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**Transgressing the limits of paleoenvironmental data for Southeast Asian Pleistocene faunal assemblages: a critical review to go further.**

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**Abstract**

For the Pleistocene of South-east Asia, the ‘savannah corridor’ hypothesis put forward by Lawrence Heaney in 1991 on the basis of a few pollen records rightly aroused a certain amount of enthusiasm and was the source of many attempts to confirm or refute a significant regression in forest cover, depending on the taxa considered, during the Last Glacial Maximum. The work carried out to verify this hypothesis used a number of tools, including palaeontology, the results of which seem to us to have been greatly embellished given the paucity of reliable data available. Indeed, it is clear that the hypothesis concerns a geographical area that is largely inaccessible today, located at a depth of 120 meters in the South China Sea, and that the faunal assemblages taken into account remain imperfectly defined to allow such a hypothesis to be tested. We provide a summary of the main work carried out to date and a critical assessment of the articles published over the last few decades. It emerges that the fossil series considered (essentially mammals) are neither well chronologically set nor well defined from a taphonomic point of view, notably because they are based on unsatisfactory references, which are themselves poorly dated or based on mixtures of different faunas. These shortcomings also call into question the renewed and attractive hypothesis of the flexibility of the diet and change of habitat (ecological niche) of certain taxa, based on isotopic analyses, as recently proposed. We advocate the implementation of systematic fine excavations that take into account the taphonomy of the sites, but also show that progress has been made to go further.

**Key-words:** South-east Asia- continental biostratigraphy – Quaternary - Best practices - Tropical palaeontology

## **Résumé**

Pour le Pléistocène de l'Asie du Sud-est, l'hypothèse d'un « corridor de savane » avancée par Lawrence Haeney en 1991 sur la base de quelques enregistrements polliniques a suscité à juste titre un certain enthousiasme et a été à l'origine de nombreuses tentatives pour confirmer ou infirmer une régression significative du couvert forestier, selon les taxons considérés, lors du Dernier Maximum Glaciaire. Les travaux menés pour vérifier cette hypothèse ont fait appel à plusieurs outils, notamment la paléontologie, dont les résultats nous semblent avoir été largement embellis compte tenu de la rareté des données fiables disponibles. En effet, il est clair que l'hypothèse concerne une zone géographique en grande partie inaccessible aujourd'hui, située à 120 mètres de profondeur en mer de Chine méridionale, et que les assemblages fauniques pris en compte restent imparfaitement définis pour permettre de tester une telle hypothèse. Nous proposons une description synthétique des principaux travaux réalisés à ce jour et une évaluation critique des articles publiés au cours des dernières décennies. Il apparaît dès lors que les séries fossiles prises en compte (essentiellement des mammifères) ne sont ni bien calées chronologiquement, ni bien définies du point de vue taphonomique, notamment parce qu'elles sont basées sur des références insatisfaisantes, elles-mêmes mal datées ou basées sur des mélanges de faunes différentes. Ces lacunes remettent également en question l'hypothèse renouvelée et attrayante de la flexibilité du régime alimentaire et du changement d'habitat (niche écologique) de certains taxons, basée sur des analyses isotopiques, telle qu'elle a été récemment proposée. Nous préconisons la mise en oeuvre de fouilles fines systématiques prenant en compte la taphonomie des sites mais montrons également que des progrès importants ont été apportés.

**Mots-clés :** Asie du Sud-est – Biostratigraphie continentale – Quaternaire - meilleures pratiques - Paléontologie tropicale.

## **1. Introduction**

Globally, the level of our palaeontological knowledge varies from one region to another, depending on the geological context and also on the different investments made over time by researchers for economic, historical or political reasons. If these factors are not taken into account, some colleagues who are unfamiliar with South-east Asia may have a false vision, or even be disappointed by the impossible progress made in this region of the world, which is of major interest particularly where the Pleistocene terrestrial fauna is concerned. Others may be misled by the emphasis of some publications, which suggest that the local palaeontological foundations and references are perfectly well known and mastered for this Pleistocene fauna. While Louys and Roberts (2020) emphasize that palaeoecological data are essential for understanding the evolution of megafaunal adaptations during the Quaternary in South-east Asia, they agree that regional data are not as well developed as in other regions.

If the progress of palaeontology was at one time synchronous in South-east Asia and in the Western world where the discipline was born, this is due to colonial history. The post-colonial period, with its different histories from one nation to another, will have welcomed or practised the discipline in different ways. As far as the Quaternary is concerned, the most fragile basis is that of its 'antiquarian' period (cf. Trigger, 1984): a phase during which it was

simply a matter of collecting fossils without always bothering about the context of their discovery (cf. Zeitoun, 2023). At the same time, when the work has been carried out correctly, it has often taken an enormous amount of time and tedious work on the archives of the time to restore the exact location of certain sites or fossils (cf. Huffman et al., 2005, 2006, 2010, 2022). Unfortunately, historical collections and series are still used as references and still bias the bulk of newly acquired data, even though the collection of fossil teeth in pharmacies or the constitution of reference collections from mixtures of several provenances has already been highlighted (cf. Colbert, 1943; de Vos, 1983, 1984; Kahlke, 1961; Orchiston and Siesser, 1982; Patte, 1928; Pei, 1957). De facto, mixtures introduce confusion into the chronological accuracy of the different assemblages and make it impossible to carry out palaeoecological or palaeogeographical work of palaeoenvironmental interest. The bad practice of mixing source data has even been perpetuated to the present day in order to increase the corpus of studies, as has recently been pointed out (see the detailed description of cases of deliberate mixing in Zeitoun et al., 2019).

The general problem of mixing of palaeontological assemblages, whether deliberate or accidental, or the uncertainties in the age estimates of assemblages that often indiscriminately encompass several glacial-interglacial cycles (Carstens and Knowles, 2007) pose problems. The poor reliability of the corpus, as indicated by Meijaard (2003) and acknowledged by Flenley (1998) for palynology or geomorphological formations (De Dapper, 1985), helps to mask the reality of incompleteness. As a result, it is still not possible to provide a well-founded discourse on the issue of environmental evolution and to assess the true value of the erosion or evolution of Pleistocene biodiversity in South-east Asia. Locally, in Sumatra, Wilting et al. (2012) deplore the fact that the absence of a complete fossil record limits hypotheses on large-scale extinctions. Thus, to date, our knowledge of fauna and environments and how they are changing does not allow us to contribute equally, from one region to another, to the debate on the current or even future evolution of our planet in relation to global climate change. The current tropical zone is important for this debate. In this respect, South-east Asia, which has remained tropical at least since the PETM (Paleocene Eocene Thermal Maximum) (Lohman et al., 2011; Morley, 2018), is a valuable laboratory. After an introduction to define South-east Asia, we will explain how savannah is defined there, and then outline the limitations of the various tools used in palaeontology – modelling, palaeogeography and isotopes – to test the hypothesis of a savannah corridor during the LGM. At the same time, we will point out the limitations of the paleontological records themselves, for each tool, we will make a number of suggestions for improving these approaches in order to be able to demonstrate whether or not a savannah corridor existed.

## **2. South-east Asia and the Sundaland**

### *2.1. Geographical entities that vary in time and space*

Over the last few thousand years, the physiography of South-East Asia has changed considerably. South-east Asia (Fig. 1) currently includes Myanmar, southern Yunnan, Thailand, Laos, Cambodia, Vietnam, Malaysia, Singapore, Brunei, the Philippines, the Andaman and Nicobar Islands as well as Kalimantan, Java and Sumatra. The region has long been divided into Indochinese, Sundaic and Philippine (Wallacean) zoogeographic sub-regions (Wallace, 1876), with mammal communities sharing a common biogeographic history. The main natural environments in South-east Asia are tropical rainforests, tropical seasonal forests, tropical deciduous forests, savannah forests and grasslands, montane forests, mangrove forests and

