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Lower Cretaceous terrestrial outcrops with fossil insects from Lebanon and China

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Terrestrial ecosystems acquired their modern structure during the Early Cretaceous, with the diversification and progressive distribution of extant organisms in the continental niches that they nowadays occupy. Traditionally, it is admitted that the Early Cretaceous is also the period that witnessed the appearance or at least the beginning of radiation of the flowering plants. During this period, referred to as the Cretaceous Terrestrial Revolution, the patterns of the modern-like terrestrial ecosystems did settle along with the beginning of a significant global warming and the apparition of most orders of flowering plants (Barba-Montoya *et al*. 2018), together with the radiation of key families of pollinators within insects (flies, butterflies, beetles, and bees) (Condamine *et al*. 2016). This period is as well marked by a shift from gymnosperm-dominated ecosystems to angiosperm-dominated ones (Condamine *et al.* 2020; Benton *et al.* 2022). These diverse and widespread flowering plants profoundly reshaped continental trophic networks, transformed herbivore communities, and fostered conditions resembling modern terrestrial ecosystems (Labandeira 2007; Labandeira 2014; Benton *et al*. 2022).

Lebanon is famous in palaeoentomology for its numerous amber outcrops from the Lower Cretaceous (lower Barremian more precisely) and recently for its contemporaneous lacustrine dysodile deposits (Maksoud *et al*. 2022). It is noteworthy to state that Lebanon during the Early Cretaceous was an equatorial area in the North-East of the Gondwana supercontinent. Dysodiles are sedimentary rocks formed by the superposition of finely laminated millimetric layers. They are characterized by their richness in organic matter and in well-preserved fossils (Cordier 1808). Dysodiles are found in different lacustrine deposits in various areas of Lebanon, from the lower Barremian stages. However, their documentation was restricted to a few old references mentioning their presence and their richness in fossils (Botta 1831; Fraas 1878; Janensch 1925; El Hajj *et al*. 2019, 2021). Subsequently, dysodiles were totally forgotten until recently, when extensive geological fieldwork led to their re-discovery in Lebanon. The rediscovery of dysodiles, unusual Lower Cretaceous continental deposits in Lebanon, brought important and exceptional palaeontological assets (Azar *et al*. 2019; Azar & Nel 2023; El Hajj *et al*. 2021; Hakim *et al*. 2022; Rasnitsyn *et al*. 2022). Lower Barremian dysodiles crop out in five localities across Lebanon, at the base of the "Grès du Liban" unit; an outcrop in the North of Lebanon (Qrayn), another in the center of the country (Tarchich), and the three remaining in the South of Lebanon (Jdeidet Bkassine, Sniyya and Zehalta). To date these outcrops (but especially the one of Jdeidet Bkassine) allowed the collection of several tetrapods (anourans, chelonians, lizards, and possibly archosaurian remains), a rich "fish" grouping including a certain number of coelacanths, possible polypteriforms, and small new and important teleosts, pulmonate gastropoda, diverse aquatic related insect assemblage, plant debris (macroflora and palynomorphs) including large assemblage of ferns, algae and spermatophytes, but also ostracods and a high concentration of various coprolites. A primary examine of the fossil assemblage permits to understand the depositional environment: a freshwater lake aside volcanic edifices, surrounded by a typical Early Cretaceous flora. The study of the Lebanese dysodiles is also a rare contribution to continental large diversity (plants, vertebrates and other animals) in the understudied African realm this early in the Lower Cretaceous, possibly revealing much of the transitory floral/faunal communities on this southern continent, under marked tropical climates.

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Amber, a fossilized plant resin, has been preserved throughout geological time (Langenheim 1969). Its unique chemical compositions allow for the exceptional preservation of biological inclusions in their three-dimensional, pristine, and minute details (Langenheim 2003). Amber occurs all over the world and its age ranges between a few millions and 320 million years (mid-Carboniferous) (Sargent Bray & Anderson 2009). Lebanon is well known for its very numerous Lower Cretaceous amber deposits (Azar 2012; Azar *et al*. 2010; Maksoud & Azar 2020, 2022; Maksoud *et al*. 2017, 2022), and to date about 500 amber outcrops have been found in Lebanon. Lebanon with its small territories and its multiple amber outcrops is relatively the richest country with amber. Approximately 10% of the land in Lebanon contains amber. Traditional Lebanese songs describe rightly Lebanon as the "mountains of amber". Maksoud & Azar (2023) proclaimed Lebanon as the land of amber. Astonishingly, despite the numerous Lower Cretaceous (lower Barremian amber deposits found throughout Lebanon, 32 of these have been discovered to contain biological inclusions (30 of which have already been published), while the discovery of two new outcrops in July 2024 will soon be published.

