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The origin of the Malesian fossil turtle diversity: Fossil versus molecular data

L'origine de la diversité des tortues de Malésie : données fossiles versus données moléculaires

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ABSTRACT

The origin of the turtle fauna of Malesia is analysed here through a review of the literature, a re-evaluation of previously described material, and the description of new material. Very few data are available prior to the Quaternary. While the Early Pleistocene record is largely dominated by reports of giant tortoises, the Middle Pleistocene record provides reports of the first occurrences of most extant taxa living in the area. Most, if not all, of the faunas have stronger relationships with Indochinese than with East Asian taxa, suggesting that colonisation largely followed the Siva- or Sino-Malayan routes, allowing turtles to invade the Sunda Shelf and disperse further east during periods of low sea-level. On the other hand, there is nearly no fossil data to understand the origin of the six endemic Malesian species, but molecular studies suggest that most of these taxa may have evolved in Malesia well before the Quaternary dispersal of the Indochinese fauna. In addition to clarify several fossil identifications, we provide evidence that the box turtle of the "*Cuora amboinensis*" species complex arrived in the Philippines before the early Middle Pleistocene. We also confirm that *Duboisemys isoclina* is an endemic extinct genus and we discuss its relationship to continental and endemic turtles.

Mots clés :
Herpétofaune
Asie du Sud-Est
Colonisation
Dispersion
Tortues

RÉSUMÉ

L'origine de la faune de tortues de Malésie est analysée ici à travers une revue de la littérature, une réévaluation du matériel déjà décrit et la description de nouveaux fossiles. Très peu de données sont disponibles avant le Quaternaire dans cette région. Alors que le registre du Pléistocène Inférieur est largement dominé par les tortues terrestres géantes, le registre du Pléistocène Moyen présente les premières apparitions de la plupart des taxons actuels vivant dans la région. La plupart des faunes ont des relations plus étroites avec les espèces indochinoises qu'avec les taxons d'Asie orientale, indiquant que les faunes se sont dispersées au travers la Sonde et plus à l'Est via la route Siva ou Sino-Malaisienne au moment où les terres étaient émergées. D'autre part, il n'y a pratiquement pas de données fossiles pour comprendre l'origine des six espèces endémiques, mais les études moléculaires suggèrent que la plupart des taxons ont évolué en Malésie bien avant la dispersion quaternaire de la faune indochinoise. En plus de clarifier l'identification de plusieurs fossiles, nous apportons la preuve que les tortues-boîtes du complexe

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d'espèces « *Cuora amboinensis* » sont arrivées aux Philippines avant le début du Pléistocène Moyen. Nous confirmons également que *Duboisemys isoclina* appartient à un genre endémique éteint et nous discutons de sa relation avec les tortues continentales et endémiques.

1. Introduction

Malesia (or insular Southeast Asia) consisting of the Philippines, Indonesia, Brunei and Timor-Leste, is a biogeographical province located between the Indomalayan and the Australasian or Sahul realms. The identity of that province is supported by its flora (Brummitt, 2001) and studies of the fauna seem to confirm it (Turner et al., 2001). The biogeographical complexity within this region and its location relative to the Sahul and Indomalayan realms makes it a remarkable area for the study endemic patterns, past dispersals, connectivity between land masses and associated vicariance patterns (Turner et al., 2001). In this area, sea-level changes and tectonic events (including subsidence) are known to have shaped the distribution of land masses and landscapes and consequently the biogeography of animal and plant communities (Woodruff, 2010; Husson et al., 2020; Salles et al., 2021). Parts of Malesia have been recursively connected and disconnected from other continental areas until the beginning of the Holocene (Sathiamurthy and Voris, 2006). In that respect, the nature and roles of several biogeographic boundaries (Wallace line, Huxley line, or Lydekker line among others) and of various dispersal paths from the continental to the insular part are widely debated in the literature (e.g., Ali and Heaney, 2021; Morwood, 2014). Malesia is itself divided in smaller areas of endemism and the connection between these areas is the object of important research. Turner et al. (2001) recognized nine areas of endemism within Malesia, namely: the Malay Peninsula, Sumatra, Java, Borneo, the Philippines, Palawan, Sulawesi, the Lesser Sunda Islands, and the Moluccas. These areas of endemism are often grouped into three main regions: Sundaland (Malay Peninsula, Sumatra, Java, and Borneo), Philippines (Palawan and remainder of the Philippines) and Wallacea (Moluccas, Sulawesi and Lesser Sunda Islands).

The origin of the non-marine mammalian fauna (including hominins) in Malesia has been investigated by several authors who have considered the Quaternary mammalian fossil record in the region (e.g., von Koenigswald, Sondaar, Soejono, de Vos, Hooijer, van den Bergh). The distribution and origin of reptiles have been discussed in certain cases (e.g. Delfino and de Vos, 2010; Siler et al., 2012), but rarely at the scale of Malesia, even though they can form a conspicuous part of both living and fossil assemblages. Among reptiles, the giant tortoises have attracted the most attention (e.g., Sondaar, 1981; Hooijer, 1982), but the freshwater species have only been partially described (e.g., Jaekel, 1911 and other references in this paper). Nevertheless, the non-marine turtle diversity in Malesia is relatively rich (at least 23 modern species) and its biogeographic structure in space has not been fully investigated, especially in light of the fossil record. The purpose of this work is therefore to assess how the fossil turtle record in Malesia (insular Southeast Asia, including peninsular Malaysia) can help to further understand the biogeography and evolution of the group in this part of the world. To this end, this paper is based on a review of the literature, the description of new material, and the phylogenetic assessment of the unique single endemic fossil genus, the enigmatic turtle *Duboisemys isoclina*, first described by Dubois in 1908 (Dubois, 1908).

2. Current day diversity and biogeography

2.1. Distribution of the modern fauna

Four continental families are currently represented in Malesia: the semi-aquatic and aquatic Geoemydidae, the terrestrial Testudinidae (tortoises), the freshwater Trionychidae (softshell turtles) and the freshwater Chelidae. The distribution of these continental turtle species is shown in Table 1 (excluding introduced species).