swamp forests (Corlett, 2009; Demangeot, 1999). Today, Sundaland (*id est* Main continental South-east Asia and islands) has a humid tropical climate with seasonal monsoons and, together with the Amazon basin, the Congo basin and New Guinea, it still forms one of the largest equatorial rainforests in the world (Richards, 1996). Its biodiversity is one of the richest in the world (Myers et al., 2000; Woodruff, 2010; Mittermeier et al., 2011; de Bruyn et al., 2014) as a result of its geological history (Holloway and Hall, 1998; Morley, 2018), which is marked by major changes in its surface area, extending over some 1,800,000 km as a result of eustatic variations linked to global climate change during the Quaternary (Molengraaff, 1921; Molengraaff and Weber, 1920; Beaufort, 1926; Verstappen, 1975a, 1980; Tjia, 1980; Hanebuth et al., 2009). The current island nature of Sundaland is therefore only recent and anecdotal over the long-term (Cannon et al., 2009; Molengraaff and Weber, 1921; Voris, 2000; Woodruff, 2010). Although this definition gives the impression of a homogeneous whole, in reality, there are differences depending on the hydrographic network, the topography or the proximity to the sea, and these differences have been more or less accentuated over time, as illustrated for example by the following two Quaternary periods: Lower Pleistocene and Late Pleistocene. Indeed, constant and periodic climatic changes took place during the Quaternary (Dam et al., 2001), which saw around fifty distinct glacial cycles (Woodruff, 2010). Thus, in one hand, between 1.25 Ma and 700 ka, the transition from low-amplitude 41 ka-year cycles to high-amplitude 100 ka cycles was accompanied by a considerable drop in sea surface temperatures, an increase in ice volume and an increase in aridity and monsoon intensity in Asia (Clark et al., 2006). As a result of these changes, the climate may have been drier, colder and more seasonal during the different glacial periods interspersed with warm, wet interglacial periods, as is the case today (Heaney, 1991; Morley, 2000; van der Kaars and Dam, 1995; Verstappen, 1975b, 1980, 1997; Stuijts et al., 1988; Thorp et al., 1990; Thomas et al., 1999). On the other hand, during the Last Glacial Maximum (LGM), with the emersion of the bathymetric zone currently located at – 120 m, the land then emerging between Kalimantan, Sumatra, Java and the continent could have been covered by savannah-type vegetation (Muller, 1975; Morley, 1981; Morley and Flenley, 1987; Broecker et al., 1988; Caratini and Tissot, 1988; Heaney, 1991; Gathorne-Hardy et al., 2002). However, monsoon forest (Whitmore, 1981; Whitten et al., 1996; Taylor et al., 1999) and lowland rainforests and mangroves (Morley, 2000; Sun et al., 2000; Kershaw et al., 2001) have also been suggested. As savannah and tropical forest are antinomic (Peel et al., 2007), we will review the various arguments put forward for reconstructing these palaeoenvironments. Nevertheless, some nuances need to be taken into account, because while temperatures at the LGM may have been 6 to 9°C lower in the highlands (Morley, 2000; Hope, 2007), in the lowlands the drop was only 1 to 2°C (Pickett et al., 2004). Specific geographical features may also have affected local climates (Meijaard, 2003). For example, the mountainous sites of Java and Sumatra show no sign of reduced rainfall (Heaney, 1991) in southern Sundaland, when those of Yunnan and Nepal at the northern margin of Sundaland show wet conditions (Walker, 1986). It should also be pointed out at the outset that savannah can take different forms from one continent to another or within a given territory and, in the fossil record, it is above all the question of the openness of the environment as opposed to the dense forest that is addressed and it is still very difficult to define the environment with any degree of precision using the various palaeontological tools available.



**Figure 1**

Map of the Sundaland with the different zoogeographic areas and a potential savannah corridor during the Last Glacial Maximum, modified according to Bird et al. (2005), Heaney (2001), Tougaard (2001), Voris (2000) and Suraprasit et al. (2021).

Carte du Sundaland avec ses différentes zones biogéographiques et un potentiel corridor de savane au dernier maximum glaciaire, modifiée d'après Bird et al. (2005), Heaney (2001), Tougaard (2001), Voris (2000) and Suraprasit et al. (2021).

## 2.2. Biodiversities in South-east Asia during times

Although biodiversity has evolved over time as a result of changes in physiography, it remains a hotspot in South-East Asia. According to Woodruff (2010), understanding the palaeobiogeography of this global biodiversity hotspot is just as important for long-term conservation objectives as ecology and evolution are for understanding current patterns and processes. The many current hot spots are thought to be the result of refugia from the colder ice ages of the Pleistocene (Whitmore, 2003; Woodruff, 2010), particularly the last one when only Mount Kinabalu in Kalimantan and a small area of sufficiently high altitude in northern

Sumatra were covered by ice (Hope, 2007; Lohman et al., 2011). The tropical forest would then have been found mainly on the rest of the high relief of the Malaysian peninsula, in western Sumatra and central Kalimantan. During periods of low temperatures, the tropical forest was replaced by more open environments. As we shall see, these general points are nuanced and even challenged for different reasons and on different scales. However, there is a consensus on the current existence of a marked biogeographic boundary between the west (Malay Peninsula and Sumatra) and east (Kalimantan) of Sundaland (Fernando et al., 2003; Hirai et al., 2005; Lim et al., 2011; Steiper, 2006; Woodruff, 2010; Zhi et al., 1996), even if its origin is debated. It is thought to be due to a more or less significant separation between a dense forest domain and a more open vegetation corridor oriented north-south in the center of Sundaland during the LGM (Adams and Faure, 1997; Bird et al., 2005; Brandon-Jones, 1996; Gathorne-Hardy et al., 2002; Heaney, 1991; Meijaard, 2003; Wurster et al., 2010). Various interpretations of the data are produced depending on the taxa and sites studied, and the chronological or geographical resolution that can be used. The deep valleys created by the major rivers crossing Sundaland at the time of its maximum emersion (with gallery forests (Colwell, 2000; Inger and Voris, 2001; Kuenen, 1950; Lim et al., 2011) are likely to have altered the continuity of the presumed more open space.

Although the past environments of Sundaland are difficult to assess insofar as much of it is submerged today (Cannon, 2012), we propose to begin by reviewing the various arguments for proposing one or other reconstruction of the evolution of its environment. Since we are mainly interested in mammalian faunal assemblages, we will then look at the various direct or indirect elements concerning Pleistocene fauna in relation to savannahs.

### *2.3. Paleogeographic and climatic evolution of Sundaland since the Miocene*

Global tectonic events and their climatic consequences have strongly shaped Southeast Asia over the last million years. The major geological changes of the Miocene have had an impact on the climate of the whole of Sundaland (Hall, 2013). Since Miocene the tropical rainforest of South-east Asia has contracted (Heaney, 1991) and for Sundaland, despite the Kalimantan uplift, there has been a progressive increase in the area of shallow seas and a reduction in the land area of Sundaland during the Miocene to the Pliocene (Lohman et al., 2011). This was accompanied by climatic changes with cooler temperatures and altered precipitation patterns during the Pleistocene. On a large scale, when few palaeontological sites were yet known, Medway Lord (1971) argued that the Lower Pleistocene mammals of the Siwaliks in India, adapted to scrub and savannah vegetation, were prevented from migrating to Java by a forest barrier that had existed since the Pliocene, with the herbivores of Java adapted to riparian forest edges or forested habitats (Verstappen, 1980).

Thus, a large forest barrier would have separated savannah areas to the north and south in such a way that monsoon forest and wooded savannah are considered to have been the characteristic environment for vertebrates during the ice ages (Petersen, 1969). We have to reiterate here that what is being discussed is more the opening up of the landscape in relation to a dense tropical forest than the degree of afforestation of the savannah itself. And undoubtedly one of the issues indeed is certainly that not everyone refers to the same concept whenever authors talk about savannah that we could reduce the definition to an area whose the tree canopy is not closed and the understorey is grassy.

For northern Sundaland during the Pliocene, an increasingly arid climate would have been caused by the surrection of the Himalayas (Poole and Davies, 2001) but for southern Sundaland a number of large freshwater lakes appeared in Java, Sulawesi and Mindanao during their Plio-Pleistocene emergence. Nevertheless, the ages of the lakes remain uncertain (Lohman et al., 2011). Climatic drying and savannah expansion in Central Java have been suggested at the Pliocene-Pleistocene boundary (Rahardjo, 1999), with palaeosol studies (Bettis et al., 2009) indicating an increase in dry season duration during the early Pleistocene in the same region. According to Morley (2018), it is very likely that a seasonal climate corridor developed more strongly in the late Pliocene or early Pleistocene, when climates in the region were probably drier than in the late Quaternary. The condition of glacial periods has become more pronounced since 0.9–0.8 Ma (van den Bergh et al., 1996; Bintanja et al., 2005) and during periods of high sea level, the Java stands were intermittently isolated, limiting the migration of continental fauna (but see Husson et al., 2022 for an alternative view-point).

An open grassland fauna managed to occupy the whole of the Javanese region during the Lower and Middle Pleistocene until the arrival of a new fauna associated with the tropical forest from continental South-east Asia, as shown by the replacement of several mammal species (Badoux, 1959; van den Bergh et al., 2001). De Vos et al. (1994) refer to the Siva-Malayan route to describe this process of migration from the south-eastern margin of the continent towards Sundaland in the Quaternary. Around 400 ka the subsidence of Sundaland (Sarr et al., 2019) reduces exposed land and decreases albedo, which increases atmospheric convection and regional precipitation (Di Nezio et al., 2016). suggested that a Pinus savannah was probably widespread on the Malay Peninsula on several occasions: 660, 480, 200 and 22 ka based on palaeobotanical data. Based on pollen analysis of a borehole drilled in the alluvium of the Khorat plateau in Thailand, Yang and Grote (2018) suggest the presence of temperate forest and savannah at  $172,739 \pm 22,400$  and  $88,661 \pm 10,600$  BP, followed by deciduous and mixed forests with aquatic species from  $52,296 \pm 6800$  to  $28,150 \pm 7860$  BP. Finally, they describe the period  $27,332 \pm 3000$  BP as dry and cold. During that time, in Java, other clues to the evolution of environments are given by the evolution of lakes. For example, near Bandung, a large lake formed 135 ka ago has disappeared over the last few thousand years (van der Kaars and Dam, 1995). The Middle Pleistocene is a period when sea level was comparable to the LGM and Morley and Flenley (1987) indicate that a palynological study near Kuala Lumpur shows the presence of a pine savannah and grassland similar to the open forests of Thailand and the northern Philippines, rather than the present-day lowland rainforest. Then, according to pollen found in interglacial deposits dating from around 80 and 55 ka (Kamaludin and Azmi, 1997), the lowlands of the Malay Peninsula must have had a climate similar to that which prevails today. The transition period between 60 and 20 ka was characterised by a relatively humid and unstable climate, with temperatures colder than today (about 2 to 6°C lower) (Heaney, 1991; Penny, 2001; White et al., 2004; Cook and Jones, 2012). This is confirmed by pollen sequences dated between ~52 and 45 ka in North Kalimantan with the periodic replacement of forest by drier, more open habitats, including savannah (Hunt et al., 2007) whereas in West Kalimantan, large fan-shaped stretches of sand bordering the rocky relief of colluvial origin suggest more open vegetation with significant seasonal rainfall between 60 and 27 ka (Thorp et al., 1990; Thomas et al., 1999; Thomas, 2000). Peat and wood samples dated between 41.2 and 36.4 ka (Ayob, 1970) indicate that a type of vegetation with evergreen leaves and to a lesser extent gymnosperms (Hing and Leong, 1990) was present in the Kuala Lumpur region.



