmark	\checkmark	\checkmark			
	Bounomys ulantatalensis								\checkmark					
	Bounomys cf. ulantatalensis							\checkmark	\checkmark					
	Bounomys bohlini						\checkmark							

(Continued on following page)

TABLE 1 (Continued) Stratigraphic levels of selected small mammals identified from Saint Jacques.

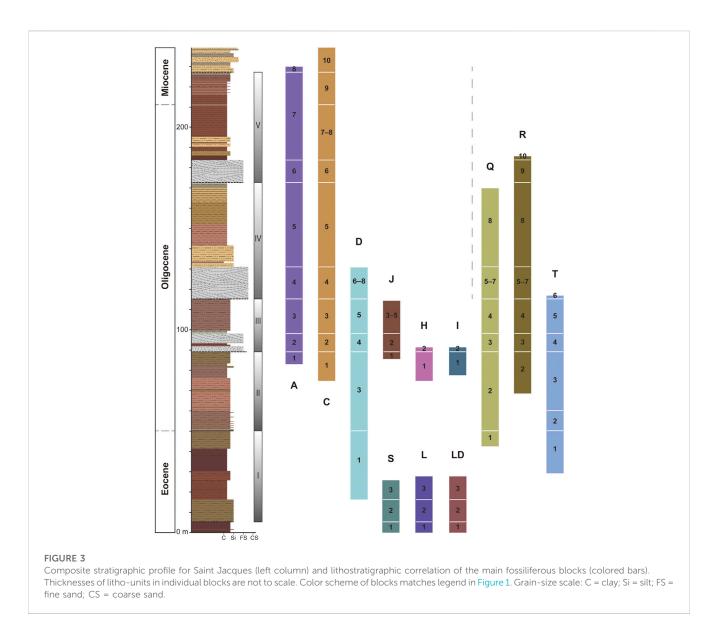
	Taxon	Eocene			Oligocene								Miocene		
		L1 S1 LD1	L2 S2 LD2	D1 Q1 T1	R2 Q2 H1 D3 T2+3	R3 Q3 J2 D4 T4	A3 R4 Q4 J5 D5 T5	A4 D6 Q5+6+7 R5+6+7	A5 C5 Q8 R8	A6 C6 R9	A7 C7 R10	C8+9	C10		
	Bounomys cf. bohlini					\checkmark	\checkmark								
	Tataromys sigmodon							\checkmark	\checkmark						
	Tataromys plicidens							\checkmark	\checkmark						
	Tataromys						\checkmark	\checkmark	\checkmark						
	Tataromys minor					\checkmark	\checkmark	\checkmark	\checkmark						
	Tataromys cf. minor			\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark						
	Karakoromys				\checkmark	\checkmark	\checkmark								
	Karakoromys decessus			\checkmark	\checkmark	\checkmark	\checkmark								
	Karakoromys cf. decessus		\checkmark	\checkmark	\checkmark	\checkmark	\checkmark								
Aplodontidae	Promeniscomys							\checkmark							
Cylindrodontidae	Anomoemys					\checkmark	\checkmark	\checkmark	\checkmark						
	Anomoemys lohiculus					\checkmark	\checkmark	\checkmark							
	Ardynomys				\checkmark										
Tsaganomyidae	Tsaganomys altaicus						\checkmark	\checkmark	\checkmark						
	Tsaganomys				\checkmark	\checkmark	\checkmark	\checkmark	\checkmark		\checkmark				
	Cyclomylus				\checkmark	\checkmark	\checkmark	\checkmark							
	Cyclomylus lohensis				\checkmark	\checkmark		\checkmark							
Dipodidae	Heosminthus				\checkmark										
	Parasminthus					\checkmark	\checkmark	\checkmark	\checkmark						
	cf. Parasminthus		\checkmark	\checkmark	\checkmark	\checkmark									
	Allosminthus		\checkmark	\checkmark	\checkmark	\checkmark	\checkmark								
Gobiomyidae	Gobiomys		\checkmark												



Si = silt; FS = fine sand; CS = coarse sand; G = gravel.

