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Snail diversity and paleoenvironment of the 12-meter-thick freshwater gastropod bed, Middle Miocene, Mae Moh Basin, Thailand

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ABSTRACT: The purpose of this study is to investigate snail fossils collected from a 12-m-thick freshwater gastropod bed of the Middle Miocene in the Mae Moh Basin, Northern Thailand, in order to investigate gastropod diversity, paleoecology, and paleoenvironment using stable isotope data. Gastropod individuals of 7,532 were analyzed, representing 3 families of freshwater snails (Viviparidae, Bithyniidae, and Planorbidae), indicating freshwater paleoenvironments such as ponds or lakes with intermittent river influx. *Bellamya* is the most dominant genus (62.75%), followed by *Bithynia* (28.92%), *Idiopoma* (7.08%), *Cipangopaludina* (0.76%), and *Mekongia* (0.50%), respectively. The stable isotopic analysis of *Bellamya* shells revealed $\delta^{13}C$ values ranging from 2.10‰ to 5.54‰ and $\delta^{18}O$ values from −2.99‰ to −6.89‰. The positive $\delta^{13}C$ values could result from dissolved inorganic carbon uptake from the dissolution of marine limestone surrounding the Mae Moh paleo-lake. The $\delta^{18}O$ values confirm that the gastropods inhabited a freshwater environment in a humid climate. The findings provide valuable insights into the Middle Miocene thick gastropod deposition.

KEYWORDS: freshwater snail, *Bellamya*, Cenozoic, climate change, paleoecology

INTRODUCTION

Mae Moh coal mine in the Mae Moh Basin, Lampang Province, Thailand, is the largest coal deposit in Southeast Asia and uses coal mainly in power plants. The mine is located 630 km north of Bangkok at 18°18′21″ N and 99°44′02″ E (Fig. S1A,B) [1]. Sedimentary rocks deposited in the Mae Moh Basin, namely the Mae Moh Group [2]. It mainly comprises lignite and claystone (Fig. S1C) with several Cenozoic fossils, including a thick gastropod bed deposited in the southern flank of the mine (Fig. S1D). The Mae Moh Group is subdivided into 3 formations from lower to upper, including the Huai King Formation, Na Khaem Formation, and Huai Luang Formation (Fig. S2A). The economic coal seams, K-, Q-, and J-Zones, are in the Na Khaem Formation [1].

The mine has yielded a diverse middle Miocene vertebrate fauna. Fossils of the Galericinae (Erinaceidae) include *Galerix rutlandae* and 2 species of *Lantanotherium*, representing their first discovery in Southeast Asia and providing evidence of faunal exchanges with South Asia [3]. The Carnivora assemblage features *Siamogale thailandica*, *Maemohcyon potisati*, *Vishnuonyx maemohensis*, *Pseudarctos*, *Siamictis* (a new genus of Asian palm civet), *Leptoplesictis peignei* (a mongoose), and an unidentified Feliformia [4]. The Viverridae include *Semigenetta thailandica* and *S. qiae*, representing a Southeast Asian clade with European origins, thriving in warm, humid, and wooded environments [5]. The first Bovidae fossils from Mae Moh include *Eotragus lampangensis*, *Eotragus* cf. *lampangensis*, and an indeterminate bovid, marking the first Southeast Asian record of *Eotragus* and suggesting a preference for ecotones between grassland and forest [6]. The proboscidean fauna consists of *Stegolophodon nasaiensis* and *S. praelatidens* dominate. The Mae Moh Gomphotherium shares affinities with *G. browni* from Indo-Pakistan [7]. The primates include *Tarsius* sp., *Tarsius sirindhornae*, *Siamoadapis maemohensis*, and rodents (*Prokanisamys* and *Neocometes* cf. *orientalis*), with a primitive deer *Stephanocemas* cf. *rucha* and a pig *Conohyus thailandicus* [8–10]. The K- and Q-Zone coals are the primary deposits of these fossils, and the beaver *Steneofiber siamensis* was found in the I-Zone coal in the Huai Luang Formation [11]. The fossil assemblages indicated the age of the Neogene. These findings enhance our understanding of Miocene faunal exchanges, paleoenvironmental conditions, and mammalian evolution in Southeast Asia.

Stable isotope analysis of tooth enamel from pigs, rhinoceros, and proboscideans from the K- and Q-Zones suggested that these animals lived in diverse habitats, ranging from woodlands to grassland, and consumed C_3 plants, such as trees, shrubs, and cool-season grasses, which use the C_3 carbon fixation pathway. They likely inhabited more humid environments and experienced a low-seasonal climate during the late Middle Miocene [12]. Magnetostratigraphic analyses have been extensively conducted in the Mae Moh Basin [13]. Paleomagnetic data indicate that the sediments of the Mae Moh Group were deposited between 11.6 and 14.2 million years ago (Myr). This time interval corresponds to the R-Zone (14.2–14.1 Myr), the Q- and K-Zones (13.4–13.2 Myr), the J-Zone (12.8–12.2 Myr), and the I-Zone (12.0–11.6 Myr) [13]. The paleoclimate and paleoenvironment interpretations based on palynological data suggested that the lower part of Mae Moh Group was deposited in a warm temperate climate and gradually transitioned to a tropical environment in the upper part, which aligns with the climatic change from the Oligocene to the Miocene [14]. Significant plant variation indicated that the Mae Moh Basin primarily consisted of deciduous-, evergreen-, and needle-leaved tree forests [14]. Stable carbon and oxygen isotopes of viviparid shells from the Q- and K-Zone coals reflected warmer conditions at high elevations or latitudes [15].