Before 34 ka Rugmai et al. (2008) identified closed habitat/rainforest, but grassland slightly present in Songkhla province in southern Thailand while Westaway et al. (2007) observed an enrichment of  $\delta^{18}\text{O}$  values in speleothems in East Java at 38 ka, indicating a prolonged dry period followed by a return to wetter conditions towards the end of the Late Pleistocene. For their part, using  $\delta^{18}\text{O}$  analysis of a freshwater bivalve, Marwick and Gagan (2011) show that northern Thailand experienced a predominantly wet and unstable climate between 33 and 20 ka, followed by a drier environment until the early Holocene. A savannah was recognized by Caratini and Tissot (1988) in the hinterland of the Mahakam delta in East Kalimantan and, in South-east Kalimantan, by Sun et al. (2000) around 20 ka. Then, climate change around  $\sim 11.5$  ka is associated with the strengthening of the Asian summer monsoon and leads to the rapid expansion of tropical forests across South-east Asia (Cook and Jones, 2012) and the reduction of open savannahs in the region (Kealhofer and Penny, 1998; Penny, 2001). The evolution of vegetation cover seems fairly accurate, although Flenley (1996, 1998) acknowledges that the dating of the pollen sequences used is uncertain. As we shall see later, we should probably consider that the historical development of the vegetation landscape of Sundaland in the Late Pleistocene is complex and locally varied (McAllister et al., 2022). This is supported by Puspaningrum et al. (2020) unless the differences result from issues specific to the proxies used.

### **3. The properties and the evolution the savannah in Asia**

#### *3.1. Savannah biomes today in Asia and their particularities*

While all savannah environments have some points in common, there are some specificities from one continent to another. All intertropical savannahs are found in hot regions where rain-fall distribution is highly seasonal, with a rainy summer season (Scholes and Walker, 1993). The coexistence of woody and herbaceous plants is made possible by the separation of rooting niches. Grasses use only the moisture in the upper layer of the soil, while woody plants use subsoil moisture (Walter, 1971; Walker et al., 1981; Walker and Noy-Meir, 1982; Eagleson and Segarra, 1985). The horizontal extent of the roots of savannah trees is around 10 times greater than the extent of their canopy (Smit, 2004). This constrains their establishment to edaphic parameters. Edaphic and topographic parameters influence the formation of a savannah (Demangeot, 1999; Soares et al., 2015; Thomas-Barry et al., 2021). Field studies on root distribution and water uptake have shown great differences in the degree of niche separation, depending on abiotic factors and the species concerned (Hesla et al., 1985; Knoop and Walker, 1985; Mordelet et al., 1997), but the establishment of savannahs and their evolution with respect to woody taxa could also be determined by competition between trees (Wiegand et al., 2006). However, it would also be possible to explain the coexistence of trees and grasses by the fact that the savannah is an unstable state maintained by relatively frequent disturbances (Jeltsch et al., 2000) even if this instability depends on the scale of observation (Scholes and Archer, 1997; Skarpe, 1992). Thus, on a landscape scale, savannahs can be in stable equilibrium and persist for millennia because of their composition as a “moving” mosaic between herbaceous and woody dominance (Remmert, 1991; Scholes and Archer, 1997; Turner et al., 1993; Watt, 1947). This last point may help us to understand some of the differences between authors, depending on the scale taken into account when reconstructing palaeosciapes. One point we must make clear here is that African, South American and Asian savannahs have different properties (Solbrig et al., 1996; Sankaran et al., 2005) and, according to Ratnam et al. (2016), although tropical Asia is dominated by monsoon climates with average annual rainfall of over 700 mm and is home to

dense, tall forests, many types of savannah formations are still present today in a patchy and fragmented manner. In Asia, three different savannah communities can be distinguished: deciduous broadleaf savannahs, deciduous thin-leaved and thorny savannahs and evergreen pine savannahs, which range from sparsely-treed grasslands to densely-treed forests, generally along a gradient of increasing rainfall. Tropical savannahs can be defined as mixed tree-grass systems where the herb layer is generally dominated by grasses that use the C4 photosynthetic pathway to fix carbon, while trees use the C3 pathway (Ratnam et al., 2011). Their defining characteristic is that the tree canopy is not closed and the understorey is grassy (Hirota et al., 2011; Lehmann et al., 2014; Staver et al., 2011). Fossil and molecular evidence suggests that C4 herbaceous vegetation was established in different parts of Asia at quite different times (Edwards et al., 2010; Morley, 2012, 2018) which sometimes leads to confusion in the use of palaeontological data to answer palaeoecological questions.

### *3.2. The savannah corridor hypothesis: the forest of the discord*

For three decades, the hypothesis of a savannah corridor in Sundaland has been the focus of various scientific communities. The existence of savannah in central Sundaland at the LGM evoked and then put forward by Heaney (1991) has been controversial depending on the methods or media used, the taxa and regions studied or the chronological or geographical resolution that can be taken into account. Depending on their preference for one argument or another, authors have put forward arguments opposing the existence of this savannah (Kershaw et al., 2001, 2007; Meijaard, 2003; Meijaard and Groves, 2006; Wang et al., 2009), some indicating that forests quite similar to those found in the region today were present (Anshari et al., 2000; Emmel and Curray, 1982; Geyh et al., 1979; Kershaw et al., 2001; Taylor et al., 1999, 2001; Page et al., 1999; Whitmore, 1981; Whitten et al., 1996). Others have highlighted the factors favouring the presence of open vegetation landscapes, including lowland savannah (Adams and Faure, 1997; Bird et al., 2005; Broecker et al., 1988; Caratini and Tissot, 1988; Clark et al., 2006; Cranbrook, 2010; Dubois et al., 2014; Frenzel et al., 1992; Gathorne-Hardy et al., 2002; Gorog et al., 2004; Heaney, 1991; Morley, 1981, 2000; Morley and Flenley, 1987; Muller, 1975; Piper et al., 2011; Russell et al., 2014; Singham et al., 2017; Suraprasit et al., 2019; Verstappen, 1975a,b; Wicaksono et al., 2017; Wurster et al., 2010; Wurster and Bird, 2014) with varying degrees of nuance regarding the extent of a savannah corridor linking the present-day South-east Asian islands to the mainland at LGM.

Anshari et al. (2004) and Dommain et al. (2014), consider that the absence of peat accumulation in the lowlands of the region during the LGM suggests drier and presumably more seasonal climatic conditions for the whole of Sundaland during the lowest eustatic levels thus reducing the occurrence of "super-humid" climates. But, according to Meijaard (2003), although geomorphological, biogeographic, geochemical and geophysical data do not support this view, the existence of a savannah corridor at the time of the LGM has been confirmed as, biogeographic, geochemical and palynological data, as well as vegetation modelling, indicate that drier conditions prevailed in insular South-east Asia. During the last ice age there is limited support for the hypothesis of a continuous savannah corridor at the scale proposed by Heaney (1991). Contradictory arguments that a large continuous rainforest, instead of savannah, was present even under conditions of full glaciation have indeed been reported (Cannon et al., 2009; Slik et al., 2011; Morley, 2012) and palynological (Cannon et al., 2009; Prentice et al., 2011; Sun et al., 2000; van der Kaars et al., 2001; Wang et al., 2007, 2009), isotopic data (Dubois et al., 2014; Wurster et al., 2010), biogeographic data (Gathorne-Hardy et al., 2002; Meijard, 2003) and abiotic conditions suitable for maintaining viable populations of

Dipterocarpaceae at the LGM would strongly call into question the intertropical savannah corridor hypothesis (Raes et al., 2014; Slik et al., 2011).

The continuity of a north-south savannah corridor in central Sundaland has also been questioned by coupled vegetation-climate reconstructions (Cannon et al., 2009; Crowley and Baum, 1997; Crucifix et al., 2005; Hope et al., 2004; Otto et al., 2002; Prentice et al., 1993). The question of the role of palaeorivers in interrupting the savannah corridor itself has been raised (Colwell, 2000; Inger and Voris, 2001; Kuenen, 1950; Lim et al., 2011). Heaney (1991) agreed with this from a geographical point of view, and Whitmore (2003) from a chronological point of view, but Slik et al. (2011) suggest that the edaphic component has been neglected and that heath forests have persisted in place of savannah in central Sundaland. However, Ashton (2005) has shown that several *Dipterocarpaceae* species can grow on sandy soils. This makes it possible for dense forest to continue even on the Sundaland sea bed during the LGM. Thus, discordant point elements exist at the various currently accessible margins of the area concerned, between the south and north of Sundaland but also within these two margins. The continuity of forest cover is associated with an increase in rainfall (Turney et al., 2006; van der Kaars, 1991) and a decrease in  $\delta^{18}\text{O}$  values in speleothems during the LGM indicating the persistence of wetter conditions conducive to the persistence of forest vegetation at Flores (Ayliffe et al., 2013). It is consistent with the results of isotopic analysis of guano in Sarawak (Wurster et al., 2010) and with the  $\delta^{13}\text{C}$  values of fatty acids from an off shore record (Dubois et al., 2014). According to Raes et al. (2014) the possibility of a *Dipterocarpaceae* environment off the west coast of Kalimantan at LGM is supported by palynological data (cf. Cannon et al., 2009; Sun et al., 2000; Wang et al., 2007, 2009). Conversely, Hunt et al., 2007, 2012 suggest a "highly disturbed open forest" during the last glaciation in North Kalimantan and, Caratini and Tissot (1988) suggested that during the LGM, the hinterland of the Mahakam delta probably consisted of grassland or savannah.