Each area of endemism contains a different number of turtle species. From the Malay Peninsula, diversity decreases successively in Sumatra, Borneo, Java, the Philippines and the Moluccas. Four areas of endemism contain endemic turtles and have low diversity, suggesting the effects of isolation. Sulawesi has two (*Indotestudo forstenii* and *Leucocephalon yuwonoi*); Palawan has one (*Siebenrockiella leytensis*); the Philippines have one (*Cuora philippinensis*); and the Lesser Sunda Islands have one endemic species (*Chelodina mccordi*) restricted to Timor Leste and Roti Island. In addition, *Cuora amboinensis* previously considered as the subspecies *Cuora amboinensis amboinensis* is restricted to the Mollucas and to Sulawesi. According to molecular phylogenetic hypotheses, of the six endemics, five (*Indotestudo forstenii*, *Leucocephalon yuwonoi* – both in Sulawesi –, and *Siebenrockiella leytensis* in Palawan, *Cuora amboinensis* in Sulawesi and the Mollucas and *Cuora philippinensis* in the Philippines) have their sister groups in continental Southeast Asia, whereas the Lesser Sunda Islands endemic (*Chelodina mccordi*) is rooted in the Melanesian/Australian fauna (Guillon et al., 2012; Colston et al., 2020; Thomson et al., 2021). The Wallace and Weber lines can explain the peculiar composition of Sulawesi compared to the rest of the fauna, with its two endemic species, and the Huxley line can explain the special composition of Palawan by comparison to the Philippines. Apart from the six endemics, the 19 other modern turtles of Malesia have distributions that extend across mainland Southeast Asia. Within these 19 species, and with the exception of *Pelochelys cantorii*, whose distribution extends from India and Indochina to Southern China and Vietnam, none extends its distribution to Japan, China, northern Vietnam and Taiwan. The origin of most turtle diversity in Malesia is therefore related to southern continental Indochina. The Philippine biogeography (Palawan excluded) merits to be detailed even if it is apparently only mostly made up taxa with a wide geographical distribution. Of the five (to potentially 6) taxa present, two are restricted to the Sulu Archipelago (*Heosemys spinosa* and *Cyclemys dentata*), and. As these two are known from Borneo but absent elsewhere in the Philippines, they could have arrived from the West via the Sunda shelf. *Cuora couro* might correspond to a recent introduction by the pet trade (Blanck et al., 2023). If we exclude that species, only three reached the main islands of the Philippines: *Cuora philippinensis* and two softshell turtles (*Pelochelys cantori* and *Dogania subplana*). While the two softshell turtles are good swimmers and may have a greater dispersal capacity, this may not be the case for the small freshwater turtles of the "*Cuora amboinensis*" species complex. In that species complex, *Cuora philippinensis* is related with *Cuora amboinensis sensu stricto* from Sulawesi and the Moluccas. This indicates that *Cuora phippinensis* is not recently derived from the populations from Borneo or from Java/Lesser

Table 1
Distribution of turtle species in Malesia (data from Turtle Taxonomy Working Group, 2021 et de Blanck et al., 2023); ! corresponds to taxa for which the introduction/indigenous status is unclear, * indicates the "*C. amboinensis*" complex recently revised,? indicates uncertain taxonomic status).
*Distribution des espèces de tortues en Malésie (données issues du Turtle Taxonomy Working Group, 2021 et de Blanck et al., 2023; les points d'interrogation correspondent aux taxons pour lesquels le statut indigène est douteux (introductions possibles), * indique les espèces du complexe* C. amboinensis *révisées récemment, ? Indique des populations pour lesquelles le statut taxonomique n'est pas clair).*

Turtle/area	Malay Peninsula	Sumatra	Borneo	Java	Palawan	Philippines	Sulawesi	Moluccas	Lesser Sunda Islands
Cuora amboinensis *							X	X	
Cuora couro *	X	X	X	X	?	?/Sulu !			X
Cuora philippinensis						X			
Pelochelys cantori	X	X	X	?	X	X	?		
Dogania subplana	X	X	X	X	X	X			
Cyclemys dentata	X	X	X	X	X	Sulu			
Amyda cartilaginea	X	X	X	X			?		
Cyclemys enigmatica	X	X	X	X					
Siebenrockiella crassicolis	X	X	X	X					
Notochelys platynota	X	X	X	X					
Heosemys spinosa	X	X	X			Sulu			
Batagur borneoensis	X	X	X						
Manouria emys	X	X	X						
Orlitia borneensis	X	X	X						
Chitra chitra	X	X		X					
Batagur affinis	X	X							
Indotestudo elongata	X								
Manouria impressa	X								
Heosemys annandalii	X								
Heosemys grandis	X								
Malayemys macrocephala	X								
Indotestudo forstenii							X		
Leucocephalon yuwonoi							X		
Siebenrockiella leytensis					X				
Chelodina mccordi									X
Malayemys subtrijuga		?		?					
Total	19	14 (15)	12	8 (10)	5	5 (6)	3 (5)	1	2

Sunda Islands now assigned to the species *Cuora couro* but that it comes from an old split occurring in the North East of Malesia (Blanck et al., 2023) that separated *Cuora philippinensis* from *Cuora amboinensis*. In addition, molecular data suggest that these species for a long time all identified as *Cuora amboinensis* were differentiating well before recent times despite fossil data have not been yet described in the Mollucas, Sulawesi or the Philippines (but see section 3.3.2 and discussion). Except for that unique case, it should be noted that no strong vicariance patterns are observed for the 18 species shared between the continental and Malesian faunas, implying that genetic flow between the continental part and the insular part was ensured for a large part of the Sunda shelf in the non distant past (Quaternary).

2.2. Origin for the endemics: nearly no fossil record, but molecular data suggest an old origin for Palawan and Sulawesi endemics

Except for *Chelodina mccordi,* none of the endemic species has a fossil record within or outside their present distribution. The origins of all other endemics have therefore to be inferred from phylogenetic results based on molecular data. *Chelodina mccordi* (represented by two distinct subspecies–one in Timor Leste (*Chelodina mccordi timorensis*) and one on Roti Island (*Chelodina mccordi mccordi*), may have diverged in the Pleistocene, whereas they may have been isolated from their New Guinea relatives during the Quaternary according to the dated tree of Thomson et al. (2021). *Chelodina mccordi timorensis* is reported from the Late Pleistocene of Timor-Leste (Samper Carro et al., 2023), which involves that the arrival of this group in the Lesser Sunda Islands should be anterior to the end of the Pleistocene and should, in addition, be constrained in the Pleistocene by molecular data. In comparison, molecular data show that the divergence between *Siebenrockiella crassicolis* (mainland and Sunda) and *Siebenrockiella leytensis* (Palawan) may be Late Oligocene or Early Miocene in age, so the origin of the Palawan endemic may be quite ancient (Thomson et al., 2021). The origin of these endemic taxon may coincide with the separation of Palawan from the continent (Hall, 2002) and with the divergence of other groups such as geckoes (Siler et al., 2012). Without fossil evidence; it is unclear whether Palawan plays the role of a refugium for *Siebenrockiella leytensis* and whether it has been hosting this species for a long time. In the latter case, it would mean that Palawan, or part of it, was emerged since at least Late Oligocene or Early Miocene. Finally, the Wallace line may have sufficiently isolated Sulawesi endemic fauna to allow a re-dispersal of the endemics to the west since the Miocene. *Indotestudo forstenii*'s closest relatives are *Indotestudo elongata* (mainland Southeast Asia) and *Indotestudo travancorica* (India), that form a clade from which the *I. forestenii* lineage may have diverged during the Miocene (Thomson et al., 2021). The phylogenetic relationships of *Leucocephalon yuwonoi*, based on molecular data, are weakly supported within the Geoemydidae (Guillon et al., 2012; Colston et al., 2020; Thomson et al., 2021). If the phylogenetic hypothesis of Thomson et al. (2021) is correct, it diverged from *Notochelys platynota* during the Late Oligocene-Early Miocene. These two endemics have an ancient origin and may have been present in Malesia at least since the end of the Oligocene for *Leucocephalon yuwonoi* and the Miocene for *Indotestudo forestenii*. *Cuora amboinensis* and *Cuora philippinensis* interrelationships with continental and sundaic *Cuora* species (*C. lineata*, *C. praschagi* and *C. couro*) requires additional studies as mitochondrial DNA and nuclear DNA deliver different messages, but preliminary data indicate that *C. amboinensis* + *C. philippinensis* split from other sundaic *Cuora* in the Middle Miocene and that the species from the Philippines differentiated itself from the species from the Mollucas and Sulawesi during the Middle to Late Miocene (Blanck et al., 2023). Nevertheless, all testudinoid endemics have a close relative of Indochinese or Indian rather than eastern origin, suggesting that early dispersal events may have occurred via the Siva- and Sino-Malayan routes (de Vos et al., 2007), and that the Taiwan-Philippine land bridge may not have functioned for turtles even in the distant past (van Koenigswald, 1956).