Freshwater gastropods are found commonly in coal seams and mudstones throughout the stratigraphic succession of the Mae Moh Basin. *Margarya* fossils from the I-Zone coal indicate deposition in a fluvial system with swampy areas, while *Melanoides* sp. and *M*. cf. *tuberculata* in the J-Zone point to a freshwater lake environment. In contrast, the *Bellamya*-Planorbidae-*Paludina* assemblage in the K-Zone reflects a swamp or shallow lake environment in a lacustrine setting [16]. Notably, the feature of a 12-m-thick gastropod bed is a part of paleoenvironment interpretation. The location of the gastropod bed is between the K-3 and K-4 Subzones on the southwestern flank of the coal mine (Fig. S1D). This bed predominantly contains viviparid gastropods, including *Bellamya corpospira* and *Bellamya lampangensis*, with minor occurrences of *Bithynia* [1]. Remarkably, this may represent the thickest documented freshwater shell bed globally [16]. Electron Spin Resonance (ESR) dating of the bed estimates its age at approximately 13.02 ± 1.03 Myr [17].

While many studies have explored the Mae Moh coal mine, few have specifically focused on the thick gastropod bed. This study investigates the 12-m-thick gastropod bed, concentrating on its gastropod diversity, paleoecology, and paleoenvironment, which remain poorly understood. The goal is to offer valuable insights into the thickest freshwater shell bed, highlighting the importance of this distinctive gastropod deposit.

Geological setting of the study area

Mae Moh Basin is approximately 16 km long and 7 km wide, more than 900 m thick of Cenozoic sediment deposited over the marine Triassic limestone, shale, and sandstone of the Lampang Group and overlain by Quaternary basalt and unconsolidated fluvial sediment (Fig. S1C) [18].

The Mae Moh Basin, including the Cenozoic basins in Thailand, was formed around 55–30 Ma due to rifting and tectonic extension driven by the Indian-Eurasian plate collision, which also created the Himalayas [19, 20]. Tectonic compression extruded Indochina and Northern Thailand [19, 20] (Fig. S1A). The Cenozoic sediments in the Mae Moh Group have been divided into 3 formations. Each of these formations has different lithology, sedimentary structures, degree of consolidation, and fossils [18, 21]. The succession from the lower to the upper formation is as follows (Fig. S2A):

The Huai King Formation represents the basal unit of the Mae Moh Basin, unconformably overlying the basement Lampang Group. Its thickness varies significantly, ranging from less than 15 m along the basin margins to approximately 150 m in the central basin. The formation comprises a fining-upward sequence of mudstone, siltstone, sandstone, conglomeratic sandstone, and conglomerate. It is characterized by a variegated color palette, including red, gray, green, yellow, blue, and purple hues. Calcrete formations are commonly observed within the unit, accompanied by localized occurrences of calcareous cement. Gastropod fossils have been identified in the lower portion of the Huai King Formation, particularly in exposures located in the southern part of the basin [18].

The Na Khaem Formation is characterized by the presence of 5 coal zones interbedded with semi-consolidated mudstone, with a thickness ranging from 250 to 400 m. This formation is rich in fossils, including gastropods, fish, ostracods, plant remains, and other vertebrate fossils. It is stratigraphically divided into 3 members: III, II, and I.

Member III ranges in thickness from 150 to 230 m and consists of gray to greenish-gray claystone and mudstone, interspersed with thin sub-bituminous coal layers. The prominent coal seams in this member include the R-Zone coal (2–6 m thick) and the underlying S-Zone coal (1–2 m thick). These beds exhibit lamination to thick planar bedding and are highly calcareous. The upper portion of Member III contains abundant gastropods, including *Brotia* and *Bellamya*, alongside fish remains, ostracods, and plant roots [18].

Member II hosts the most economically significant coal sequence and is subdivided into 3 units: the Q-Zone, Interburden, and K-Zone.

The Q-Zone has a total thickness of 25 to 30 m and consists of brittle, sub-bituminous coal ranging from black to brownish black. It is rich in diatoms, pyritized gastropods, Planorbidae mollusks, and plant remains. The coal seams within the Q-Zone are categorized into 4 distinct units, designated Q-1 through Q-4 [18].

The Interburden of the Na Khaem Formation comprises a 10 to 30 m thick sequence of claystone, varying in color from brown and brownish gray to gray, green, and greenish gray. These claystone beds exhibit laminated to thick planar bedding and contain lignite flakes, fish remains, plant roots, rare ostracods, and gastropods of the genus *Bellamya* [18].

The K-Zone is a fossiliferous coal sequence characterized by black to brownish black, brittle, and highly calcareous coal interbedded with light yellowish gray to gray silty claystone partings. This zone is 10 to 30 m thick but exhibits regional variability; in the northern and southern parts of the basin, the silty claystone partings are thicker and transition laterally into carbonaceous claystone. The K-Zone contains a diverse fossil comprising *Planorbis*, *Melanoides*, *Bellamya*, fish, turtles, and plant remains. The sub-coal beds within the K-Zone are designated as K-1 to K-4 coal seams.

The K-4 coal seam, the thinnest in the sequence, contains sparse mollusk fossils and is part of the Planorbidae Molluscan Zone, indicative of swamp and lake deposits. A 12-m-thick *Bellamya* and *Bithynia* fossil bed occurs between the K-3 and K-4 Subzones, situated along the southwestern margin of the Mae Moh coal pit. Planorbidae fossils are present in the K-3 and K-2 Subzones, with the K-2 Subzone additionally containing *Paludina* within carbonaceous claystone. In contrast, the K-1 Subzone lacks mollusk fossils, and its boundary with the overburdened claystone is defined by the presence of the *Melanoides* sp. cf. *M. tuberculata* Molluscan Zone [15]. This overburdened claystone subsequently transitions into the J-Zone. Sulfur isotopic analysis of pyrite within the Q-, K-, and the lower part of the J-Zones indicates that the sulfur originated from organic sources, suggesting deposition within a freshwater environment [22].

Member I forms the uppermost part of the Na Khaem Formation and comprises the Overburden and the J-Zone coal. The coal beds of the J-Zone are thin and hold limited economic significance. Stratigraphically, the J-Zone consists of gray to greenish-gray claystone and mudstone with occasional occurrences of siltstone. These sedimentary layers exhibit laminated to massive planar bedding and are highly calcareous. Certain sections frequently exhibit fine-grained pyrite spots. This zone hosts a rich fossil assemblage, including gastropods (*Melanoides*, *Physa*, and *Viviparus*), fish remains, ostracods, plant remains, and reptile skeletons. The J-Zone has a thickness ranging from 100 to 150 m and features 2 thin argillaceous layers, each less than 2 m thick, interspersed with thin coal seams designated as J-1 through J-6. Sulfur isotopic analysis from the middle portion of the J-Zone suggests a volcanic sulfur source. However, evidence of a marine incursion during coal deposition in the upper part of the zone indicates a shift in environmental conditions [22].