In the northern Sundaland, in northern Thailand, Suraprasit et al. (2019) indicate a possible open landscape from mammalian assemblages and Morley (1998) suggested that *Pinus* savannah was probably widespread on the Malay Peninsula at 22 ka. According to Penny (2001), the arid zone flora of north-eastern Thailand, consisting of a mixture of tropical, dry deciduous and savannah taxa, as well as temperate, tropical-montane or Eurasian taxa, then saw the advent of tropical deciduous forest dominance at the Pleistocene/Holocene boundary. The analysis of the cenogram of the Thum Wiman Nakin fauna (Tougaard and Montuire, 2006) shows as lightly open forest environment, but according to these authors the species richness in *Muridae* were not consistent with the palynological records from southern China (cf. Wang et al., 1999; Zheng and Lei, 1999).

It is the different interpretations of data concerning environmental barriers that are the source of controversy or different interpretations. For example, Meijer and Withington (1981) state that the southernmost location of *Pinus* is restricted in the central highlands of Sumatra and van der Kaars et al. (2010) consider that its range was probably more extended during the LGM. Whereas Bodribb and Field (2007) consider that tropical evergreen forests constitute an impassable ecological barrier to the movement of *Pinus* southwards, where its absence can be explained by the permanent presence of dense forests in the equatorial region. From a genetic point of view, strong biogeographical barriers are thought to persist, particularly between Sumatra and Kalimantan, or more generally between east and west (Fernando et al., 2003; Hirai et al., 2005; Steiper, 2006; Zhi et al., 1996). For Slik et al. (2011), the dispersal barrier is mainly based on soil properties, as suggested in particular by Bird et al. (2005), Cannon et al. (2009) and Wurster and Bird (2014). Although plant distribution in

tropical environments is mainly dictated by temperature and rainfall (Araújo and Peterson, 2012; Araújo et al., 2013; Boucher-Lalonde et al., 2012), the edaphic reality is a prelude to the possibility of having dense forests or savannahs. If there are barriers, there are also refuge possibilities (Haffer, 1987; Prance, 1979; Colinvaux et al., 2001), the relevance of which is reiterated by Morley (2018). Nevertheless, the origin and age of these refuges is subject to various interpretations which in turn interfere with the development of the vicariance or dispersal models taken into account (cf. Brandon-Jones, 1996; Bibi, 2013; de Bruyn and Mather, 2007; de Bruyn et al., 2013; Esselstyn and Brown, 2009; Fernando et al., 2003; Gilbert et al., 2006; Gorog et al., 2004; Harrison et al., 2006; Heaney, 1991; Hirai et al., 2005; Leonard et al., 2015; Mason et al., 2019; Patou et al., 2010; Quek et al., 2007; Ruedi, 1996; Singham et al., 2017; Steiper, 2006; Wurster et al., 2010; Xu and Arnason, 1996; Zhang et al., 2001; Zhi et al., 1996).

Ultimately, the hypothesis of a savannah corridor is based on climatic conditions during the different glacial maxima, when land area was at its maximum, *id est* a biogeographical reality limited to ~ 17% of the last 250,000 years according to Voris (2000) who proposes a probabilistic approach of the variation of eustatic levels. For the supporters of a savannah corridor in the heart of Sundaland, the nuances concern its width and continuity, depending on the adaptability of the taxa taken into account. To take up the founding point put forward by Heaney (1991) to promote this hypothesis, Wurster and Bird (2014) point out that the evidence put forward was limited to five palynological studies of varying reliability and Bird et al. (2005) were forced to take indirect evidence into account to support this hypothesis when other models (cf. Cannon et al., 2009 or Raes et al., 2014) suggest the presence of continuous forest cover across Sundaland. The question is not so much whether to accept or reject this or that conclusion, but rather to note that some studies use data that are limited, contested or questionable. As a result, despite the quality or relevance of the analyses produced, their results are in turn open to question. What matters above all is to identify the limitations or weaknesses of the primary data used to contradict this or that argument. What about the validation of models that are often used as credit in one-off studies?

#### **4. Limitations of palaeontological tools**

##### **4.1. Modelling, methods and limitations**

Modelling requires different types of data. Bioclimatic envelope models use associations between aspects of climate and occurrences of taxa to estimate the conditions conducive to maintaining viable populations. Once bioclimatic envelopes have been characterized, they can be applied to a variety of issues. The question arises as to the usefulness of these models, or at least their construction, especially as they may be based on unprovable hypotheses or may be contradicted by empirical evidence (Araújo and Peterson, 2012). Numerical simulations of palaeoclimate at the LGM (Bush and Fairbanks, 2003; Crucifix et al., 2005; Otto et al., 2002) indicate that most of Sundaland globally shows evergreen tropical forest landscapes. Wurster and Bird (2014) and O'Connell et al., (2020) also indicate that montane forest increased due to generally cooler climates during the LGM and that the area of lowland tropical rainforest almost doubled through expansion on the plateau linking Kalimantan to mainland Asia. The models proposed by Cannon et al. (2009) also show an expansion of the main forest types rather than a contraction during glacial phases. Using *Dipterocarpaceae* species distribution models to estimate the geographical extent of suitable climatic conditions for the Sundaland rainforest at LGM, Raes et al. (2014) conclude that the presence of an intertropical savannah corridor is unlikely.

Different simulations (Cannon, 2012) in fact give different scenarios, with or without savannah, due to the lower spatial and topographic resolution of the global climate model, which does not incorporate a narrow corridor and Handiani et al. (2012) show that the simulation of a savannah corridor in Sundaland only appears in one of their models, depending on whether or not it is associated with an unusual hydrological cycle in the tropics and a southward shift of the ITCZ (Intertropical Convergence Zone) (cf. Behling et al., 2000). Bird et al. (2005), who accept that the degree of northward contraction of the south/south-east forest boundary varies considerably between models, critically reviewed the evidence for drier and more seasonal climates during the LGM but were forced to consider indirect evidence to arrive at the savannah corridor hypothesis. Furthermore, in their modelling, Cannon et al. (2009) 'forced' the model to generate an expansion of seasonal vegetation or savannah and more generally, there may also be disagreement in the interpretation of palaeovegetation (Sun et al., 2000), which has an impact on palaeoclimate reconstructions and modelling.

Although we are far from being able to refine the meaning of the term savannah in the fossil record, the study by Ratnam et al. (2016), aimed at improving management in terms of conservation, indicates that none of the models used manages to correctly represent the present-day savannahs of the islands of South-east Asia, and that Asian pine savannahs seem to be located in different climates to those of other southern continents. A lack of data for the reconstruction of the tropical Asian biome makes a thorough comparison between the model and the data difficult. For Handiani et al. (2012), the failure to take into account the topographical specificity of places can lead to errors due to a lack of sufficient resolution, but the application to the incomplete fossil record remains imperfect. Wurster and Bird (2014) also note that vegetation models specific to Sundaland during the LGM fail to take edaphic factors into account, as has been previously noted (Heaney, 1991; Bird et al., 2005).

The most inclusive models using palynological data, dynamic vegetation models, mammal and/or insect communities, and isotopic compositions of vascular plants and guano remain incomplete. Indeed, a lower atmospheric CO<sub>2</sub> concentration at the LGM compared with the pre-industrial CO<sub>2</sub> concentration (Bragg et al., 2013) is difficult to take into account. However, this parameter is important since the advantage of plants with C<sub>4</sub> metabolism over plants with C<sub>3</sub> metabolism increases with lower CO<sub>2</sub> concentrations. Furthermore, according to Kershaw et al. (2001) at the LGM, pollen records indicate lower precipitation than today, while mean temperatures may have been globally reduced by 6 to 7°C, but assuming that the reduction in CO<sub>2</sub> in the atmosphere had little influence. It is noticed that authors indicated that the temperature reduction is not the same in the highlands: 6 to 9°C lower (Morley, 2000; Hope, 2007) and in the lowlands: only 1 to 2°C lower (Pickett et al., 2004). However, Louys and Roberts (2020) admit that a subtle variation in the partial pressure of atmospheric CO<sub>2</sub> will affect interpretations of δ<sup>13</sup>C values as being exactly equivalent to forest cover when this is not the case. Furthermore, as Bocherens et al. (2017) point out, the Suess effect, which describes the possible shift in carbon isotope values in atmospheric CO<sub>2</sub> due to CO<sub>2</sub> emissions from fossil fuel combustion and land use change, is a parameter to be taken into account when comparing recent and ancient materials. Finally, Sarr et al. (2019) have shown that due to its subsidence, Sundaland was not inundated during the Pleistocene until ~400 kya with a cyclic inundation repeating thereafter approximately every 100 kya (Voris, 2000; Woodruff, 2010).