3. The fossil record

3.1. The pre-Pleistocene fossil record (Fig. 1)

The pre-Pleistocene fossil record is extremely poor. The earliest fossil turtles, known from vertebrate assemblages from the Early Cretaceous of Peninsular Malaysia in the state of Pahang (Teng et al., 2019), remain undescribed. Later, Eocene deposits in Sumatra have yielded a vertebrate fauna including fish, birds, turtles, and mammal remains in the Ombilin Basin near Talawi. Most of these have not been studied or described in detail, but the turtles have been identified as carettochelyids (Zaim et al., 2014). Carettochelyids are not known from the Late Eocene-Early Oligocene of Krabi in Thailand or from the Eocene of Vietnam, but they are known from the late Middle Eocene Pondaung Formation in Myanmar and from the Late Eocene of China (Hutchison et al., 2004; Claude et al., 2007; Tong et al., 2010; Claude et al., 2012; Böhme et al., 2013). As the fossils from Sumatra are not described, it is difficult to know how they could link the modern *Carettochelys insculpta* from New Guinea/Australia with other fossil lineages. The Miocene fossil record for the freshwater and terrestrial turtle fauna is limited to a single find reported from the Late Miocene Seria Formation at the Jalan Pak Bidang site in Brunei Darussalam (Borneo) (Kocsis et al., 2021). It corresponds to a large caudal vertebra of a trionychid. Part of that Miocene assemblage have been found at Penanjong beach, but it is reworked and mixed with more recent material. Fragments of Late Miocene geoemydids and trionychids are most likely present in the reworked Miocene material, but could not be identified at the generic level (Kocsis et al., 2021). The only genus that could be recognized in the reworked material is based on an epiplastron of *Cuora*, but the age of this fossil is more likely Pleistocene or Holocene owing to its preservation state. Finally, a new pig-nose turtle, *Carettochelys niahensis*, has recently been described from supposed Oligocene or Miocene rocks of Niah cave in Sarawak and might be a close relative of *Carettochelys insculpta*, the only living species of that family in Australia and New Guinea (White et al., 2023). *Carettochelys niahensis* might have been the last carettochelyid living in South-East Asia.

3.2. Early Pleistocene (Fig. 1)

The documented Early Pleistocene fossils in Malesia are giant tortoises and a few unidentified softshell turtles. Giant tortoises of the genus *Megalochelys* have been recorded from several places. The oldest records to date are from the Early Pleistocene (Gelasian) of the Wallanae Formation in South Sulawesi (van den Bergh and Aziz, 1995; van den Bergh, 1999), together with a trionychid (fragments of plastron and carapace plate). The age of the latter taxon could be older if reworked (Webb and van Dijk, 2004), and morphology of the fossils is considered consistent with *Pelochelys* but not *Chitra*. The giant tortoise was first named *Testudo margae* by Hooijer (1948) based on a scapula. Later, with the discovery of more material, it was placed in *Geochelone atlas* (Hooijer, 1954). More specimens have been found since then (van den Bergh and Aziz, 1995). The plastral material and the appendicular skeleton are known (Setiyabudi, 2016). The epiplastron is not complete enough to know if a well-developed furca was present, which would be completely consistent with *Megalochelys sivalensis* from Indo-Pakistan (see Vlachos, 2019 for use of *Megalochelys sivalensis* instead of *M. atlas*). Giant tortoises have also been described from the Lower Pleistocene Kaliglagah Formation in Bumiayu, Central Java (van der Maarel, 1932; Setiyabudi, 2009; Setiyabudi, 2016). A partial plastron, associated with a partial carapace, a pelvic girdle and a femur are known. So far, the described material consists of a single individual with an epiplastral process well developed as a furca, and most of the characters match well with *Megalochelys sivalensis*. The specimen was assigned to *Megalochelys* cf. *sivalensis* by Setiyabudi, 2009. In Java, giant tortoises have also been found in the Lower Pleistocene Sangiran beds, although not described in detail (de Vos et al., 1994; van den Bergh, 1999). Still in Java, Testudinidae and Trionychidae are reported from Lower Pleistocene beds around Patiayam but are not described (Siswanto and Noerwidi, 2016). Elsewhere in Indonesia, giant tortoises are also known from Flores, in the Ola Bula Formation of the Soa Basin, specifically from the tuff member dated to the late Early Pleistocene. Here, *Megalochelys* sp. is found below levels containing artefacts (Sondaar et al., 1994). The giant tortoises of Flores were placed in *Megalochelys* sp. by Setiyabudi (2016). Setiyabudi (2016) noted strong similarities with *M. sivalensis* but remained cautious in assigning the material to *Megalochelys* sp. The material comes from several individuals. Epiplastral morphology varies between individuals, suggesting sexual dimorphism (see Naksri et al., 2019), and there is also significant variation in furca morphology. To date, this is one of the best known sample to estimate the importance of sexual dimorphism and maturity on epiplastral morphological variation. Setiyabudi (2016) noted that the thickness of the carapace of the Flores specimens could be thinner than other *Megalochelys* found in Malesia or on the mainland, but he further pointed ontogeny could also explain the differences. The material also includes limb bones, a scapular girdle, and a complete lower jaw. A small geoemydid, tentatively assigned to *Cuora amboinensis*, was also described based on a pelvic girdle (pubis and ischium) and a carapace fragment (that fragment did not appear on figures or plates of Setiyabudi paper). We regard this as plausible, but more comparisons are required to confirm it.