The Huai Luang Formation represents the uppermost stratigraphic unit of the Mae Moh Basin, comprising semi-consolidated to unconsolidated strata. This formation is predominantly red to brownish red with occasionally interbedded gray layers in certain areas. The primary lithologies include claystone, siltstone, and mudstone, with sandstone and conglomerate lenses present in the central part of the basin. The formation contains abundant gypsum, pyrite, plant roots, and flame structures. The thickness of the Huai Luang Formation varies considerably, ranging from less than 5 m to approximately 350 m. The I-Zone within this formation defines the *Margarya* Molluscan Zone, characterized by the presence of *Hyriopsis* and bivalves of the family Unionidae, as well as gastropods such as *Melanoides*, *Margarya*, and *Brotia* [16, 23].

MATERIALS AND METHODS

Sample collection

The 12-m-thick gastropod bed that deposited in between the K-3 and K-4 Subzones was subdivided into 17 sub-beds (designated as MM1 to MM17) based on color variation and the degree of shell preservation and bed compaction (Fig. S2B). Sixteen gastropod shell samples (each weighing approximately 1–1.5 kg) were collected for analysis. However, the MM3 sub-bed was excluded due to its composition as a coal seam and the absence of gastropods. Each sample was sieved to categorize the gastropods into 3 size ranges (large, medium, and small) before conducting detailed studies on shell morphology and species identification. Observations from fieldwork and laboratory analysis revealed that gastropod shells within the sub-beds were preserved in varying conditions, ranging from large and small complete shells to fragmented remains (Fig. S2C,D). Opercula were notably well-preserved and commonly encountered throughout the sub-beds.

Shell morphology and identification

The snail fossils were analyzed to evaluate their morphological features. Key shell measurements: shell height (SH), shell width (SW), apertural height (AH), and apertural width (AW) (Fig. 1A′), were taken in millimeters using a digital vernier caliper, following the methods described by Brandt (1974) [24]. A scanning electron microscope (SEM) obtains high-resolution images of the shells. Species identification was carried out by comparing the fossil specimens with modern species [24] and fossil records [1]. Additionally, the specimens are to be cross-checked against relevant reference collections and similar specimens for confirmation.

Sample preparation and analyzed method for stable carbon and oxygen isotopes

Sample selection and preparation

Bellamya shells were chosen as control variables for isotopic analysis due to their abundance and excellent preservation. Only shells that were well-preserved and free from visible recrystallization, secondary mineralization, or contamination were selected. The shells were carefully cleaned with a soft brush to remove debris and surface contaminants. After purifying and drying, the shells were ground into a fine, uniform powder using an agate mortar and pestle. The powdered carbonate was then placed into clean, labeled