Cannon et al. (2009) have already highlighted the need for long, well-dated terrestrial archives capable of providing indirect and direct evidence of local vegetation. A major problem

is that many sites considered to be indicative of conditions during the LGM remain poorly dated, or even completely lacking in any real dating control. Such sources must be treated with greater caution, and the decision to accept them or not is ultimately subjective and potentially biased by preconceived ideas (Adams and Faure, 1997). Finally, from the various attempts at synthesis produced in recent years it is possible to identify a consensus to express dissent or more accurately to accept that significant climatic heterogeneity exists in the region, with high sensitivity to glacial-interglacial forcing (Wurster et al., 2019). Lohman et al. (2011) summarize the problem in one formula, indicating that the parameterization of the model guides the results and the neontological data add a level of uncertainty.

#### 4.2. Phylogeography, methods and limits

Phylogeography has produced a number of results that are sometimes complementary but can also be interpreted in contradictory ways. The test of the savannah corridor hypothesis is based on the climatic conditions of a maximum area of Sundaland that has only covered ~37% of the last million years, *id est* ~17% of the last 250 ka (Voris, 2000) and makes it unlikely that it is solely responsible for the biogeographic pattern observed in Sundaland (Lohman et al., 2011). The available evidence consists of sites located on the Sundaland margin and a few marine cores (Sun et al., 2002; Wang et al., 2009; Zachos et al., 2001). This raises the question of the basis for the phylogeographic studies that are often invoked. In our opinion, this type of study is more relevant for raising new questions than for answering the subject we are dealing with here, because of the large number of ad hoc hypotheses used to interpret the models themselves, or even the primary data integrated into the models, most of which are already interpretations.

The study by Singham et al. (2017) suggests that different dispersal events and genetic isolation have shaped current biogeography and that different dispersal pathways affected terrestrial fauna during the Pleistocene whereas molecular data have revealed that Sulawesi taxa are frequently basal groups clustering with Asian ones (Randi et al., 1996). Several taxa have been studied on their own or in groups to answer the question of ecological or geographical connections or barriers, but according to Leonard et al. (2015) the chronology of divergences between populations of different landmasses varies considerably and cannot be attributed to a single event, such as a particularly extreme glacial cycle or a massive volcanic eruption. The wide variation in the dates attached to divergences from one taxon to another suggests that a stochastic factor may have led to different rates of population survival over tens of thousands to several million years. Geographical changes may have reduced biomes and population numbers, thereby increasing the risk of extinction, particularly in narrow areas of the Malay Peninsula where species diversity is now low (Woodruff and Turner, 2009) or on islands (Mays et al., 2018). Geneticists estimates refer to fairly large ages, which makes it difficult to use certain taxa to answer the question of connectivity between island and the South-east Asian continent during the LGM. For example, orangutans from Kalimantan and Sumatra (Groves et al., 1992; Uchida, 1998; Xu and Arnason, 1996; Warren et al., 2001; Zhang et al., 2001; Zhi et al., 1996) are thought to have been very distinct and probably genetically separated for 1 to 2.5 million years. Similarly, assemblages constructed from recent molecular phylogenies estimate that cervids and cattle diversified in Asia after the beginning of the Pliocene, and that species now isolated on islands across South-east Asia diverged in the Pleistocene perhaps more than 1 Ma ago (Bibi, 2013; Gilbert et al., 2006). Gorog et al. (2004) used a phylogeographic approach to account for the possible Pleistocene terrestrial connections of three rainforest-influenced *Muridae* rodents, which would indicate that the

Pleistocene migrations of these taxa were instead replaced by a vicarious evolutionary history corresponding to the fragmentation of Sundaland in the Pliocene. This vicariance has been suggested repeatedly and usually against the prior expectation of younger Pleistocene patterns (Clouse and Giribet, 2010; Gorog et al., 2004; Shih et al., 2009). At the Isthmus of Kra, the few studies that have explicitly estimated divergence time support a vicariant scenario (de Bruyn et al., 2014; Patou et al., 2010). An additional difficulty is therefore noted here, which will inevitably affect the interpretations of the analyses carried out. Although many local taxa are endemic (Myers et al., 2000), many others are widespread throughout the region (Heaney, 1986).

Another parameter to be taken into account upstream in phylogeographic models is genetic differentiation. For example, widely distributed terrestrial arthropods that are genetically differentiated show little intraspecific genetic variation in continental South-east Asia north of the Kra Isthmus (Azuma et al., 2006; Lohman et al., 2008; Su et al., 2007). Numerous studies on vertebrates have highlighted genetically distinct lineages and/or cryptic species, notably *Paradoxurus hermaphroditus* (Patou et al., 2010), *Panthera tigris* (Luo et al., 2004) and birds (Fuchs et al., 2008). However, according to Lohman et al. (2011), the differences in the rates of discovery of cryptic species are more a reflection of the different research traditions of vertebrate and invertebrate taxonomists. Mason et al. (2019) suggest that a much higher sampling density of Sundaic taxa would shed more light on the geographic discrimination of cryptic species. Geographic disjunctions generate barriers at the origin of butterfly cladogenesis (Müller et al., 2010) and cryptic genetic differentiation of mammalian subspecies (Luo et al., 2004) or arthropods (de Bruyn et al., 2014). The notion of refuge has also been interpreted or discussed in work that has served as a basis for the creation of models. For example, landforms may have acted as refuges during the drier periods of the Plio-Pleistocene (Cannon and Manos, 2003; Lim et al., 2011; Moyle et al., 2005; Quek et al., 2007), enabling ancient lineages to be preserved and spurring the genesis of new taxa with restricted ranges (Fjeldsa and Lovett, 1997). Changes in the hydrographic network (Barber et al., 2000; Crandall et al., 2008; Dodson et al., 1995) itself and its extensions in the form of estuary, mangrove or peat swamp habitats have resulted in the connectivity of aquatic taxa. Finally, phylogeography mobilizes a spectrum of multiple indirect inferences (stochastic, tectonic, volcanic, climatic, etc.) that are difficult to test in the fossil record, providing numerous examples and making paleontological transposition that is not ad hoc even more difficult, according to the authors.

#### 4.3. Isotope, methods and limitations

Isotope analyses are routinely used in palaeontology, but many new parameters and new methodological constraints are emerging in an effort to take more aspects of reality into account. As indicated by McAllister et al. (2022), stable isotope techniques applied to sediments, guano, dental enamel, speleothems or biomolecular material are making it possible to develop palaeoenvironmental reconstructions, but are still in their infancy for answering palaeoenvironmental and biodiversity evolution questions. While the diagenetic controls associated with the hot, humid environments that characterize the intertropical region are not yet fully understood, the availability of stable isotope sources also varies from site to site. In addition, subtle variation in the partial pressure of atmospheric CO<sub>2</sub> and  $\delta^{13}\text{C}$  values may have occurred over time and affect interpretations of  $\delta^{13}\text{C}$  values as being exactly equivalent to forest cover when this is not the case (cf. Louys and Roberts, 2020). By way of

illustration and prospectively, the favorable influence of the CO<sub>2</sub> rate for the forest with respect to the savannah has been modelled by Kumar et al. (2021).

In the 1990s, the isotopic adventure remained reluctant to take on the Asian tropical world despite our requests and endeavored to develop studies on the temperate environment (Bocherens, 1999). The psychological barrier was then broken (Martin et al., 2008) by correlating the  $\delta^{18}\text{O}$  values of carbonates and phosphates, making it possible to identify inter-taxonomic differences and/or differences linked to body temperature, initially as a diagenetic test. This was followed by a straightforward application, including on sites where the establishment of faunal assemblages had not been taken into account, to the point of supporting the classic hypothesis in palaeontology of flexibility in diet via isotopic analyses (Bocherens et al., 2017). In order to demonstrate this, it was necessary to postulate that isotopic analytical results were references for inferring one diet or another. Several developments were then proposed (see Ma et al., 2019; Suraprasit et al., 2020). To see whether these developments are legitimate, we need to go back to the basic principles of isotopic analysis.

Discrimination in the isotopic composition of carbon makes it possible to determine the evolution of plant cover and, over-all, the  $\delta^{13}\text{C}$  values of plants are closely linked to C4 production (Cerling et al., 2011). Thus, C4 plants (tropical and subtropical grasses and arid-adapted shrubs) minimize photorespiration by separating initial CO<sub>2</sub> fixation with  $\delta^{13}\text{C}$  values between  $-17\text{‰}$  and  $-9\text{‰}$  (Ehleringer et al., 1997). The majority of plants (trees, most shrubs, temperate grass) have a so-called C3 physiology of photorespiration with  $\delta^{13}\text{C}$  values between  $-32\text{‰}$  and  $-20\text{‰}$ . Within tropical C3 plants there are also distinct carbon isotope ranges, due in part to edaphic factors (Cornwell et al., 2018), so that there is an increasing value of  $\delta^{13}\text{C}$  values from tropical rainforests to tropical seasonal forests to tropical deciduous forest and then xeric woody scrub (Diefendorf et al., 2010). Depending on the trophic chain, it is then possible to distinguish the value of  $\delta^{13}\text{C}$  among herbivores between those consuming exclusively C3 plants (below  $-10\text{‰}$ ), those of mixed C3/C4 habitats (between  $-10\text{‰}$  and  $-2\text{‰}$ ), and finally pure C4 diet (above  $-2\text{‰}$ ) (Lee-Thorp et al., 1989; Cerling and Harris, 1999; Cerling et al., 1997, 1999; Koch, 1998; MacFadden et al., 1999). Beyond this, the diet of carnivores is in turn recomposed. It should be noted that all isotopists make it clear that the trophic chain must be calibrated according to the local parameters available. While this is the basic toolbox for isotopists, there are a number of drawbacks. If succulents are present in the environment, as is the case in the tropics, they use an alternative photosynthesis pathway, CAM (Crassulacean Acid Metabolism), which gives carbon isotope ratios similar to those of C4 plants (Tykot, 2004). Furthermore, although  $\delta^{13}\text{C}$  values of facultative CAM plants have long been known to extend well into the range below  $-20\text{‰}$ , this value is often tentatively used as threshold for character coding to distinguish C3 from CAM species in studies of CAM evolution, Messerschmid et al. (2021) conclude that the evident continuum between CAM and C3 photosynthesis cautions against the usage of a  $\delta^{13}\text{C}$  threshold in macroevolutionary studies.