Fossil collection started in 2011. Two collection methods are used: in situ collecting and surface collecting. When fossils are found in situ, we record the coordinates and elevation of the location and consider it a fossil locality. A locality is typically an area of a few meters across or less. Each locality is tied to a block and a stratigraphic level. Fossils that have been washed out from the place of burial and transported for a short distance were also collected from the surface. In these cases, we can

usually still determine the lithological layer that the fossils are from, even though we cannot pinpoint an exact location. During each field season, we sorted through our findings daily and made field catalogue. Further identification and research were conducted after returning from the field. In order to minimize preservation bias, we made efforts to collect more thoroughly from blocks and layers in which fossils were not as abundant.



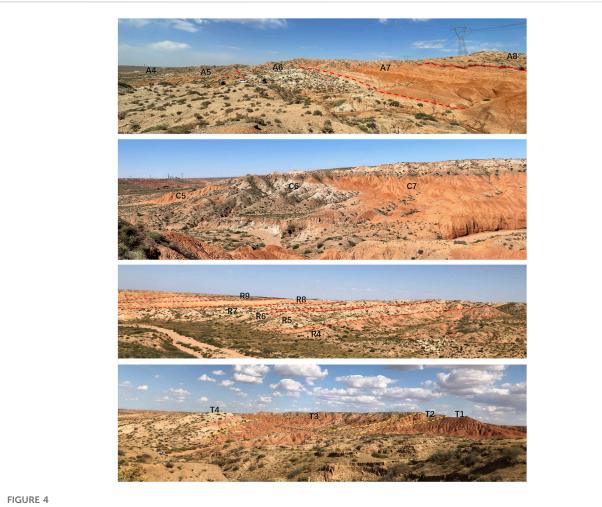
We measured five stratigraphic sections using a Brunton compass, a tape measure, and Jacob's staff. Rock strata in Saint Jacques gently dip north-northeast at 5-20°. Because the dip of the beds is generally low, we measured sections primarily with a tape measure and then corrected for dip. Where the exposure is suitable, we used Jacob's staff to measure the thicknesses of beds directly. The measured sections combined encompass nearly the entire stratigraphic sequence exposed in Saint Jacques. Three of the five measured sections are in Langhaogou, the E-W trending gully along which previous discoveries were made. The other two sections are located in what we refer to as Sanshenggongbei, approximately 4 km to the northeast of Langhaogou, a fossiliferous area that we newly discovered. The measured sections span about 100 m in elevation, close to the total topographic relief in Langhaogou. We mapped the locations of stratigraphic sections using a GPS device and described lithologies in detail as we measured sections. We recognized correlations of measured and unmeasured sections on the basis of the lateral and vertical relationships of facies sharing similar lithological properties and fossil evidence.

Results

Across the 22 fossiliferous blocks in Saint Jacques, we have documented 1635 fossil localities (Figure 1). The Sanshenggongbei area is divided into blocks Q, R, and T, which all have densely packed localities (Figure 1C). The other 19 blocks are distributed in Langhaogou, where more faults are present. Here, blocks A, C, D, J, and I have the most number of localities. Older strata in Langhaogou are generally in more southerly located blocks.

Lithostratigraphic correlation and classification

The five measured lithostratigraphic sequences are in blocks A, C, S–D, R, and T (Figure 2). Blocks S and D are stratigraphically continuous, only separated by a gully, and S3 partially overlaps with the lower part of D1. Fossiliferous layers are continuously numbered, except in two cases. D2 is a band of light colored



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Outcrop photographs of selected measured sections.
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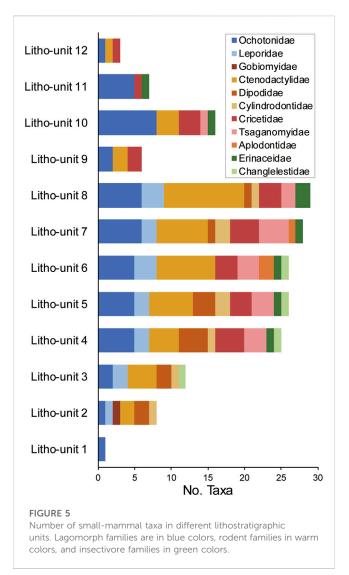
siltstone sandwiched by reddish beds below and above. Vertebrate fossils are rare in D2; this layer is primarily used to separate D3 from D1, thereby achieving a higher stratigraphic resolution. The other exception is C8, a large lens of channel sandstone that cuts into the upper part of C7. Blocks A and C are largely comparable in lithology, only block C is thicker and includes more strata at the top. A5 and C5 have a distinctive brownish yellow color that differentiates this layer from strata below and above. This color is also observed in R8 in northern Saint Jacques. A7 and C7 are characterized by multiple bands of reddish mudstone (Figure 4). Additional fossiliferous areas that have been correlated to the measured sections similarity in lithology and fossil composition include blocks H, I, J, L, LD, and Q (Figure 3). Block E, representing the lower-most strata in this area, produced some remains of Gomphos but can not be correlated with any other blocks, and it is here excluded from the composite profile. Altogether, 12 lithostratigraphic units are recognized in ascending order:

Litho-unit 1 (S1, L1, LD1): Dark red muddy siltstone. The sedimentary structure is uniform with no visible lamination. This unit is rich in turtle fossils, while mammalian fossils are scarce. No underlying strata are exposed in block S or block L.

Litho-unit 2 (S2, L2, LD2): Brownish yellow fine sandstone interbedded with variably thick lenses of siltstone mixed with dark red muddy pebbles, carbonate nodules, and coarse sand. Cross bedding and lamination are developed in this unit. This unit includes the earliest occurrences of Leporidae, Ctenodactylidae, and Dipodidae in the sequence and the only occurrence of *Gobiomys*.

Litho-unit 3 (D1, S3, T1, L3, Q1): Thick layer of brownish red muddy siltstone to dark red silty mudstone. The color becomes lighter upwards with increasing amount of muddy siltstone. Massive, with no visible lamination. Fossils are sporadically discovered without any particularly rich locality. *Karakoromys decessus* and *Ordolagus* first occur in this unit.

Litho-unit 4 (A1, C1, D3, T2+3, R2, Q2, J1, H1, I1): The basal part of this unit is represented by thin layers of light brown siltstone with lamination; the upper part is composed of massive, structureless lighter brownish red muddy siltstone and darker brownish red silty mudstone. This unit contains well-preserved small mammal fossils, including relatively complete skulls and jaws. Species richness is markedly higher than in the underlying unit. *Cricetops, Selenomys, Cyclomylus* and other taxa begin to appear in the sequence.



Litho-unit 5 (A2, C2, D4, T4, R3, Q3, J2, H2, I2): Grayish white fine-to medium-grained sandstone with large-scale cross bedding, interbedded with lenses of coarser-grained sands with carbonate nodules or muddy pebbles. Vertebrate fossils are rich, including fish, frog, salamander, turtles, birds, and mammals. The mammalian fauna is similar to that of litho-unit 4.

Litho-unit 6 (A3, C3, D5, R4, T5, Q4, J3+4+5): Pale brownish red muddy siltstone or silty mudstone. Massive and structureless. Fossils are sporadically distributed. In block Q, a large lens of siltstone and fine sandstone is observed within the Q4; the lens is pinched off eastwards. *Desmatolagus*, *Tataromys*, and *Karakoromys* are abundant.

Litho-unit 7 (A4, C4, D6+7+8, R5+6+7, T6, Q5+6+7): Grayish white fine-to medium-grained sandstone with large-scale cross bedding. The reddish silty mudstone bed in between the sandstone varies in thickness from 0 to 2–3 m in different blocks. Fossils are rich in the sandstone. *Karakoromys* disappears from this unit.

Litho-unit 8 (A5, C5, Q8, R8): Thick layer of yellowish brown muddy siltstone and silty mudstone, massive and structureless, with

manganese nodules. Small mammals are sporadically distributed in this unit. *Sinolagomys* first appear from the upper part of this unit.

Litho-unit 9 (A6, C6, R9): Grayish white fine-to coarse-grained sandstone with large-scale cross bedding. Large mammalian fossils are rich, including skulls and postcranial of giant rhinos. *Tachyoryctoides* are first documented from this unit.

Litho-unit 10 (A7, C7+8, R10): Massive brownish red silty mudstone interbedded with bands of reddish mudstone. C8 is composed of fine or coarse sandstone, pinched off westwards, thickening eastwards, and punctuated by a fault on the west side. Fossils of *Sinolagomys* and large-sized *Yindirtemys* are abundant in this unit.

Litho-unit 11 (C9): Alternating light brownish red muddy siltstone and dark brown silty mudstone. *Sinolagomys* remains abundant while *Yindirtemys* disappears in this unit.

Litho-unit 12 (C10): Pale orange fine-grained sandstone, with light brown muddy siltstone in the upper part. Small-sized *Sinolagomys*, *Prodistylomys*, and some insectivores are documented in this unit.