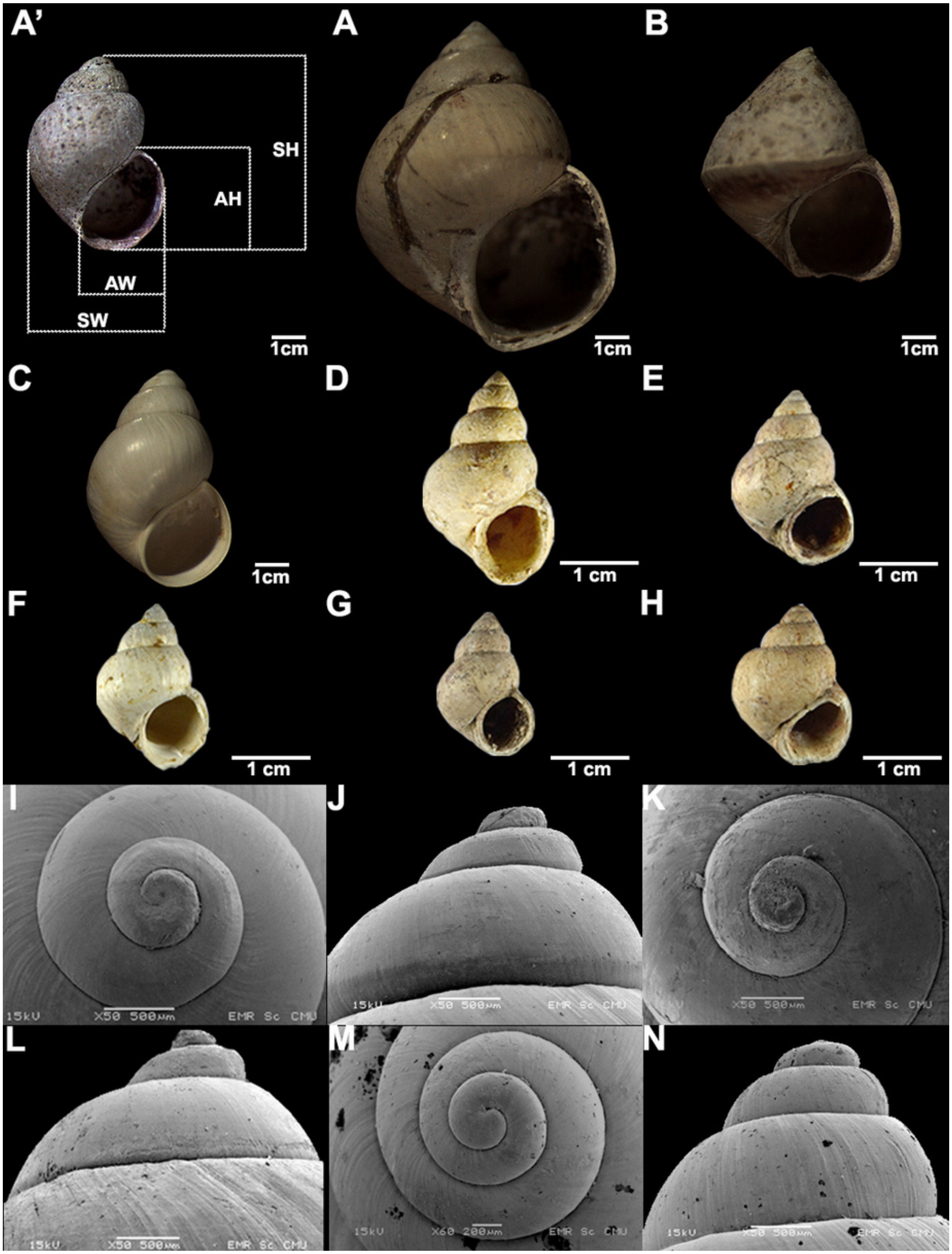

Fig. 1 The image set presenting gastropod genera from the thick gastropod bed, including shell measurements (A′), young *Idiopoma* (A), Young *Bellamya* (B), *Bithynia* (C), *Cipangopaludina* (D), *Bellamya* (E), *Bellamya* (F), *Idiopoma* (G), and *Mekongia* (H). Scanning Electron Microscopy (SEM) images revealed detailed morphological characteristics of the protoconch and teleconch for *Idiopoma* (I, J), *Bellamya* (K, L), and *Bithynia* (M, N).

plastic vials to ensure proper handling and avoid contamination.

Analytical procedure

The isotopic analyses were conducted at the Stable Isotope Laboratory, Department of Geological and Atmospheric Sciences, Iowa State University, USA. A Thermo Finnigan Delta Plus XL mass spectrometer, operating in continuous flow mode and connected to a Gas Bench with a CombiPAL autosampler, was used for measurements. Reference standards (NBS-18, NBS-19, and LSVEC) were employed for isotopic calibration and consistency of the appropriate isotopic scales. The analysis included at least one reference standard for every 5 samples to ensure accuracy and consistency. The combined uncertainty (analytical uncertainty and average correction factor) for the isotopic measurements was ±0.04‰ for $\delta^{13}C$ (VPDB) and ±0.14‰ for $\delta^{18}O$ (VPDB), respectively.

The $\delta^{13}C$ and $\delta^{18}O$ values derived from shell carbonates were interpreted to infer environmental, ecological, and physiological conditions. The $\delta^{13}C$ values indicate the carbon sources and the relative contributions of terrestrial and aquatic vegetation, reflecting primary productivity and habitat dynamics. The $\delta^{18}O$ is a proxy for paleotemperature and hydrological conditions, including variations in precipitation, evaporation, and water sources influencing the lake or swamp system. Isotopic data plays a crucial role in reconstructing past environmental conditions and understanding the paleoecological settings that supported the thriving of *Bellamya*. The equation for calculating the isotopic ratio is:

$$\delta^{X} = \left(\mathrm{R}_{\text{sample}}/\mathrm{R}_{\text{standard}} - 1\right) \times 1000,$$

where X is the isotope of interest (either $\delta^{13}C$ or $\delta^{18}O$); $\mathrm{R}_{\text{sample}}$ is the ratio of the heavy to light isotope in the sample ($\delta^{13}C/^{12}C$ for $\delta^{13}C$ or $^{18}O/^{16}O$ for $\delta^{18}O$); $\mathrm{R}_{\text{standard}}$ is the ratio of the heavy to light isotope in the standard reference, which this study is Vienna Pee Dee Belemnite (VPDB) for both $\delta^{13}C$ and $\delta^{18}C$; andthe δ-values are expressed in parts per thousand (per mille, ‰). This formula allows for the comparison of isotope ratios in the sample relative to a known standard.

RESULTS AND DISCUSSION

Gastropod diversity and habitat

A total of 7,532 individual gastropods were classified into 3 families (Table 1): Viviparidae, Bithyniidae, and Planorbidae. The Viviparidae family is the most abundant, comprising approximately 62.75% *Bellamya*, 7.08% *Idiopoma*, 0.76% *Cipangopaludina*, and 0.50% *Mekongia*. The second most abundant family is Bithyniidae, which accounts for 28.92% of *Bithynia*. The *Planorbidae* family is the least represented, with only 2 fragmented snail samples (Table 1 and Fig. 1) *Bellamya*, *Bithynia*, *Idiopoma*, and Planorbidae have been reported in the previous studies [1, 15]. However, this is the first report of *Cipangopaludina* and *Mekongia* found in the Mae Moh Basin.

All the snails appeared to be in a freshwater environment with salinity levels of less than 0.5 parts per thousand (ppt) [25]. Different gastropod species have varied environmental preferences and life behaviors, indicating specific ecological niches. *Bellamya* and *Idiopoma* can thrive in both lotic (flowing water) and lentic (still water) habitats, including rivers, ponds, and small lakes with little vegetation [26, 27]. *Mekongia* and *Cipangopaludina* prefer flowing waterways, such as rivers and creeks, typical of lotic environments [28]. In contrast, *Bithynia* exhibits greater adaptability and inhabits various freshwater environments. It frequently associates with aquatic plants that differ from those preferred by *Bellamya* and *Idiopoma* [29]. Bithynia primarily inhabits calcareous lacustrine environments and occurs in silts and muds deposited in river settings. Because the genus has a limited range, it can be utilized as a climatic-stratigraphic indicator when examining Middle Miocene deposits for malacology. The gastropod fossil assemblage from the Mae Moh Basin supports the interpretation of a freshwater lake environment throughout the depositional sequence. *Mekongia* and *Cipangopaludina* in samples MM1, MM6, MM16, and MM17 suggest intermittent water inflow, indicating a dynamic lacustrine system with episodic river inflows.