Large fosssil tortoises were first identified in potential early Pleistocene deposits of the Philippines between Caloocan and Quezon by von Koenigswald (1956) but were not described. Large tortoises were briefly listed close to this area at Antipolo in the province of Rizal (de Vos and Bautista, 2003). More recently and still in this area, fossils from the Laguna Formation of Luzon were described under the name *Manouria sondaari* (Karl and Staesche, 2006). The specimen is known by a coracoid bone, a part of the scapula, a peripheral bridge plate, dermal ossicles, a humerus (30 cm-long) and a femur ($\sim$ 20 cm-long). This specimen would reach half the size of the giant turtles from Bumiayu, for which the plastron is 174 cm-long. It was first thought to belong to *Manouria* that was supposed to have evolved a large size in Luzon as a result of insularity (Karl and Staesche, 2006). It is now recognized as a small species of the genus *Megalochelys* (Turtle Extinctions Working Group, 2015). The estimated size (70–90 cm) of Turtle Extinctions Working Group (2015) may be a correct or slightly underestimated, as the carapace is usually longer than the plastron. More material is needed to know if there is a clear evolutionary unit in the Philippines in the Early Pleistocene.

3.3. Middle Pleistocene (Fig. 1)

3.3.1. Trinil, Java

Most of the known and described turtles come from Trinil in Java and were collected by the Dubois and Selenka expeditions. There has been a long debate over the existence of a single or two bonebeds at Trinil and this debate is still open. According to Huffman et al. (2022) the fossils from Trinil are coming from one layer dated late Early Pleistocene or early Middle Pleistocene. However, Hilgen et al. (2023) recent dating suggests that fossils are coming from two layers with two different ages. This being said, the fossil age would also be constrained from the late Early Pleistocene to the early Middle Pleistocene (Hilgen et al., 2023). Dubois (1908) himself named one species *Hardella isoclina*, while several species were identified and described in detail by Jaekel (1911). Jaekel's list included five taxa: *Batagur siebenrocki*, *Batagur signatus*, *Chitra minor*, *Chitra selenkae,* and *Trionyx trinilensis*;