The  $\delta^{18}\text{O}$  of carbonates is influenced by several factors such as latitude, altitude, aridity, precipitation and evaporation (Dansgaard, 1964; Gonfiantini et al., 2001; Longinelli, 1984; Luzet et al., 1984; Pederzani and Britton, 2019; Rozanski et al., 1993). Provided these conditions are met, the  $\delta^{18}\text{O}$  carbonate of tooth enamel is commonly used to investigate the isotopic composition of ingested water. Thus, grassland-inhabiting grazers may have higher  $\delta^{18}\text{O}$  enamel values than forest-dwelling browsers. Obviously, the first step is to check that the signal obtained and the vector studied are geographically consistent. For example, on the Kalimantan coast, vegetation at the start of MIS 3 was interpreted as alternating montane



forest and savannah for the glacial period and as rather dry lowland forest, sometimes with the presence of mangroves (Hunt et al., 2007), whereas, according to isotope analyses of guano, forest habitats would have persisted during the Late Pleistocene. However, as Wurster et al. (2010) point out, these data may be biased because most bats and swifts only feed in wooded environments. What about the signals conveyed in the fossil record with the central aim, which interests us, of being able to report on the evolution of environments and biodiversity?

According to Puspaningrum et al. (2020) all Lower Pleistocene *Proboscidea* from Java have  $\delta^{13}\text{C}$  values compatible with the range expected for herbivores from closed canopy forests to open grasslands, while the values for taxa from the Sangiran Formation are indicative of savannah-type vegetation. Furthermore, for the Middle Pleistocene assemblages of Kedung Brubus, in the Bapang Formation and those of Trinil, Sunggu and Ngandong attributed to the Upper Pleistocene, the  $\delta^{13}\text{C}$  values of *Stegodon* and *Elephas*, are concentrated in the range of C4 plants associated with herbaceous vegetation with the exception of rare specimens that indicate a mixed diet. It would therefore seem that *Proboscidea* were able to live in different environments and that they adapted over time. However, as these authors illustrate (fig. 3, p. 5 and fig. 5, p. 9), the chronological spectrum of the different assemblages taken into account covers several climatic variations and the answers provided remain global and limited to the rare samples selected. The same applies to faunal data from Niah caves in Kalimantan taken into account by Cranbrook and Piper (2007) who suggest a rainforest habitat during the Late Pleistocene associated with montane elements and signs of disturbance, but the chronological resolution of this work is extremely low compared with the palynological series used as a reference.

The use of stable carbon isotopes in the enamel of mammalian teeth from mainland or island South-east Asia has unfortunately focused on series whose dating is controversial or, more often, whose chronological resolution is imprecise or too great, indiscriminately mixing different climatic stages in a single assemblage (see Bacon et al., 2018a; Bocherens et al., 2017; Janssen et al., 2016; Pushkina et al., 2010; Suraprasit et al., 2018, 2019). This general point has been discussed, both from the point of view of the actual coexistence or otherwise of certain taxa in an assemblage at a given time and their supposed ecological values (cf. Zeitoun et al., 2010, 2015) and, more generally, from the point of view of the necessary chronological resolution that is essential for comparing primary palaeontological or isotopic data with global climate cycles (cf. Zeitoun et al., 2019). We briefly return to this point here, particularly when it was put forward to test the hypothesis of a glacial effect in the South-east Asian tropics or, more specifically, the existence of a savannah corridor during the LGM.

According to Janssen et al. (2016) the correlation observed between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of herbivores confirms that enriched precipitation and  $\delta^{18}\text{O}$  values of vegetation coincided with C4 abundance during the presumed glacial periods and that a relative break in vegetation balance is related to the contrast between glacial and interglacial precipitation due to the rapid flooding of Sundaland. However, if we go back to the sites studied by these authors, we see that, for Wajak, the dates are uncertain. They indicate a MIS 3 glacial origin according to Storm et al. (2013) or a Holocene interglacial origin according to Shutler et al. (2004). This could correspond to a mixture of specimens from glacial and inter-glacial periods in the collection considered. For the Padang and Sibrambang sites, taxonomic correlation with the Punung fauna is used as a criterion, whereas Punung shows taxa from different environments. For Trinil HK, Joordens et al. (2015) indicate an age between  $0.43 \pm 0.05$  Ma and  $0.54 \pm 0.1$  Ma but assume that there is a possibility of diagenetic alteration and mixing in

the series considered. As for the Sangiran specimens, they come from a stratigraphic sequence that may extend over several hundred thousand years, spanning several glacial or interglacial episodes. Furthermore, it is not stated whether the specimens studied come from the Sangiran Formation, the younger Bapang Formation or whether they are of mixed origin (Janssen et al., 2016).

In a study dedicated to testing the existence of the savannah corridor on the basis of mammalian faunal assemblages from the Boh Dambang site in Laos, Bacon et al. (2018b, p. 422) state: “*it was not clear if the deposit represented a mix of older and younger fauna or just older fauna that had been eroded into a younger deposit*”. Furthermore, the choice of sites for comparison is not relevant to answering the question posed. Indeed, for the age of the other Laotian sites taken into account, Bacon et al. (2015, p. 117) themselves state : “*Despite being major fossil sites in the Southeast Asian Pleistocene record, Tam Hang and Nam Lot have only ever been discussed using estimated chronologies (Bacon et al., 2008b, 2011, 2012; Durringer et al., 2012)*”. For the Duoi U’Oi site in Vietnam, the date of  $63 \pm 3$ ka of one calcitic floor does not correspond to the assemblage itself and, moreover, according to Bacon et al. (2008a) the faunal corpus is made up of remains from three locations (*id est* 1, 2 and 3) in the cavity, brought together in a single collection. For the Sibrambang site in Sumatra, the same authors state: “*Despite recent attempts to relocate it in western Sumatra, its location and geological context are currently unknown*” (Bacon et al., 2015, p. 103). Finally, at the Thum Wiman Nakin site in Thailand, the ages obtained for the faunal assemblage indicate a very broad chronological spectrum, from 8 to 350 ka (Esposito et al., 2002), encompassing several climatic phases and probably indicating mixing in the series taken into account.

Using Zn isotopes, Bourgon et al. (2020) seem to indicate a case of good preservation of the trophic level between the different taxa from the Laotian site of Tam Hay Marklot, but the authors specify that the taphonomic origin of the remains, between primary deposit or reworking of ancient fossiliferous deposits, is unknown. Several loci appear to have been collected, and it is not possible to distinguish between them in a single faunal list. If the series is complete, it is ideal since it is dated on both sides of the LGM, *id est* between 26.5 and 19 ka. The isotopic results logically suggest an environment ranging from dense tropical rainforest to open savannah. The primary data could have indicated a succession of distinct environments over time if they had not been amalgamated into a single batch. It would then have been possible to monitor whether there had been an evolution in biodiversity or, whether or not, a mosaic landscape had persisted on either side of the LGM. It is also regrettable that a sequential sampling was not carried out to compare intra-individual and inter-individual variations to account for any climatic seasonality or flexibility in the diet of the various taxa. This question is central. Indeed, as can be seen by comparing the spectra of the isotopic data produced by Bacon et al. (2018b, Fig. 10) and that of Suraprasit et al. (2021, Fig. 4), for the Gaur (*Bos gaurus = Bos frontalis*), we see that the distribution of point values of  $\delta^{13}\text{C}$  is from  $-3$  to  $+1.5$  ‰ for the different specimens at Boh Dambang while it is  $-2$  ‰ to  $+1$  ‰ for sequential data from a single individual at Tham Lod. This high overlap of values between a single individual and several individuals suggests that the data from Boh Dambang are not exploitable as indicators of the diet and consequently the environment of this site used to test the savannah corridor hypothesis during MIS2.

Although there are four main deposits in Yai Ruak cave, Suraprasit et al. (2019) chose to deal with the faunal assemblage of breccia level 2, which guarantees the homogeneity of the assemblage under consideration. While the isotopic data provide valuable information, particularly as a result of the sequential sampling of the teeth, the impossibility of quantifying

the age and, above all, the duration of the assemblage is a major obstacle to palaeoenvironmental interpretation. Indeed, according to these authors while analyses of  $\delta^{18}\text{O}$  obtained from the Rhinoceros allow them to identify a prolonged or non-contrasting wet season and  $\delta^{13}\text{C}$  a slight gradient in a habitat remaining closed for this taxon, the global data indicate a variety of the ecosystems ranging from closed forests to open environments dominated by C4 plants. It is therefore not possible to say whether there was a mixed habitat for which the different taxa are indicators or whether it is a mixture of habitats that have succeeded one another over time. Suraprasit et al. (2019, p. 3) agree, stating that “*the existence of savanna grasslands in the continent of Peninsular Thailand during the Pleistocene has never been demonstrated because the available proxy data are scarce*”. We do not use the comparisons made by these authors to calibrate their assemblage over time, as the references they use for this purpose are of lesser quality than their own, both from the point of view of the analyses (which are not sequential sampling) and of the way in which taphonomic conditions are taken into account.