Fossil *Bellamya* from the Mae Moh Basin provides crucial insights into the evolutionary history and biogeography of the genus. During the Middle Miocene (approximately 13 Myr), *Bellamya* thrived in Thailand but later became extinct while continuing to flourish in other parts of Asia and Africa. Fossils from China dated 12–7 Myr, while those from East Africa are younger, with an age of 4.2 Myr. Phylogenetic analyses suggest that *Bellamya* populations in East Africa diverged from their Chinese counterparts during the Early Miocene, between 20 and 15 Myr [30]. This divergence coincides with the tectonic connection between the Afro-Arabian plate and Eurasia, which occurred between 20.5 and 14.8 Myr and facilitated faunal exchanges between these regions [31]. Gu et al [30] proposed that *Bellamya* likely originated in Southeast Asia, particularly Thailand, and subsequently spread to China and Africa, driven by tectonic and environmental shifts.

Stable carbon and oxygen isotope and paleoenvironment

The results of bulk stable isotope analysis ($\delta^{13}C$ and $\delta^{18}O$) from 16 shell samples ($n = 16$) are summarized in Table 2. The $\delta^{13}C$ values ranged between 2.10‰ and 5.54‰, with an average of 3.79‰. The $\delta^{18}O$ values ranged from −2.99‰ to −6.89‰, with an average of −5.07‰. These isotopic measurements offer valuable information about the paleoenvironmental

Table 1 Gastropod taxa with size measures and number of individuals. Abbreviation: shell height (SH), shell width (SW), aperture height (AH), aperture width (AW), and number of individuals (NI) with 7,532 individuals in total.

Sample no.	Gastropod taxa	Average size				NI
		SH (cm)	SW (cm)	AH (cm)	AW (cm)	
MM1	*Bellamya*	1.98	1.66	0.91	0.83	399
	Cipangopaludina	2.54	1.89	1.01		44
	Bithynia	0.62	0.38	0.29	0.22	100
MM2	*Bellamya*	0.82	0.61	0.48	0.37	4
MM4	*Bellamya*	1.94	1.43	0.81	0.66	100
	Idiopoma	1. 49	1.22	0.70	0.56	21
	Bithynia	0.607	0.416	0.308	0.243	20
MM5	*Bellamya*	0.44	0.38	0.185	0.16	158
	Bithynia	0.6	0.401	0.304	0.251	3
MM6	*Bellamya*	1.87	1.3	0.88	0.72	399
	Mekongia	1.78	1.68	0.75	0.80	8
	Bithynia	0.697	0.447	0.339	0.288	343
MM7	*Bellamya*	2.07	1.44	0.91	0.77	100
	Bithynia	0.656	0.388	0.322	0.239	10
MM8	*Bellamya*	2.44	1.66	0.81	0.77	190
	Idiopoma	2.32	1.58	0.71	0.62	59
	Bithynia	0.642	0.41	0.301	0.248	443
MM9	*Bellamya*	2.01	1.44	0.88	0.72	183
MM10	*Bellamya*	2.58	1.66	0.88	0.72	376
	Bithynia	0.769	0.485	0.355	0.278	25
MM11	*Bellamya*	1.91	1.29	0.72	0.66	1000
	Idiopoma	1.88	1.15	0.65	0.59	380
	Bithynia	0.639	0.451	0.317	0.282	238
MM12	*Bellamya*	2.11	1.44	0.88	0.72	185
	Bithynia	0.743	0.417	0.344	0.3	94
MM13	*Bellamya*	2.11	1.5	0.88	0.77	399
	Idiopoma	1.073	0.841	0.577	0.471	14
	Bithynia	0.746	0.646	0.362	0.354	50
	Bithynia	0.586	0.403	0.305	0.243	100
MM14	*Bellamya*	2.08	1.5	0.99	0.72	500
	Idiopoma	1.93	1.68	0.47	0.39	59
	Bithynia	0.649	0.527	0.324	0.291	119
	Bithynia	0.702	0.406	0.289	0.236	200
MM15	*Bellamya*	1.98	1.39	0.77	0.69	195
	Bithynia	0.692	0.458	0.324	0.257	206
MM16	*Cipangopaludina*	2.22	1.57	0.94	0.83	13
	Bellamya	2.01	1.32	0.87	0.66	230
	Bithynia	0.67	0.43	0.36	0.26	68
MM17	*Bellamya*	1.99	1.5	0.91	0.66	308
	Mekongia	0.83	0.667	0.443	0.4	30
	Bithynia	0.32	0.24	0.19	0.14	159

conditions and water chemistry of the Mae Moh paleo-lake during the time of deposition period.

Changes in respiration, calcification physiology, CO_2/O_2 ratios, and DIC content influence isotopic variation in gastropod shells. These factors differ from those in land snails and other air-breathing organisms, which mainly obtain their carbonate from respired CO_2 [32]. These physiological and environmental factors may reflect changes in salinity or other aspects of the paleo-lake's water chemistry [33]. Aquatic mollusks, like gastropods, primarily build their carbonate shells from ambient DIC, including $CO_{2(aq)}$, HCO_3^-, and

Table 2 Stable $\delta^{13}C_{shell}$ and $\delta^{18}O_{shell}$ from *Bellamya* in each sub-bed.

Sample no.	δ^{13}C ‰ VPDB	δ^{18}O ‰ VPDB	Remark
MM1	5.40	−4.95	
MM2	4.55	−5.17	
MM4	3.93	−5.66	
MM5	4.53	−6.16	
MM6	3.68	−6.36	
MM7	4.10	−5.52	
MM7_2	4.20	−5.28	* Repeat
MM8	2.43	−3.72	
MM9	3.10	−4.44	
MM10	3.52	−4.31	
MM11	5.54	−4.56	
MM12	4.25	−6.08	
MM12_2	4.37	−6.05	* Repeat
MM13	3.48	−6.89	
MM14	3.51	−5.46	
MM15	2.45	−4.54	
MM16	3.00	−2.99	
MM17	2.10	−3.21	
Average	**3.79**	**−5.07**	
SD	**0.95**	**1.09**	
Max	**5.54**	**−2.99**	
Min	**2.10**	**−6.89**	

The analytical uncertainty for δ^{13}C is ±0.04‰ (VPDB) and δ^{18}O is ±0.14‰ (VPDB), respectively.