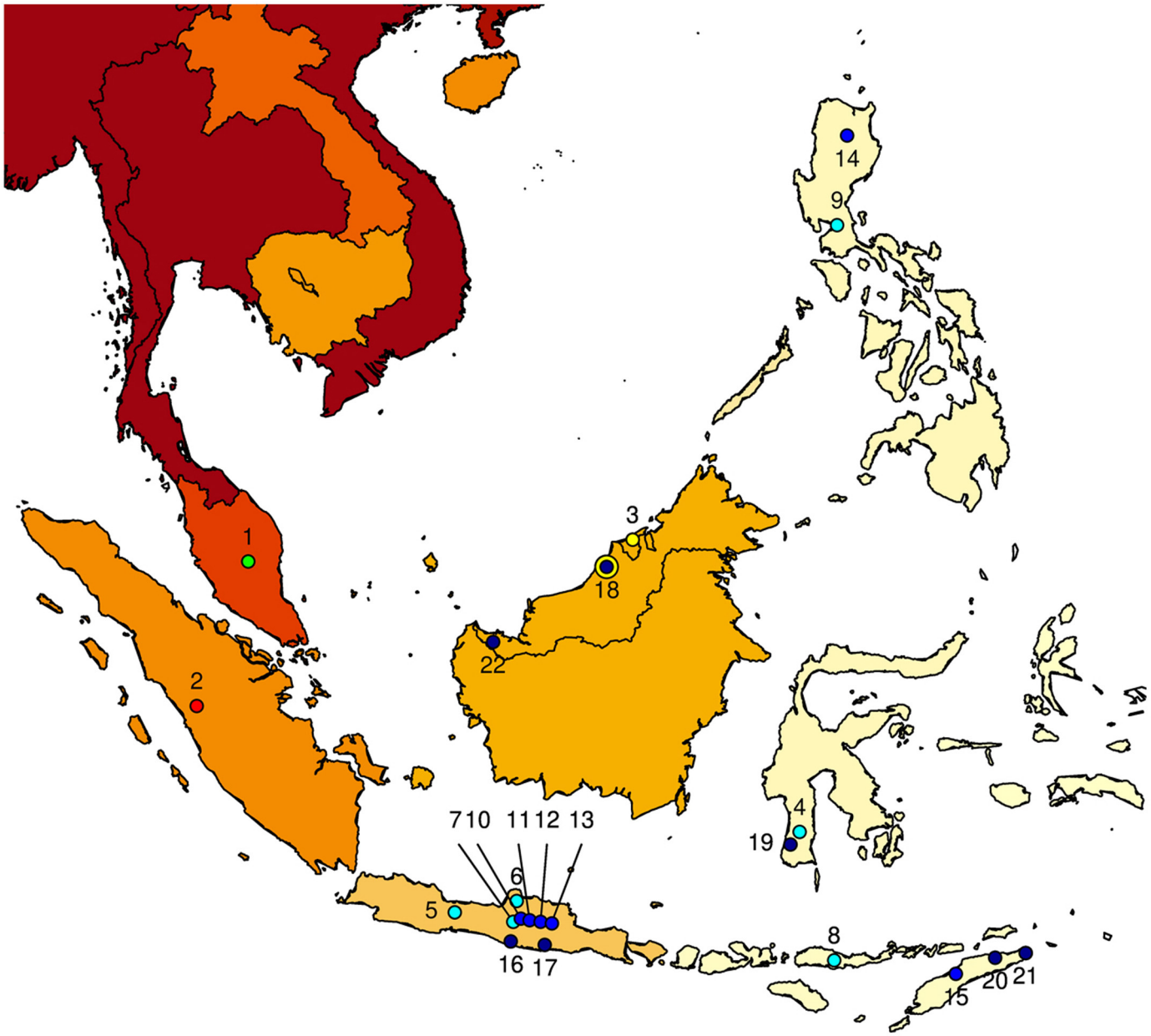

Fig. 1. Main localities for fossil turtle from Malesia. The colors of countries are proportionally darker when current day species richness increases. 1. Early Cretaceous of Pahang, 2 Eocene of Talawi (Umbilin basin), 3 Jalak Pak Bidan (Miocene Seria Formation), and Penanjong beach, 4 Wallanae Formation, 5 Bumyayu along Kali Glagah river (Early Pleistocene), 6 Patiayam (Early Pleistocene), 7 Sangiran (Early Pleistocene and Middle Pleistocene), 8 Flores (Soa Basin, Early Pleistocene), 9 Tres Hermanas (Early Pleistocene), 10 Cemeng (Middle Pleistocene), 11 Trinil (late Early Pleistocene and Middle Pleistocene), 12 Kedung Brubus (Middle Pleistocene), 13 Bangle (Middle Pleistocene), 14 Kalinga (early Middle Pleistocene), 15 Atambua (Middle Pleistocene), 16 Braholo (Late Pleistocene), 17 Gamping (Late Pleistocene, Wajak), 18 Niah (Cenozoic and Late Pleistocene), 19 Laeng Burung 2 (Late Pleistocene), 20 Laili (Late Pleistocene), 21 Matja Kuru 2 (Late Pleistocene), 22 Paku flat (Late Pleistocene or Holocene).
Localités ayant livré des tortues fossiles en Malésie. Les couleurs des pays sont d'autant plus foncées que la richesse spécifique est élevée. 1. Crétacé Inférieur de Pahang, 2 Eocène de Talawi (Bassin de Umbilin), 3 Jalak Pak Bidan (Miocène; formation de Seria Formation), et plage de Penanjong, 4 Formation de Wallanae, 5 Bumyayu près de la rivière Kali Glagah (Pléistocène Inférieur), 6 Patiayam (Pléistocène inférieur), 7 Sangiran (Pléistocène Inférieur et Moyen), 8 Flores (Bassin de Soa Basin, Pléistocène inférieur), 9 Tres Hermanas (Pléistocène Inférieur), 10 Cemeng (Pléistocène Moyen), 11 Trinil (Pléistocène Inférieur tardif à Pléistocène Moyen), 12 Kedung Brubus (Pléistocène Moyen), 13 Bangle (Pléistocène Moyen), 14 Kalinga (Pléistocène Moyen inférieur), 15 Atambua (Pléistocène Moyen), 16 Braholo (Pléistocène Supérieur), 17 Gamping (Pléistocène Supérieur, Wajak), 18 Niah (Cénozoïque et Pléistocène Supérieur), 19 Laeng Burung 2 (Pléistocène supérieur), 20 Laili (Pléistocène Supérieur), 21 Matja Kuru 2 (Pléistocène Supérieur), 22 Paku flat (Pléistocène Supérieur ou Holocène).

no testudinid was reported. These taxa require, however, a reassessment, part of it has been done by Karl (1987) and Karl et al. (2019), but there is still a need for several updates (see below).

Family Geoemydidae Theobald, 1868
Genus ***Batagur*** Gray, 1856

Jaekel (1911) erected *Batagur siebenrocki* on a fairly-complete material including shell, plastron, and pelvic girdle. Unfortunately, the shell sutures are fused and the sulci may have fused and are not discernible, as is often the case in old individuals for several species of the genus (at least in *B. baska*, *B. affinis*, *B. kachuga*, and *B. trivittata*). Therefore, nearly no character can be used to distinguish *Batagur siebenrocki* from the other species of the genus. Karl (1987) first synonymized this material with *Batagur baska* and later with *Batagur affinis* (Karl et al., 2019) on the basis that *B. affinis* is spatiallygeographically closer. Karl et al. (2019) also illustrated a second carapace of *Batagur* (from Bogmi Aloi, a locality unknown to us), but on this second carapace also, most of the sulci are not

visible and the sutures are fused. The fact that the anterior lobe of the plastron is truncated in a mature specimen such as the one described by Jaekel and the absence of fontanelles in these two old individuals would be more consistent with an old individual of *Batagur affinis* or *Batagur baska* than with *Batagur borneoensis*. However, we prefer to refrain from proposing a species-level identification. Claude et al. (2019) showed that the geographic range of species in the genus has changed dramatically over time, in the Pleistocene and even during the Holocene. Furthermore, *Batagur trivittata* had an expanded range during the Pleistocene (Claude et al., 2011) and could have reached Java. As for *B. affinis* or *B. baska*, the morphology of old individuals is not incompatible with the fossils that was described: it can have an anteriorly-truncated plastral lobe, the fontanelles can disappear and the suture can be fused (Claude et al., 2011; Naksri et al., 2023). Furthermore, Java does not host any *Batagur* representatives today, and it is not impossible that the species living there in the Pleistocene were differentiated from others from Sumatra and from the Malay peninsula.

Genus?***Orlitia*** Gray, 1873 or ***Siebenrockiella*** Lindholm, 1929

Batagur signatus is based on a small nuchal bone. Karl (1987) and Karl et al. (2019) recognized that this plate should not be related to *Batagur*. Indeed, the genus does not show a triangular cervical scute, the vertebral lateral sulci never diverge anteriorly within the nuchal bone, and the first vertebra is not strongly convex anteriorly. In the fossil, the first vertebral scute is widened anteriorly, and the triangular and narrow cervical scute may correspond to the morphology observed in juvenile individuals of *Orlitia borneensis*, as proposed by Karl et al. (2019). However, we agree with Setiyabudi et al. (2016) regarding their doubts about this material. The first vertebral scute is generally broader in *Orlitia borneensis*. On the other hand, the specimen does not fit *Siebenrockiella crassicolis*, in which the vertebral scute is narrower posteriorly. Finally, the ratio of maximum width to anterior width seems to be lower than in *Malayemys* for which the vertebral and cervical scute pattern could also match. The morphology of the specimen matches well with *Siebenrockiella leytensis*, but this species has a more pronounced nuchal emargination (at least in adults). The specimen being small, it could be a juvenile of that species. The specimen should therefore be considered as ?*Orlitia* or *Siebenrockiella*.

Genus ***Duboisemys*** Karl, Safi and Philippen, 2019

Duboisemys isoclina (Dubois, 1908)