The Khok Sung site is located in a sand pit that is currently being exploited and has benefited from methodological developments for its dating (Duval et al., 2019), combined US-ESR dating provides two possible ages of  $130 \pm 29$  ka and  $217 \pm 36$  ka for some of the fossils but no sediments associated with the measured samples were available, nor was it possible to carry out in situ gamma dose rate measurements due to the high water level. The sandpits in which it is located were deposited in the form of two sets of sinuous channels in which six units were distinguished. The faunal assemblage present in unit 4 and at the top of unit 3 is made up of fluvial contributions, some of which have a polished structure indicating reworking prior to deposition, but almost complete skeletons are also present, indicating taphonomic heterogeneity (Duangkrayom et al., 2014). Isotopic analysis by Suraprasit et al. (2018) indicates a variety of diets, ranging from pure C3 to C4 plants. The stable isotopic distinction between C3 and C4 plants suggests that the Pleistocene habitats ranged from closed forests to open grasslands but once again it is not possible to distinguish contemporary landscape mosaics or landscape evolution over time. If the intra-tooth variability in enamel  $\delta^{18}\text{O}$  values of certain taxa provide information about significant seasonal variations in precipitation and temperature, and humid conditions, the comparison with cenogram analyses is not relevant. Indeed, we have shown that although the approach was useful in its time (cf. Tougaard and Montuire, 2006), an application of this type of comparative analysis to assemblages that are well identified chronologically by layer differs from a global analysis encompassing all the layers (Zeitoun et al., 2019).

The work of Pushkina et al. (2010) has the advantage of producing  $\delta^{13}\text{C}$  values for modern taxa but on the other hand, comparison with the Pleistocene faunal assemblage of Thum Wiman Nakin reveals a range of habitats from closed canopy forest to open C3 and C4 habitats that is more likely the consequence of a mixture of several successive environments between 8 and 350 ka according to the dating of this assemblage (cf. Esposito et al., 2002) than of synchronous ecological mixing. Similarly, Louys and Roberts (2020) carried out a global analysis of several sites whose assemblages were mixtures and/or had uncontrolled chronologies. This they agree with, as they consider it important to note that the modern baseline data needed to correctly interpret the fossil record and to place the deep period geobiological record in a modern context is almost entirely lacking.

## 5. Perspectives

In attempting to resolve various palaeontological questions concerning climatic, palaeoenvironmental and ecological evolution, it is useful to take into account the limiting factors mentioned above in order to improve the quality of possible answers and draw conclusions that are reliable and properly supported. One of the major problems is therefore the availability of distinct faunal assemblages that are well dated and whose chronological range lies on either side of the LGM or other glacial maxima, so that their ecological realities can be quantified if they are recorded in the fossil record. Natural mixing due to taphonomic processes on the one hand, particularly in karstic environments, or deliberate mixing of fauna in collections or series to increase the corpus of specimens on the other, make it impossible to answer the question of whether or not there is a possible phasing between global climate change and the evolution of biodiversity, it is useful to take into account the limiting factors mentioned above in order to improve the quality of possible answers and draw conclusions that are reliable and properly supported. One of the major problems is therefore the availability of distinct faunal assemblages that are well dated and whose chronological range lies on either side of the LGM or other glacial maxima, so that their ecological realities can be quantified if they are recorded in the fossil record. Natural mixing due to taphonomic processes on the one hand, particularly in karstic environments, or deliberate mixing of fauna in collections or series to increase the corpus of specimens on the other, make it impossible to answer the question of whether or not there is a possible phasing between global climate change and the evolution of biodiversity.

There seem to be sufficiently effective tools for recognizing mixed habitats, such as the synecological method undertaken by Louys and Meijaard (2010). However, if a mixed habitat is detected for the Niah caves (Kalimantan), Tam Hang (Laos) and Ban Fa Suai I (Thailand) sites, the question that arises is the nature of this mix. Have Louys and Meijaard (2010) recognized mosaic landscapes, or is the mix identified merely the reflection of taphonomic mixing? Niah caves is a complex site with several distinct localities where, for example, there are no orangutans everywhere (Piper and Rabett, 2009). The mixture of different habitats is at least due to such a taphonomical point and is probably diachronic since, according to Hunt et al. (2007), the region was cyclically dominated by lowland forests, montane forests and open savannah-type vegetation. At Tam Hang, the absence of a record of the position of the various specimens means that a corpus of diachronic faunal elements has been built up. At Ban Fa Suai I, the chronological alternation of two assemblages has been described (Zeitoun et al., 2010). The mixed habitats reported by Louys and Meijaard (2010) in the latter case are therefore more the result of a mixture of data than the reality of a mosaic landscape. We therefore need to be in a position to specify whether the mixed environments reported by different media, whether palaeontological or isotopic, reflect an ecological reality or an analytical imprecision.

It has to be said that in the literature produced these trivial bases are largely forgotten. Even when effective geochronological supports are mobilized, the age of deposits containing fossils does not always correspond to that of the fossils themselves. The problem is that we are unable or unwilling to treat fossils by distinct stratigraphic units, even though this is a prerequisite for testing palaeoenvironmental hypotheses or quantifying the evolution of biodiversity (see Saegusa, 2001). Moreover, several authors had long been reluctant to consider the Indochinese paleontological assemblages as they are mixtures from different periods and environments (Patte, 1928; Colbert, 1943; Pei, 1957; Kahlke, 1961; Orchiston and Siesser, 1982; de Vos, 1983, 1984). Despite a number of methodological precautions, it is

regrettable that most of the isotopic analyses were carried out on inadequate series, as we have already seen.

Even if the Pha Bong case is a little distant from the period that interests us *id est* the LGM to test the hypothesis of a savannah corridor, it is revealing of the precautions that it will be necessary to add in the future in the use of isotopic tools. Indeed, while we can also criticise the lack of dating or duration for the Pha Bong assemblage used by Bocherens et al. (2017) on the one hand and the reference made to the Thum Wiman Nakin site, whose chronological spectrum extends over several hundred millennia, on the other hand, several methodological precautions were taken to determine the *Gigantopithecus* diet that should be followed to answer the question concerning more recent periods. Thus, it has been assumed that larger mammals tend to have lower  $\delta^{18}\text{O}$  values than smaller ones due to a lower metabolic rate (cf. Bryant and Froelich, 1995) and that folivorous primates have higher  $\delta^{18}\text{O}$  values than frugivorous *Primates* (Carter and Bradbury, 2016) and, according to Bocherens et al. (2017) the restricted range of  $\delta^{13}\text{C}$  values for *Gigantopithecus* indicates a habitat restricted to forested environments with a pure C3 diet and an absence of C4 grass. However, certain points should be noted as new restrictions. CAM plants, particularly succulents in forest environments, are not taken into account whereas Schoeninger (2014) showed that some primates consumed up to 30% of C4 or CAM foods. Furthermore, another difficulty could arise in the case of savannahs, whose genesis we have seen could be controlled by edaphic factors (Demangeot, 1999; Soares et al., 2015; Thomas-Barry et al., 2021). Indeed, according to Lloyd et al. (2015), there are differences between savannah soils, which systematically have lower concentrations of exchangeable cations and higher C/N ratios than neighboring forest plots and these differences between soils are also reflected in the average leaf characteristics of the canopy, with savannah trees generally having a higher leaf mass per unit area, but a lower mass of nitrogen and potassium, which has an impact on  $^{13}\text{C}$  isotopic discrimination. Soil potassium would therefore play a critical role in modulating the structure and function of tropical vegetation. Finally, recent studies (Fannin and Scott McGraw, 2020) also suggest that the main factor in  $\delta^{18}\text{O}$  variation in certain primates living under the canopy is not so much their diet as their vertical stratification.

Prior to their study, Bocherens et al. (2017) aimed to identify whether flexibility in the ecological niche of *Gigantopithecus* could explain its extinction, given that climate change will have a stronger impact on species with limited ecological flexibility. This flexibility is well known in *Cervidae*, which are generally considered to be adaptive and often mixed vegetation eaters (Kitchener et al., 1990; Oka, 1998). Actualist or palaeontological studies of long evolutionary periods or different environments show this (Berlioz et al., 2017; De Miguel et al., 2010; Gebert and Verheyden-Tixier, 2001; Hofmann, 1989; Uzunidis et al., 2022) so that studies of dental micro- and meso-wear are particularly worthy of development in South-east Asia. Such studies indeed indicate local and global environmental trends, such as those recognised in several taxa, particularly *Ungulates* (Fortelius and Solounias, 2000; Merceron et al., 2004; Merceron et al., 2007; Rivals et al., 2010; Rivals and Semprebon, 2011). Geographical and/or temporal variability in diet and vegetation structure has been illustrated during the Cenozoic (Mihlbachler et al., 2011; Rivals et al., 2007; Rivals and Lister, 2016; Semprebon and Rivals, 2007, 2010; Semprebon et al., 2016). And improvements have even been made to allow correlations between vegetation, climate and niche use (Calandra et al., 2008; Rivals et al., 2012). Wirkner and Hertler (2019) attempted to put the method into practice on *Muntiacus muntjak* from the E. Dubois collection preserved in Leiden, but this consists of remains brought back from the caves of Lida Ajer, Sibrambang, Jambu and more generally from the

Padang Highlands without dating and sometimes without distinction of locality. For the three Sumatran caves, the *Muntiacus muntjak* are classified as mixed feeders, which for the moment makes it impossible to assess whether this is the reflection of a seasonal phenomenon or a mixture of environments linked to a climatic evolution for lack of dating, especially as the authors specify that the differences observed for two of the caves concerned can-not be validated statistically. Finally, the study of different types of tooth wear carried out by Amano et al. (2016) on Javanese cervids and bovids in the Late Pleistocene thus succeeded in showing a certain seasonality in clear chronological contexts during the LGM. Extending these studies to Asian savannah environments would help to illustrate what seasonality looks like in these biotopes which is encouraging for us to go further.