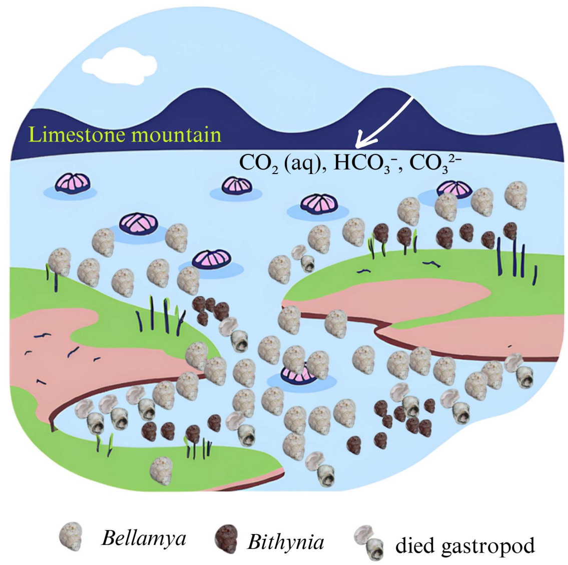

Fig. 2 Hypothesis model of the open system dynamics of the Mae Moh paleo-lake, with surrounding marine limestone, illustrating conditions that supported gastropod proliferation under high precipitation. The weathering and erosion of the limestone contributed to a substantial influx of carbon dioxide and bicarbonate into the lake, influencing carbonate chemistry and supporting a favorable habitat for gastropods.

CO_3^{2-} [34]. Freshwater and marine gastropods generally exhibit distinct isotopic signatures. Freshwater snails regularly present lower values of both stable carbon and oxygen isotopes. For instance, *Lymnaea* sp. from St. Margarethen exhibits a mean δ^{13}C value of −8.8‰, and a mean δ^{18}O value of −4.7‰, whereas the marine snail *Potamides disjunctus* has mean δ^{13}C and δ^{18}O values of 2.8‰ and −2.1‰, respectively. Positive δ^{13}C values indicate marine environments, while depleted δ^{18}O values in marine snails suggest freshwater influences [35].

Stable carbon isotope interpretation

The δ^{13} values in this range (2.10‰–5.54‰) are typical of marine carbonate systems, which supports the previous interpretation that the Mae Moh Basin may be influenced by its proximity to a sea during the Middle Miocene [17]. High δ^{13}C values can also indicate an environment with active photosynthesis, which preferentially removes ^{12}C and leaves the remaining dissolved inorganic carbon (DIC) pool enriched in ^{13}C, as observed in forest swamps where coal formed. Elevated δ^{13}C value can also result from DIC in the surrounding environment such as limestone, which is typically enriched in ^{13}C with δ^{13}C values ranging from 0‰ to +4‰ [36]. More importantly, fossil evidence from the Mae Moh Basin consistently indicates a freshwater environment, as no marine fossils are present. Therefore, the surrounding limestone likely significantly influences the δ^{13}C values of carbonates in this study area, especially in environments where DIC from limestone dissolution contributes to the carbonate system. The weathering and dissolution of limestone would release dissolved carbonate species into the paleo-lake, increasing the δ^{13}C values of the lake's DIC (Fig. 2).

In freshwater environments, δ^{13}C values typically reflect the balance between DIC sources. Higher values (e.g., 5.54‰) are likely due to DIC from limestone dissolution in surrounding rocks. Freshwater systems in contact with carbonate bedrock tend to inherit enriched δ^{13}C signatures. Lower values (e.g., 2.10‰) may result from contributions of ^{13}C enriched organic carbon from decaying plant material or soil organic matter. The overall δ^{13}C range suggests a carbonate-buffered freshwater system where limestone dissolution predominantly controls the carbon pool. The combination of moderately high δ^{13}C and strongly negative δ^{18}O values indicate that the DIC pool in the water has been influenced by both limestone dissolution and organic inputs.

Stable oxygen isotope interpretation

Negative δ^{18}O values indicated warmer water temperatures during carbonate precipitation because oxygen isotopes fractionate based on temperature. The more

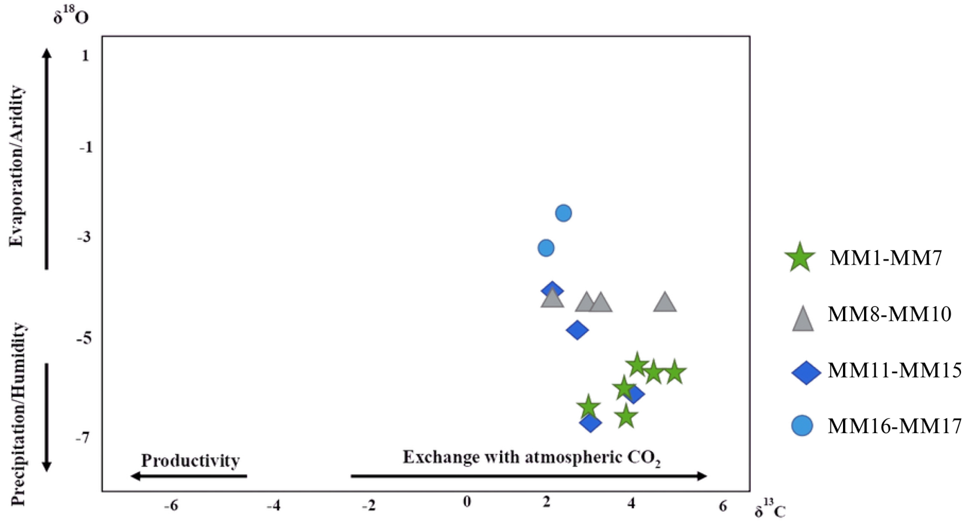

Fig. 3 The $\delta^{18}O$ versus $\delta^{13}C$ plot suggesting a humid paleoenvironment, indicating that the gastropods likely inhabited the lake for a prolonged period, exchanging CO_2 with their surrounding environment [33].

negative $\delta^{18}O$ values (−6.89‰) could suggest influence from freshwater input such as river discharge or precipitation in a wet climate (Fig. 3), typically depleted in ^{18}O compared to seawater. This evidence supports the result of gastropod taxa diversity. The $\delta^{18}O$ values from the gastropod shells in this study are comparable to those from modern viviparids collected from the Kiew Lom Dam in Lampang Province, which has a $\delta^{18}O$ value of −6.76‰ [17]. This similarity supports the interpretation of the Mae Moh paleo-lake as a freshwater with an isotopic signature reflecting local climatic and hydrological conditions. The $\delta^{18}O$ values align with the wet climatic conditions of the Miocene in Northern Tibet [37]. However, the isotopic values from Northern Tibet show greater depletion than those from Mae Moh, probably due to topographic differences between the regions. Despite the interpretation of the Mae Moh paleo-lake as an open system primarily controlled by meteoric precipitation [38], evaporative effects appear to play a minimal role in contributing to the observed positive shift in oxygen isotope values.