This species is based on a complete carapace associated with an almost complete plastron (Fig. 2). It was first described by Eugène Dubois as a new species of *Hardella* (Dubois, 1908). Dubois (1908) found similarities with the living species *Hardella thurjii* and the fossil *Hardella falconeri* from the Miocene-Pliocene of the Siwaliks. The generic assignment was mainly based on the position of the humeropectoral sulcus, which is far behind the entoplastron. *Hardella* is known from the Gange and Indus basins in Bangladesh, India, Nepal, and Pakistan. *Hardella falconeri,* from the Neogene of the same region, has been later synonymized with *H. thurjii* (Lydekker, 1885; Lydekker, 1889; Garbin et al., 2020). Claude et al. (2007) also identified a distinctive Late Eocene-Early Oligocene species of *Hardella* in Krabi, Thailand. Several authors questioned Dubois generic identity of this species (see Williams, 1957; Das, 1997 and, more recently, Karl et al., 2019). Williams (1957) was the first to question the generic identity of *H. isoclina*, noting several features that were incompatible with that genus. He noticed that the buttresses were much more developed in *Hardella* and its relatives which gave him strong ground to exclude *H. isoclina* from *Hardella*. Based on the weak buttresses and the position of the humeropectoral sulcus, he suggested that the species might be close to *Morenia* (from Myanmar, India, and Bangladesh), but he ruled out the possibility of a relationship with *Morenia*, noting that *H. isoclina* differed from *Morenia* in more characters than from *Hardella*. By elimination, he quickly considered similarities with *Mauremys mutica* (China, Japan, Taiwan, and Vietnam) and produced a comparison table listing 15 characters. On this list, excluding the last character (size), there are indeed eight differences with *M. mutica*, *contra* 10 with *Morenia* and 10 with *Hardella*. Williams (1957) himself recognized that his sample size for comparison could be biased, especially for *M. mutica* for which he knew that important phenotypic variation could occur. For example, he considered that, in *M. mutica*, the width of the first vertebral scute was much narrower than that of the first marginal and cervical scute, which is a quite unusual character state for this species (actually, the first vertebral become wider anteriorly in most individuals, reaching nearly the second marginal scute in *Mauremys*). He tentatively suggested using the name *Clemmys* for *Duboisemys* (at that time *Clemmys* also included several *Mauremys* species) and he also made a brief comparative diagnosis with *M. mutica* as a reference. With caution, Williams suggested that *Clemmys isoclina* might be a biogeographic exception in the turtle fauna, representing a “Chinese element” in the Trinil turtle fauna (dominated by genera known from Burma and India). Das (1997) briefly summarized the work of Williams (1957) and also produced a comparison table with different genera (strangely he did not discuss the absence of difference with *Morenia* in this table). His conclusions confirmed the results of Williams (1957), and he further emphasized the presence of other East Asian elements in the Malesian fauna, in particular using the distribution of *Geoemyda*, in which *Leucocephalon yuwonoi* from Sulawesi was first placed (since, we know that *Leucocephalon* and *Geoemyda* have different phylogenetic origins). More recently, in their work, Karl et al. (2019) made another revision of the *Hardella isoclina* material and placed it in a new genus: *Duboisemys*. To assess the systematic relationships of *Duboisemys isoclina*, Karl et al. (2019) were the first to perform phylogenetic analyses based on anatomical character matrices. Their first analysis reuses the taxa of Hervet (2004) and scores nine characters for 22 genera, and the second scores 10 characters for 20 extant genera. The first (including mostly European fossils) places *Duboisemys* close to *Cuvierichelys* (actually, between *Palaeoemys* and *Palaeochelys*/*Mauremys*), while the second places the fossil species between *Orlitia borneensis* and a group consisting of *Siebenrockiella*, *Malayemys*, *Mauremys*, *Cyclemys*, *Heosemys*, and other Geoemydinae. Both results are not fully contradictory, as the species composition is completely different between the analyses. Furthermore, many species used in Karl et al. (2019) first analysis were synonymized in *Palaeoemys*, a taxon considered by Claude and Tong (2004) as a potential relative of *Orlitia*, *Geoclemys* or *Malayemys*. It should be noted, however, that *Cuvierichelys* is not included in *Palaeoemys* and that Claude and Tong (2004) suggested that it may belong to a different clade. Karl et al. (2019) provided an emended diagnosis, but several details do not match the description of Williams (1957) and the observations of Das (1997). We therefore provide an emended diagnosis here and reassess the phylogeny using morphological features of species instead of genera as terminal units, to test whether the erection of a new genus is necessary and hopefully to understand the phylogenetic origin of *D. isoclina*.

Phylogenetic analysis of *Duboisemys isoclina*

The phylogenetic position of *Duboisemys isoclina* is reconstructed here using a matrix of 58 morphological characters scored

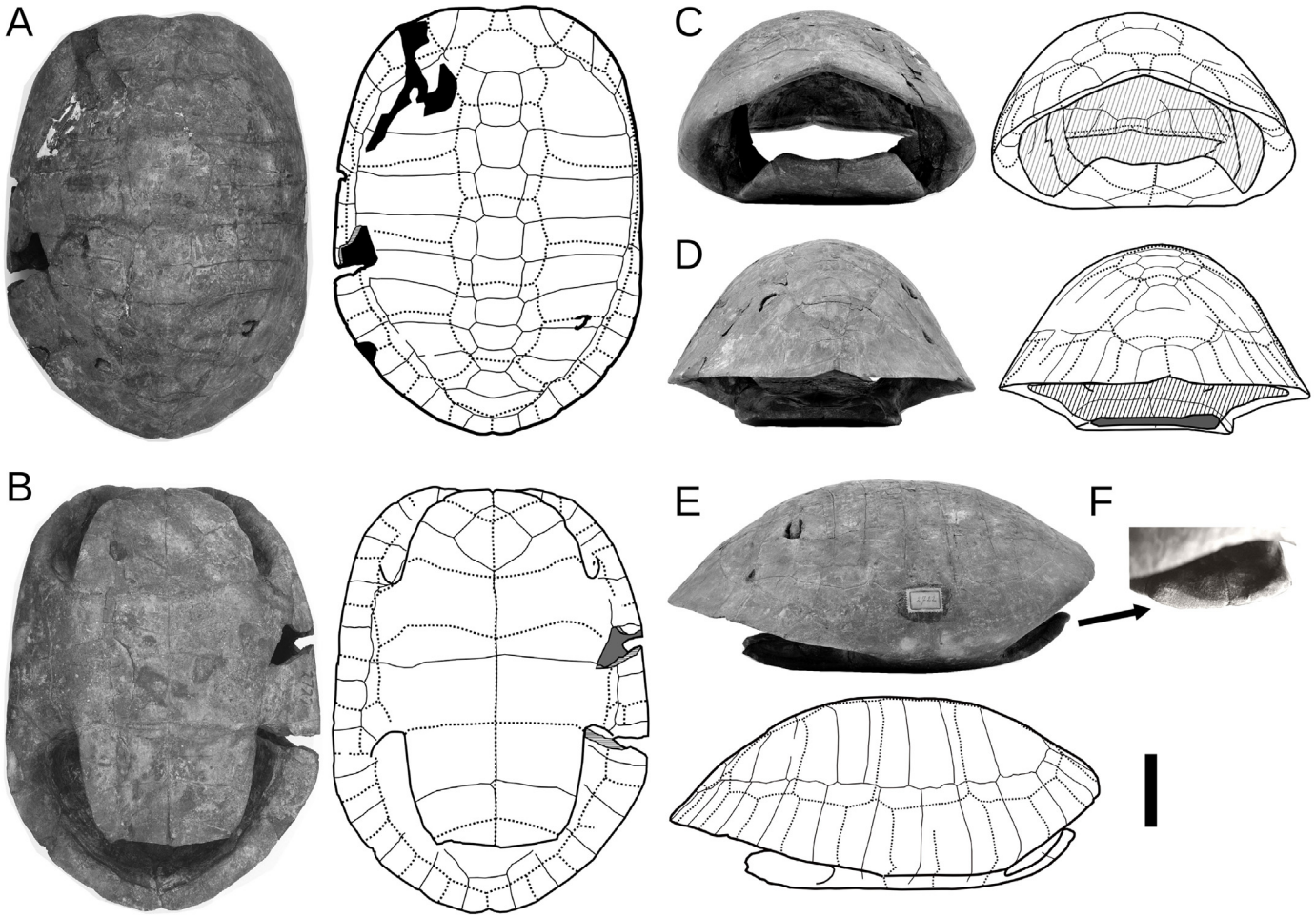

Fig. 2. *Duboisemys isoclina*. The shell in dorsal (A), ventral (B), anterior (C) posterior views (D) and detail of the dorsal view of the anterior plastral lobe (E) scale bar: 5 cm.
Duboisemys isoclina. *Carapace en vues dorsale (A), ventrale (B), antérieure (C) postérieure (D) et détail de la face dorsale du lobe antérieur du plastron (E). Barre d'échelle : 5 cm.*