Further work was also undertaken on *Naemorhedus goral*, *Naemorhedus griseus*, and *Capricornis sumatraensis* which are taxa that co-exist in Pleistocene assemblages in Thailand, suggesting a more widely overlapping distribution in the past than today. Investigating their diet and habitat preferences using stable carbon and oxygen isotope analyses Suraprasit et al. (2020) revealed different ecological patterns between both genus *Naemorhedus* and *Capricornis*, the latter taxon having a greater generalist diet (browsers and grazers) than the former that fed on pure C4 or mixed C3 and C4 plants restricted to an open landscape habitat. As far as these taxa are concerned, we can wonder about their respective abilities to adapt to altitude by remaining in place through the time even when the climate changes, rather than migrating from one area to another, especially as, during karstic erosion in tropical environments, landscape erosion helps to generate steep gradients, which explains why the cavities located highest up are the oldest (Demangeot, 1999; Dunkley, 1995).

Suraprasit et al. (2021) are finally the only ones to have carried out a sequential sampling of teeth and to have performed  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  analyses on the tooth enamel of faunal assemblages from different layers of the same site at the Tham Lod rock shelter in north-west Thailand. No doubt they are downplaying the significance of their result and that additional analyses are needed to follow the evolution of signals by taxon over time in order to obtain a more detailed expression of the synchronism or otherwise of the evolution of biodiversity on either side of the LGM. The authors limit themselves to a conclusion that is too modest from an environmental point of view. In fact, they note no significant change in  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values among mammals, nor any major seasonal variation based on the intra-dental profiles of the crowns of large *Bovidae*, whereas according to their overall interpretation in terms of diet distribution (Fig. 6, p. 8), the various Heinrich events 3, 2 and 1 are already perceptible. The Bølling-Allerød event, on the other hand, is not marked. The result of this study is that there is evidence for the existence of synchronous mosaic landscapes and that, on the other hand, not all global climatic events are recorded in faunal assemblages which is also encouraging for us to go further.

## 6. Conclusion

The palaeontology of Southeast Asia remains a field that still lacks a great deal of reliable data, while many definitive conclusions are drawn on unsubstantiated grounds. A brief historical review shows how gaps remain and have not yet been filled by sufficiently rigorous approaches. Present-day South-east Asia is characterized by two biogeographical entities (Indochinese to the north and Sundaic to the south) adjoining a Wallacean area further east and exclusively insular. Today, the Indochinese-Sundaic transition zone varies close to the Kra Isthmus depending on the plant or animal taxa considered. The region is characterized by a climate influenced by a monsoon phenomenon (Tada and Murray, 2016)

and a more or less dense forest cover depending on altitude and soil type. Throughout the Quaternary, the region was subject to eustatic changes linked to global climate change which had an impact on a significant proportion of the land (Sathiamurthy and Voris, 2006; Voris, 2000).

As far as the large mammalian fauna is concerned, the boundary between the two present-day biozones has fluctuated overtime. The region is characterised by a faunal assemblage initially identified in southern China with tropical taxa (Bien and Chia, 1938; De Terra, 1943; Fromaget, 1936; Granger, 1938; Matthew and Granger, 1923; Patte, 1928; Pei, 1935; Young, 1932) described by von Koenigswald (1938–1939) as “Sino-Malay”, which has been considered a chronological marker of the Middle or Upper Middle Pleistocene (Colbert and Hooijer, 1953; Ginsburg et al., 1982; Han and Xu, 1985; Kahlke, 1961; Pei and Wu, 1956; Schepartz et al., 2003). However, as palaeontology has developed locally over the years, the biostratigraphic correlation established between the different assemblages has long appeared unsatisfactory because it is based on mixtures of sites from different environments. As a result, the historical reference series and even most of the new assemblages unearthed cannot currently be properly used for palaeoecological or palaeoenvironmental purposes because of taphonomic gaps.

As far as the Quaternary in South-east Asia is concerned, three major questions have been addressed with regard to the biodiversity of the regional megafauna: the possible impact of humans (cf. Martin, 1967), the Toba mega-eruptions (cf. Chesner, 2012), or the more or less extensive and continuous existence of a savannah on Sundaland during the LGM (cf. Heaney, 1991). When we looked at this last point, we realized that few studies were able to answer the question because of the lack of appropriate media, or at least because of the incompleteness or relevance of the information available. After a period of positioning for or against the hypothesis of a savannah corridor during the LGM, when everyone seemed to be leaning towards the confirmation bias, the time came to note that several elements constituted either a confirmation or a denial. This then led to the current phase of a consensus admitting to disagreement, with a tendency towards conciliation proposing a more complex reality, *id est* the coexistence of local particularisms (vegetation with varying degrees of cover depending on proximity to the coast or altitude, north or south of Sundaland).

No doubt we now need to try and provide a real answer to the question of whether or not this savannah corridor exists. It cannot be both present and absent although it is still a question of everyone agreeing on his definition of the savannah in South-East Asia. So is not the real question whether or not it is possible to answer this question or to reformulate it? At the very least, it is necessary to try, if possible by remaining as close as possible to the field data. The weakness of the basic data is apparent in almost all the studies linked to primary data, and depending on the degree of interpretation, the hypothesis may or may not be accepted. Work will probably have to be undertaken that will be more arduous and time-consuming if the results are to be more reliable and lasting. Successive constructions and elaborate models often distance themselves from reality by multiplying proxies, which by definition are only approximations, without being able to reach it.

In the treatment of the savannah corridor hypothesis, phylogeography appeared to be a powerful tool, but one that implements numerous inferences that are difficult to control, with multiple ecological overlaps and several different methods. Above all, this tool raises many questions when there are incongruities from one taxon to another and sometimes provides snippets of answers, but these are based on older elements that incorporate incomplete primary data or data that has since been contested. In palaeontology, Tougard

(2001) was one of the first to use the biogeographical approach in a synthetic way to deal with Pleistocene faunas on the continent and the Sundaland islands, but on a scale that does not allow us to answer the question for the LGM. However, numerous studies have echoed her conclusions. The aim is not to accumulate studies in favour of one model or another (confirmation bias), but to determine whether we have the information we need to answer the questions posed. In this respect, and in particular with regard to the various models used, new studies are calling into question the foundations of phylogeographic or biogeographic studies by proposing that, due to its subsidence, Sundaland was not covered by the sea in the way that has been assumed until now, particularly from 400 ka onwards (see Husson et al., 2020; Salles et al., 2021; Sarr et al., 2019). From the point of view of isotopic approaches, these are carried out on media that involve numerous proxy chains, the accumulation of which makes interpretation tricky. We have highlighted the fact that CAM plants are not taken into account when reconstructing diets and environments. One major criticism that we have levelled at the application of isotopic tools in palaeontology is that they focus on series that are unsuitable for answering questions about the evolution of environments over time because of the poor taphonomic quality of the palaeontological assemblages taken into account. In terms of ecological answers, it is undoubtedly appropriate to combine the isotopic approach with that of dental micro- and meso-wear. Similarly, the sequential sampling along mammalian high-crowned teeth that can allow quantification of the importance of seasonal variations in stable oxygen and carbon isotope composition related to the then prevailing environmental conditions (Balasse, 2002; Fricke and O'Neil, 1996; Fricke et al., 1998; Kohn et al., 1998) should be systematically implemented. It is also the pitfall of taphonomic gaps that limited the scope of the pioneering cenographic study by Tougaard and Montuire (2006) to account for the palaeoenvironmental evolution of continental faunas in Sundaland during the Pleistocene. We strongly recommend the implementation of systematic fine excavations that take into account the many taphonomic factors that affect palaeontological assemblages in order to avoid considering sites as reliable environmental contexts when this is still not the case despite the proposal of some unfounded interpretations (cf. Bacon et al., 2023). By taking into account faunal assemblages layer by layer, as was done at Tham Lod (Suraprasit et al., 2021), it will be possible to see whether or not palaeoenvironmental changes were recorded in the register during the LGM. Especially since, as Stimpson (2012) pointed out, closed canopy forest habitats may have been considerably reduced and mixed with, or replaced by, wooded savannah and grassland habitats and fragmented into refugia. It is therefore a question of being able to account for a real ecological mix (mosaic landscape) or a mixing effect, in particular for the question of the existence of a savannah corridor, the scale and extent of which there is no consensus on. The important thing, therefore, is to give ourselves the means to answer the question posed, bearing in mind that the important thing is to contribute knowledge and not to make ourselves known.

#### **Disclosure of interest**

The authors declare that they have no competing interest.

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