Freshwater $\delta^{18}O$ was influenced by precipitation. Negative $\delta^{18}O$ values are typical of meteoric waters in temperate to tropical climates, while less negative $\delta^{18}O$ values (closer to −2.99‰) may reflect evaporative enrichment in shallow or stagnant water bodies. The isotopic variability suggests multiple freshwater inputs, likely a combination of rainwater, surface runoff, and groundwater, influenced by local geology.

Sedimentation rate estimation

Field and laboratory observations revealed considerable fossil fragmentation and the presence of numerous opercula, suggesting the reworking of some of the gastropods. The preservation of these fossils and the formation of thick gastropod deposits imply that the lake likely experienced gradual subsidence.

To estimate the sedimentation rate of the 12-m-thick gastropod bed, dated to approximately 13.02±1.03 Myr, researchers determined the duration of sediment deposition by calculating its minimum and maximum ages. The minimum age is 13.02−1.03 = 11.99 Myr, and the maximum is 13.02+1.03 = 14.05 Myr. This results in a deposition interval of 2.06 Myr. The sedimentation rate is calculated by dividing the thickness of the sediment layer by the deposition time interval [39]. The resulting sedimentation rate is approximately 5.83 m/Myr (or 0.58 cm/kyr), which indicates a very slow rate consistent with deposition in a distal floodplain or palustrine/lacustrine environment [40]. Slow sedimentation rate and limited sediment supply may have created favorable conditions for gastropods to thrive.

The slow subsidence would have exposed older generations of gastropods while newer generations continued to inhabit the same lake which resulted in the accumulation of multiple generations of gastropods over time and the formation of the thick gastropod bed observed.

CONCLUSION

Gastropod fossils from a 12-m-thick bed (K-Zone) were classified into 3 families and 5 genera, with *Cipangopaludina* and *Mekongia* representing new occurrences for the fossil record in the Mae Moh Basin. *Bellamya* is the most abundant genus and includes endemic species possibly related to those found in China and East Africa [30]. Isotopic data ($\delta^{13}C$ and $\delta^{18}O$) indicate the gastropods lived in a system influenced by limestone dissolution and meteoric water, with water chemistry differences controlled by local geology. These results align with exclusively freshwater snail species in the area, suggesting a paleoenvironment of ponds or lakes with occasional river influx. The reworking of some layers, indicated by fragmented shells, and the slow sedimentation that supported gastropod growth highlight key aspects of this paleoecological setting. This environment provides valuable insights into paleoclimate, paleoecology, and the depositional processes that led to the formation of thick gastropod layers.

Appendix A. Supplementary data

Supplementary data associated with this article can be found at https://dx.doi.org/10.2306/scienceasia1513-1874.2025.062.

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Appendix A. Supplementary data