Lebanese amber is one of the most important for the study of arthropod evolution, as the period of its formation is contemporaneous with the appearance of flowering plants (angiosperms) and the associated newly evolved ecosystems. Moreover, it documents the initial diversification of the modern entomofauna and the disappearance of some archaic insect groups (Azar 2012; Poinar & Milki 2001; Azar *et al*. 2010). Amber in Lebanon is found in lens of dark clay associated with lignite and plant debris, sometimes in purely fluvial deposition system, *i.e*., in channels, or riversides, and sometimes the deposition is subject to marine influences, *i.e*., in a deltaic zone, or on the littoral (in the intertidal area). In fluvial cases, no palynomorphs of marine origin are found and amber accumulation could mainly occur after storms, while several types of dinoflagellates and marine gastropods are incorporated into the sediments when the deposition undergoes marine influence. This type of accumulation could be continuous as long as resin producing forest exists aside. Lebanese amber is often buried in its primary deposit, with lignite and fossil leaves from the resin producing tree. When transported, it is for little distances, as confirmed by the exceptional preservation state of the palynomorphs.

The Early Cretaceous Jehol Biota is a terrestrial lagerstätte renowned for its exceptionally well-preserved fossils, which provide critical insights into the origin and early evolution of Mesozoic life (Zhou *et al*. 2003, 2021). As defined in Pan *et al*. (2013) that combines ecological and taphonomic aspects, the Jehol Biota is described as "organisms that lived in the Early Cretaceous volcanic-influenced environments of northeastern China and were buried in lacustrine, and occasionally fluvial, sediments, where most turned into exceptionally preserved fossils." This definition widely adopted, as it best captures the key features of the lagerstätte. Traditionally, the Jehol Biota has been defined by three hallmark taxa: the spinicaudatan *Eosetheria*, the insect *Ephemeropsis*, and the fish *Lycoptera*. However, with the advent of more refined geochronological data, the dating of the fossil-bearing strata has become more precise, placing the Jehol Biota firmly within the time frame of approximately 135 to 118 million years ago (Swisher 2002; He *et al*. 2004; Yang *et al*. 2020; Zhou *et al*. 2021; MacLennan *et al*. 2024).

Recent studies have focused on the environmental and taphonomic impacts of the North China Craton (NCC) destruction on the biota evolution of the Jehol Biota (Zhou & Wang 2017; Zhou *et al*. 2021). This geological process began approximately 160 million years ago, peaked around 125 million years ago, and was closely linked to the subduction and retreat of the Palaeo-Pacific Plate beneath the eastern Asian continent (Wu *et al*. 2008; Zhu *et al*. 2012; Zhou *et al*. 2021). The intense volcanic activity associated with this event not only facilitated the high-fidelity preservation and fossilization of the Jehol Biota but also significantly influenced its formation and evolutionary dynamics, serving as a key external driving force (Zhou *et al*. 2021). Investigating how the NCC destruction shaped the local speciation and extinction patterns of the Jehol Biota preserved in various basins remains a crucial avenue for future research (Xu *et al*. 2020; Zhou *et al*. 2021).

The Jehol Biota is well known for yielding hundreds of exceptionally preserved fossil species, offering an unprecedented window into Early Cretaceous terrestrial ecosystems. These fossils include an extraordinary diversity of organisms, such as feathered dinosaurs, stem-group birds, early mammals, pterosaurs, lizards, turtles, amphibians, and fishes, alongside diverse insects and the earliest-known flowering plants (Zhou *et al*. 2003; Meng 2014; Zhou & Wang 2017; Ren *et al*. 2019; Xu *et al*. 2020). These discoveries have profound implications for reconstructing the initial development of today's terrestrial ecosystems, revealing how key ecological relationships and ecosystem functions were established during this critical period in Earth's history (Xu *et al*. 2020).

One of the most remarkable features of the Jehol fossils is their exceptional preservation of soft tissues with extraordinary fidelity, including skin, feathers, hair, wing membranes, ovarian follicles, and lungs (Zheng *et al*.