We created a composite stratigraphic profile of Saint Jacques using measurements from blocks S, D, and C, which combined encompass the longest temporal and lithostratigraphic records (Figure 4). The composite section spans 239 m. Particle size of the sediments is generally small. Aside from the three layers of fine- to medium-grained sandstone, the sequence is mainly composed of reddish silty mudstone and muddy siltstone. Rock color is generally darker towards the bottom and lighter towards the top. Section S through the bottom of section D (litho-units 1–3) is marked by dark red silty mudstone and moderate brown muddy siltstone. Several layers of pale orange yellow muddy siltstone appear in the upper half of the sequence.

Small mammals in stratigraphic context

Fossil mammals are collected from litho-unit 1 through litho-unit 11. With a preliminary examination of the small mammals from these units, we have identified 65 taxa belonging in eleven families of small mammals, including seven families of rodents (Aplodontidae, Ctenodactylidae, Cricetidae, Cylindrodontidae, Dipodidae, Gobiomyidae, Tsaganomyidae), two families of lagomorphs (Leporidae and Ochotonidae), and two families of insectivores (Changlelestidae and Erinaceidae) (Table 1). Additionally, the basal Glires *Gomphos* has been found in block E, putting it to stratigraphically below litho-unit 1.

Taxonomic richness of small mammals increases progressively from litho-unit 1 to litho-unit 8 and then sharply declines in higher units (Figure 5). The greatest increase occurs between litho-units 3 and 4. This pattern is a result of a step increase in the number of ochotonid taxa as well as the appearance of cricetids, tsaganomyids, and erinaceids in litho-unit 4. Ctenodactylid richness increases relatively steadily across these units. Among the rodents, the aplodontids appear the latest in the sequences and have the shortest duration—they are only found in litho-units 6 and 7. An abrupt drop in taxonomic richness is observed in litho-unit 9. The abundance of relatively complete large-mammal fossils in this unit suggests that flow velocity was high and not ideal for the deposition of small-mammal material. Therefore, the decline in the richness of small mammals may reflect, at least in part, the condition of preservation rather than a true ecological signal. Faunal turnover appears to be gradual across the sequence (Table 1). Even though the taxonomic richness remains relatively stable during the deposition of litho-unit 4 through litho-unit 8, the small-mammal fauna was not static. Rather, a stepwise transition in the taxonomic composition is documented, especially for the ochotonids, ctenodactylids, and cricetids.

Discussion

Our re-exploration of the Saint Jacques area has revealed developed terrestrial sediments with rich fossils. The significance of this work is several fold. First, we have recovered fossils from a larger area at Saint Jacques than previously known. In addition to the localities in Langhaogou (roughly equivalent to the former Saint Jacques site), we discovered a fossiliferous area to the northeast that was unknown before. These areas have been intensively surveyed over 12 field seasons, as shown by the high density of new fossil localities (Figure 1). Our continuous field expeditions have yielded thousands of pieces of fossil-mammal material, all tied to specific stratigraphic units. Comparing to the existing fauna lists of Saint Jacques (e.g., Meng and McKenna, 1998; Wang and Qiu, 2003), a number of taxa are recorded for the first time, including Sinolagomys ulunguensis, S. pachygnathus, Yindirtemys suni, Yindirtemys grangeri, Gobiomys, Tachyoryctoides kokonorensis, Eucricetodon jilantaiensis, Cyclomylus lohiculus, Allosminthus, Parasminthus, Prodistylomys, and Ayakozomys. Our thorough investigation of the field area thus reveals a fuller picture of the mammalian assemblages of Saint Jacques.

Second, we conducted the first detailed study on the lithological subdivision of Saint Jacques strata. This provided a lithological context for the fossiliferous sequence and allowed for the correlation of facies across blocks. The establishment of this chronostratigraphic framework formed the basis for documenting and understanding the deposition of fossil materials, with improved temporal resolution. We recognize 12 lithostratigraphic units in Saint Jacques, and mammalian fossils have been collected from all of them (Table 1; Figure 5). Additional material (i.e., *Gomphos*) has been found in even older strata (block E) in the area. This fine division of stratigraphic units allows for analyses of faunal transition in smaller time bins and with reduced errors introduced by time averaging.