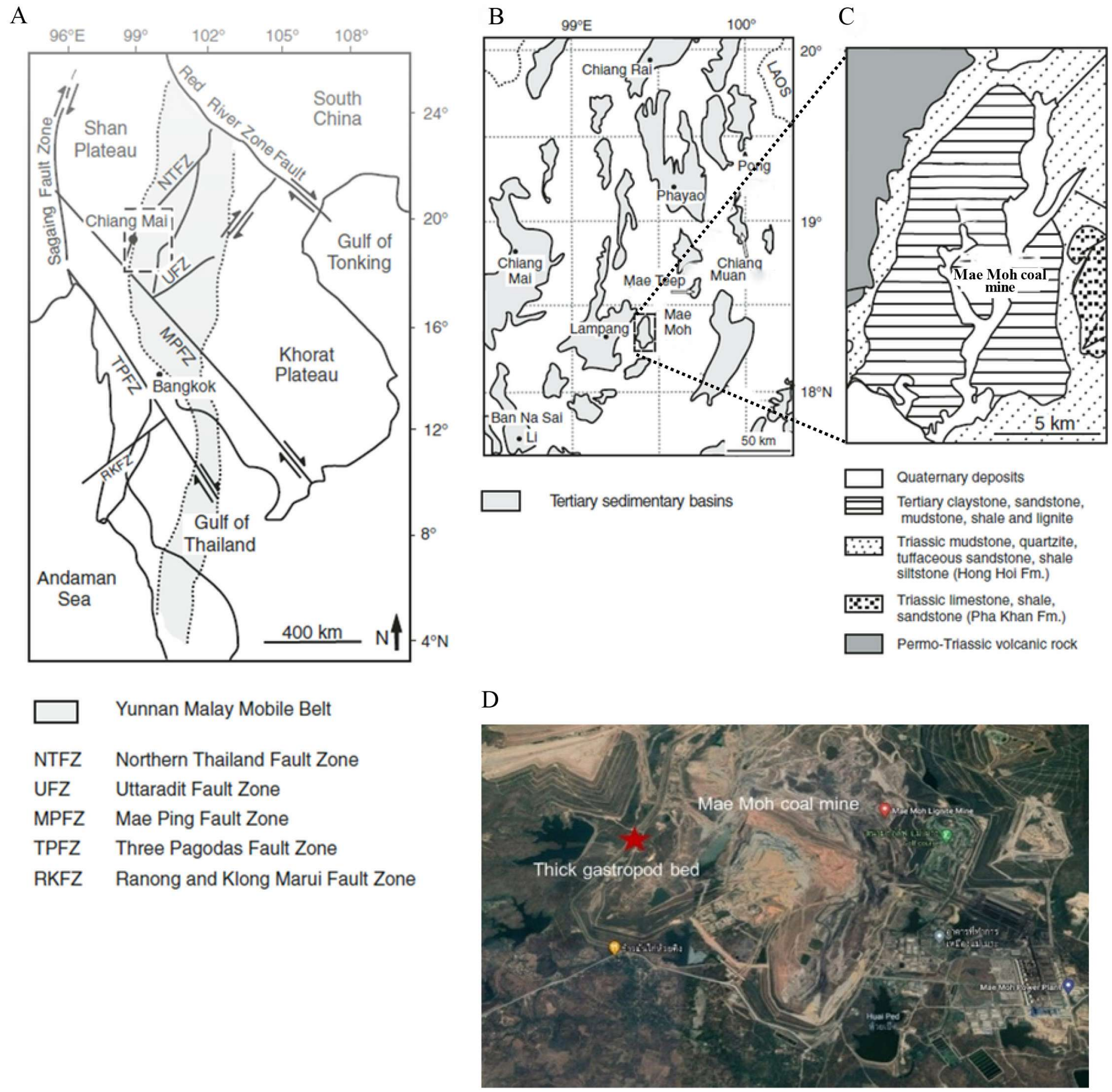

Fig. S1 The map of Thailand illustrating a geologic structure (A); Cenozoic basins in Northern Thailand (B); geologic map of the Mae Moh Basin (C) [13] with the location of thick gastropod bed (D).

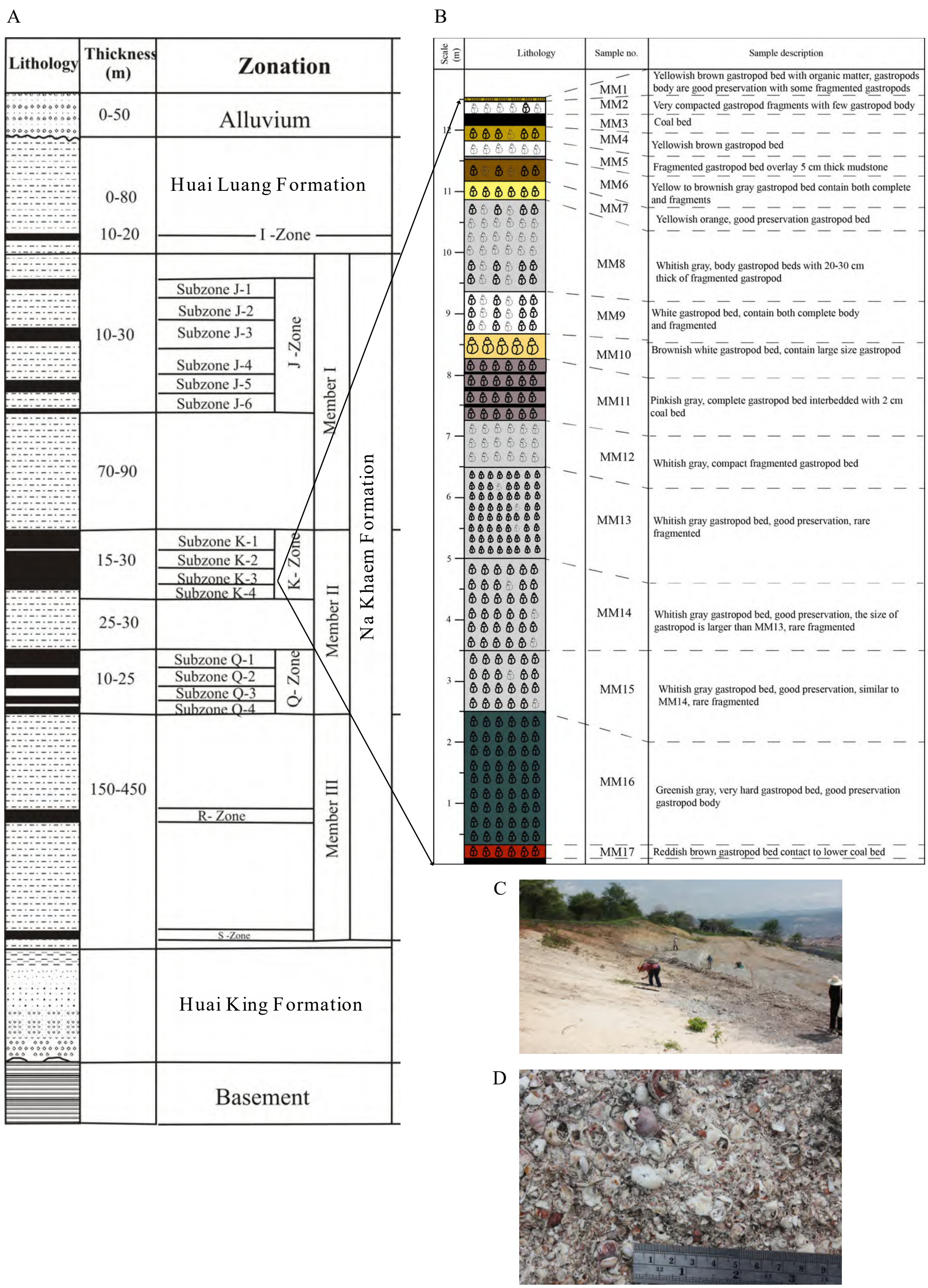

Fig. S2 The stratigraphy of the Mae Moh Group (A) [18] outlined alongside detailed descriptions of sub-beds (MM1–MM17) (B) which presents the characteristics of snail fossils by categorizing fossil sizes as small, medium, and large in each sub-bed. Fossil preservation states have distinct line types: solid lines indicate complete shells, while dotted lines denote fragmented shells. Detailed views of the gastropod bed, showcasing both wide-field and close-field perspectives (C, D).