2013; Wang *et al*. 2018). Even microscopic and nanoscale structures, such as melanosomes and beta-keratins, have been identified (Li *et al*. 2010; Zhang *et al*. 2010; Pan *et al*. 2016, 2019). This unparalleled quality of preservation has provided critical data evidence address critical questions in vertebrate evolution, such as the origin and early evolution of birds and their flight, the emergence of feathers, and the evolution of mammals and key innovation of critical traits (Xu *et al*. 2014; Wang *et al*. 2019). In addition, the Jehol fossils provide a wealth of information about the palaeoecology of Early Cretaceous terrestrial biotas, offering invaluable insights into the structure and dynamics of ancient ecosystems (Zhou 2014; Xu *et al*. 2020).

The discovery of diverse insect fossils from the Jehol Biota has significantly enhanced our understanding of insect evolution and insect-plant coevolution, shedding light on several pivotal aspects. These include the emergence of pollination relationships, the evolution of insect mimicry and parasitism (Ren *et al*. 2019), and the origins of numerous insect lineages (Gao *et al*. 2012; Huang *et al*. 2012; Gao *et al*. 2013; Cai *et al*. 2014, 2017; Ren *et al*. 2019). These fossils provide crucial evidence for reconstructing the evolutionary history of key lineages of insects, offering insights into their ecological roles and adaptations during the Early Cretaceous.

The Jehol Biota has yielded the earliest known fossil angiosperms, dating back approximately 125 million years. *Archaefructus* is an extinct genus of herbaceous aquatic seed plants that has played a pivotal role in discussions about the origins of angiosperms (Sun *et al*. 1998, 2002). Initially described as a potential sister group to all extant angiosperms, *Archaefructus* sparked significant scientific debate regarding the evolutionary history of flowering plants. Subsequent studies, however, have suggested that *Archaefructus* may be likely belongs to the crown group of angiosperms, with its unique adaptations to an aquatic habitat pointing to affinities with groups such as the Nymphaeales (water lilies) or basal eudicots (Friis *et al*. 2003). The angiosperms of the Jehol Biota remain critical to understanding the early evolution of flowering plants. Their combination of primitive and derived traits offers invaluable insights into the diversification of angiosperms and the ecological niches they occupied during the Early Cretaceous. Newly discovered specimens in recent years continually expand the already extensive diversity of the Jehol Biota. With ongoing discoveries, including new species of birds and insects, the diversity of the Jehol Biota continues to grow at a rapid pace, offering exciting prospects for further insights into this extraordinary terrestrial biota (Xu *et al*. 2020).

The fossil sites in Lebanon and northeastern China, represented by the Lebanese amber and dysodile deposits and the Jehol Biota respectively, share remarkable parallels in their palaeontological implications and offer complementary perspectives on Early Cretaceous terrestrial ecosystems. Both regions are famous for their exceptional preservation of diverse and abundant fossils, which capture intricate details of ancient life and ecosystems during the same geological period, approximately 125 million years ago.

The Lebanese dysodiles and the Jehol Biota also showcase the impact of distinct palaeogeographic and palaeoclimatic settings on biodiversity and ecosystem structure. While the Jehol Biota reflects the temperate and volcanic landscapes of northeastern Asia, Lebanese fossil sites reveal the tropical environments of the northeastern Gondwanan margin. Comparing these assemblages enables researchers to investigate biogeographic patterns, ecological adaptations, and evolutionary processes across vastly different but contemporaneous ecosystems. Future interdisciplinary research linking these fossil sites has the potential to deepen our understanding of the global biodiversity and ecological transformations of the Early Cretaceous.

The contemporaneous fossil deposits of Lower Cretaceous amber and dysodile from Lebanon, along with the Jehol Biota in China, hold global significance beyond their local contexts. These sites provide a unique opportunity to compare the tropical Gondwanan Lebanese fauna with the temperate Laurasian Chinese fauna.

Such comparisons, alongside coeval outcrops in Eurasia, such as Bernissart in Belgium, Las Hoyas in Spain, the Wealden amber of the Isle of Wight, the Purbeck Limestone Group of southern England, the Laiyang and Shouchang formations from eastern and southeastern China respectively, and the Jiuquan Basin of northwestern China, as well as the Zaza and Turga formations of eastern Russia, and fossil sites in Australia, including the Koonwarra fossil bed in Victoria (Grimaldi & Engel 2005; Tihelka *et al*. 2023), enable a comprehensive understanding of Early Cretaceous palaeobiodiversity. These fossil assemblages collectively shed light on the evolutionary and ecological dynamics of this critical period in geological history.

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