on 66 taxa. Because geoemydid morphological characters have high rates of homoplasy and significant polymorphism, phylogenetic assessment in the group is more expressive when backbones derived from recent molecular phylogenetic analyses are used (Ascarrunz et al., 2021). However, published analyses of molecular sequences (Guillon et al., 2012; Colston et al., 2020; Thomson et al., 2021) do not all agree on inter-generic relationships within geoemydids; in particular, they disagree on the (non-)monophyly of Asian Geoemydidae. Unlike previous analyses, the recent analysis by Thomson et al. (2021) finds *Rhinoclemmys* (New World geoemydids) allied with several Eurasian genera (*Melanochelys*, *Cuora*, *Mauremys*, *Heosemys*, *Cyclemys*, *Sacalia*, *Notochelys*, and *Geoemyda*) and roots that ensemble together with Asian Batagurinae within Geoemydidae, whereas older phylogenetic hypotheses indicate that the first split within Geoemydidae was with the American Rhinoclemmydinae as sister group to all other Eurasian geoemydids (eg., Claude and Tong, 2004; Spinks et al., 2004; Guillon et al., 2012). The position of several genera also fluctuated between proposed hypotheses (*Siebenrockiella*, *Geoemyda*, *Melanochelys*, *Sacalia*, *Leucocephalon*), and not all intrageneric relationships received equal support. Consequently, we chose to collapse nodes with weaker support in the phylogenies established on molecular data. Two backbones were considered from the recent results of Thomson et al. (2021), leaving unresolved the nodes that did not receive 99% and 100% Bayesian probability. We also considered one backbone from the work of Guillon et al. (2012), leaving unresolved nodes that were below 90% and 95% bootstrap confidence, respectively. This combination of different backbones allowed to test the effect of different constraints on the position of the fossil. Analyses were performed in PAUP 4.0a169 (Swofford, 2002) using the random addition sequence and the tree bisection-reconnection branch swapping algorithm over 100 replicates, with the rearrangement limit set to 10,000,000. Twenty-two multistate characters were ordered as they represent morphological clines, and these multistate characters (three to five states) were scaled to count a maximum of one step between two taxa. The backbones are given in parenthetical format in the appendix, with the matrix and character codings.

The results of the phylogenetic analyses are summarized in Table 2 and Fig. 3. When the backbones from Guillon et al. (2012) were used, we found that *D. isoclina* formed a clade with the Indochinese genus *Heosemys* and the Malesian genus *Leucocephalon* (Fig. 3). By contrast, when performed with backbones issued from Thomson et al. (2021), phylogenetic hypotheses yielded the same set of equal trees irrespective of the number of nodes fixed by the backbone. At 99% and 100%, the analyses resulted in three equal trees placing *D. isoclina* either at the base of the clade made up of Indochinese *Geoclemys*, *Morenia*, *Batagur*, *Pangshura* and *Hardella*, either at the base of the clade made up of Indochinese *Morenia*, *Batagur*, *Pangshura* and *Hardella* or as a sister group of *Orlitia* within the more inclusive Indochinese clade made of *Orlitia*, *Malayemys*, *Geoclemys*, *Morenia*, *Batagur*, *Pangshura* and *Hardella*. These latter hypotheses are closer to the one made by Karl et al. (2019).

The proximity to Batagurinae *Morenia*, *Batagur*, *Hardella*, and *Pangshura* can be understood by the position of the

Table 2
Summary of different phylogenetic analyses performed using different constraint trees backbones.
Caractéristiques des analyses phylogénétiques basées sur différentes contraintes topologiques.

Backbone	Guillon 90%	Guillon 95%	Thomson 99%	Thomson 100%
Unresolved nodes in the backbone	17	29	9	11
Number of equal trees	24	629	3	3
Parsimony score	250.17	240.18	252.1	251.51
Consistency Index	0.2484	0.2587	0.2465	0.2475

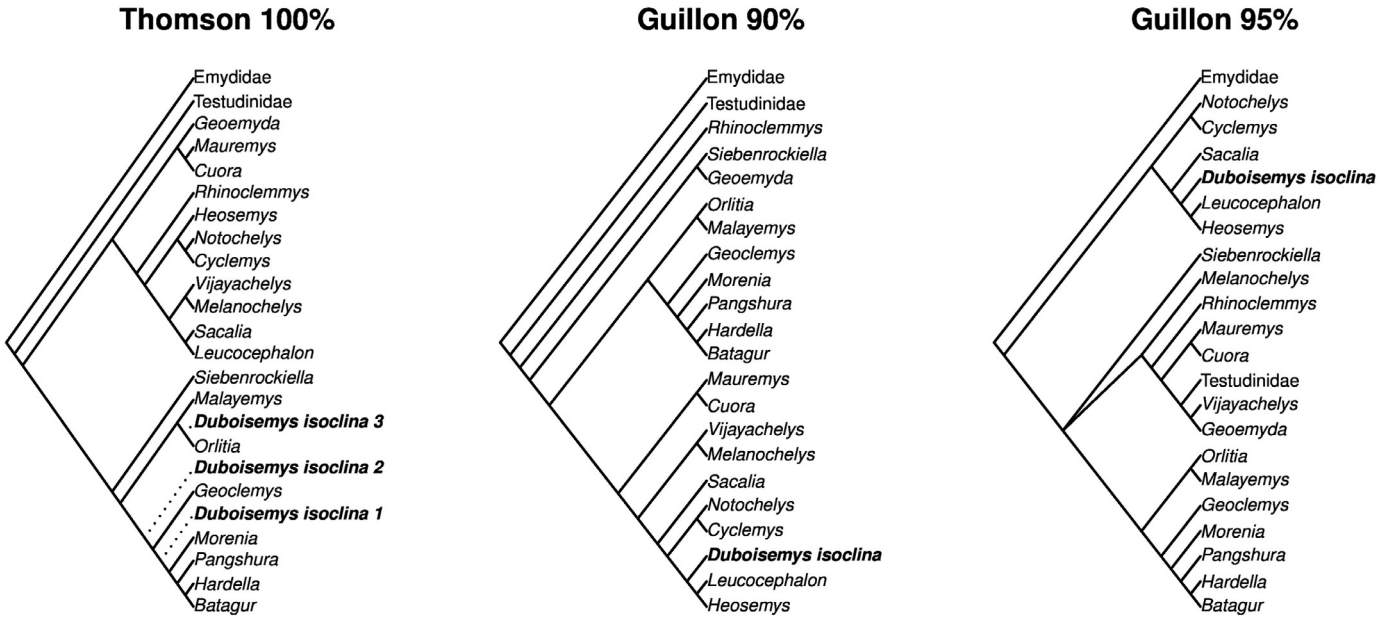

Fig. 3. Phylogenetic hypothesis for *Duboisemys isoclina.* Genera being monophyletic here, intrageneric species relationship are not provided.
Phylogenetic hypothesis for Duboisemys isoclina*. Les genres étant ici monophylétiques, les relations entre espèces intragénériques ne sont pas fournies.*