Third, a preliminary examination of the rich small-mammal materials (especially rodents and lagomorphs) reveals that faunal assemblages in Saint Jacques show successive evolutionary stages. Most taxa occur in stratigraphically continuous litho-units (Table 1), documenting the pattern of faunal succession. No prominent hiatus in the depositional sequence has been observed. This record, therefore, provides an excellent opportunity for further studying the faunal composition of continental Asia from the late Eocene through the Oligocene. Wasiljeff et al. (2020) recently provided better age constraint on the Ulantatal sequence in Nei Mongol and demonstrated that major faunal turnover preceded (instead of precisely at) the Eocene-Oligocene (E-O) boundary. Research on the magnetostratigraphy of the Saint Jacques sequence is still underway. A deeper look into the timing and pattern of faunal transition in Saint Jacques will help elucidate the potential complexity in terrestrial faunal responses to broad-scale changes in climate and environment.

Prior to our revisit of Saint Jacques in 2010, the common understanding of its paleontology was that the area contained two local faunas, one of early Oligocene age and the other late Oligocene (e.g., Wang and Qiu, 2003). In contrast, our work now suggests that the sedimentary strata in Saint Jacques likely span the Eocene through the early Miocene, bracketing a long, successive Oligocene sequence within. Bai et al. (2018) reported A. praecox from L2 (litho-unit 2), correlating this unit to the Ergilian Asian Land Mammal Age (latest Eocene). In line with this result, we have identified Gobiomys in L2 (litho-unit 2). This rodent genus is known exclusively from the Eocene of Nei Mongol (Wang, 2001; Li et al., 2022). The presence of Ardynia praecox and Gobiomys shows that the lower Saint Jacques sequence extends into the Eocene. Another taxon that sheds light on the E-O boundary is Ardynomys, a primitive cylindrodontids previously known from the late Eocene of Nei Mongol (Wang and Wang, 1991; Wang and Meng, 2009; Gomes Rodrigues et al., 2014; Wasiljeff et al., 2020; Wasiljeff and Zhang, 2022), the late Eocene to the early Oligocene of Mongolia (Dashzeveg, 1996; Daxner-Höck et al., 2017), and the late Eocene of North America (Wood, 1970; 1974; Korth, 1992). In Saint Jacques, Ardynomys occurs in litho-units 3 and 4. Considering the occurrence of other Oligocene taxa (e.g., Desmatolagus gobiensis, Eucricetodon, Cricetops, Selenomys mimicus, Tsaganomys) in litho-unit 4, the epoch boundary is most likely within litho-unit 3 at Saint Jacques. Taxa in the top layers at Saint Jacques show similarity with late Oligocene to early Miocene faunas in northern China and Mongolia. For example, T. kokonorensis, Sinolagomys pachygnathus, Eucricetodon youngi, and Y. suni are representatives of the Xiejian faunas of China, considered to be the early Miocene in age (Li and Qiu, 1980; Qiu and Qiu, 1995; Qiu et al., 2001; Wang and Qiu, 2012; Qiu et al., 2013). In Saint Jacques, these species occur in litho-units 10 and 11. T. kokonorensis (litho-unit 10), Y. suni (litho-unit 11), Prodistylomys (litho-unit 12), and Ayakozomys (litho-unit 12) occur in the Valley of Lakes, Mongolia during the latest Oligocene to the early Miocene (Daxner-Höck et al., 2015; 2017; Harzhauser et al., 2017).

To conclude, our re-investigation of Saint Jacques has greatly expanded the chronostratigraphic and taxonomic coverage of the mammalian fossil collection from this area. Our preliminary biostratigraphic analysis of small mammals shows that the area preserves faunal succession from the late Eocene to the early Miocene, making it an important record for studying mammalian faunal turnovers during both the Eocene–Oligocene and the Oligocene–Miocene transitions.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding authors.

Author contributions

Data synthesis and manuscript preparation: BW, Z-QZ, and Y-QW. All authors participated in field work and data collection.

Funding

Field work was supported by the Strategic Priority Research Program of Chinese Academy of Sciences (XDB26000000), the National Natural Science Foundation of China (41472003), and the Special Fund for Fossil Excavation and Preparation of the Chinese Academy of Sciences.

Acknowledgments

We are grateful to many individuals for their field assistance over the years: Wei Zhou, Shi-Jie Li, Qi Li, Yong-Xing Wang, Yong-Fu Wang, Xin-Yue Zhang, Ping Wang, and others. We would also like to thank the reviewers for their constructive feedback on the manuscript.

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