humero-pectoral sulcus. The buttresses compared to other members of the clade is just slightly stronger than *Morenia* (contra what was described in Williams, 1957), with the inguinal buttress reaching the costal 1 under which a continuous strong ridge is present. However, *D. isoclina* is not as advanced as this group in the relationship between the relative position of the 4th marginal scute and the second pleural scute and the relative position of the 6th marginal scute to the third pleural scute. *Duboisemys isoclina* shares some similarities with *Orlitia*, but these are mostly based on the primitive character states. Similar results were obtained in using backbones derived from Colston et al. (2020), with 90% and 95% threshold depending on bootstrap values (not shown). On the other hand, the position of *D. isoclina* within the *Sacalia*, *Cyclemys*, *Leucocephalon* and *Heosemys* lineage might also result from a combination of primitive characters. Finding phylogenetic proximity with this group may be due to several plesiomorphic features shared by *Sacalia* and *D. isoclina*, such as the shape of the neurals, the reduced gulars and extension of the visceral plastral sulci. The fact that *D. isoclina* is often allied with *Leucocephalon* might come from the reduced gular. Finding *D. isoclina* close to *Heosemys* within this clade is more difficult to explain but it might be due to the absence of a hinge and the shape of its vertebral scutes. Our preferred hypothesis is the one placing *D. isoclina* as a branch of the tree bifurcating before *Geoclemys,* before *Morenia* or as a sister taxon of *Orlitia*. The position of the sulcus and the shape of neural plates are rarely showing reversals to support a close relationship with *Heosemys* or *Leucocephalon,* furthermore the high carapace of *D. isoclina,* the absence of carapace serration, and the thick shell are more in agreement with a close relationship with *Orlitia, Geoclemys,* or *Morenia*.

In our analyses, *D. isoclina* is never found within a modern genus, suggesting it should indeed be interpreted as a separate genus (at least if we consider living forms). In none of the analyses, *D. isoclina* was detected as a close relative of *Mauremys*. Results of phylogenetic analyses using Thomson et al. (2021) or Colston et al. (2020) backbones suggest a colonization by Indochinese migrants using the Malay/Sundaic route rather than Chinese fauna migrating via the Taiwanese/Philippine route. On the other hand, in the analyses using Guillon et al. (2012), *D. isoclina* is found not far from *Leucocephalon.* Although it is not our preferred hypothesis and if this result is correct, *D. isoclina* could serve as a phylogenetic intermediate to understand the distribution of *Leucocephalon* in Sulawesi. Indeed, when using Guillon et al. (2012) backbone and keeping nodes resolved with 95% bootstrap support, *D. isoclina* (Java)*, Sacalia* (a Chinese, Laotian and Vietnamese genus), and *Leucocephalon* (Sulawesi) could form a grade. Under this scenario, the Sino-Wallacean dispersal could be accommodated and an East Asian origin for a fossil and a living endemics could be possible. It is unfortunately not well-supported by fossil evidences as *Sacalia* or *Duboisemys* have not been recorded yet in sediments of China and Taiwan (or anywhere else).

Emended diagnosis: Small to medium-sized freshwater turtle, differing from all other geoemydids by the following combination of characters: anteriorly well-developed first marginal scutes; posterior and medial corner of second marginal pinched at the contact with marginal 1 and pleural 1, nearly reaching nuchal plate; bell-shaped first vertebral; pygal widening posteriorly, inguinal and axillary buttresses present and developed at least as in *Morenia*, intergular sulcus length equals about 50 % of interhumeral sulcus; gular relatively short and covering the anterior

part of entoplastron; humeropectoral sulcus behind entoplastron; anteriorly truncated anterior plastral lobe; interfermoral sulcus longer than interabdominal sulcus; femoroanal sulcus parallel to xiphiplastron/hypoplastron suture; epiplastral lip present and continuous on the anterior visceral side of the plastron, but very short medially and widening laterally forming a small lateral bulge at the level of the visceral sulcus between humeral and gular; marginal 4 and 6 restricted in peripherals and respectively not contacting pleural 2 and 3; shell surface smooth.

Comparison with similar taxa. Several characters allow *Duboisemys* to be distinguished from living and fossil species. *Morenia* differs from *Duboisemys* in the morphology of the first marginal, the shell surface with microsculpture, the shorter and wider-than-long pygal, the femoroanal sulcus not parallel to the hypo-xiphiplastron suture, the longer visceral gular lips especially in the middle of the ventral surface of the epiplastra, the position of the second pleural scute relative to the fourth marginal, and the bridge marginals extending close to or sometimes overlapping the costo-peripheral suture. *Orlitia* differs from *Duboisemys* in the shape of the first marginal, the first vertebral much wider anteriorly than posteriorly, mushroom-shaped vertebrals 2 and 3, the stronger buttresses, the longer intergular sulcus. *Duboisemys* differs from *Hardella thujii* in the morphology of the first marginal, the weaker buttresses, the shape of the entoplastron with subequal posterior and anterior anterior halves, the wider gulars, the position of the second pleural relative to the fourth marginal, and the bridge marginals not overlapping the costo-peripheral suture. *Duboisemys* differs from *Geoclemys* and *Malayemys* by the absence of lateral carinae on the carapace and by its more posterior humeropectoral sulcus. *Sacalia* differs from *Duboisemys* in the shape of the first marginal, the anterior widening of the first vertebral, the more anterior position of the humeropectoral sulcus, the morphology of the posterior sulcus of the fifth vertebral and its position relative to the pygal plate, the weaker buttresses, and its lower carapace. *Mauremys* differs from *Duboisemys* in the shape of the first marginal, the first vertebral often widening anteriorly, the stronger gular visceral lip, and the more anterior position of the humeropectoral sulcus, the weaker buttresses, and its lower carapace. The fossil *Cuvierichelys* differs from *Duboisemys* in the morphology of the first marginal, the first vertebral being broader anteriorly, the gular not extending onto the entoplastron, the vertebrals 2 and 3 usually more quadrangular, the epiplastral lip more developed in the middle and flatter laterally, and the humeropectoral sulcus on the entoplastron or touching it. Because *Orlitia borneensis* may be present in the Middle Pleistocene of Java (see below), confusion with *Duboisemys isoclina* may occur on disarticulated elements, especially when vertebral sulci are not preserved.

Referred material: none. Williams (1957) referred an anterior plastral fragment and a posterior xiphiplastron as to *D. isoclina.* The anterior plastral fragment appears to have a fused suture and shows a very weak or almost absent epiplastral lip. For these two reasons, it would be better to assign it to *Batagur* sp. A posterior xiphiplastron is also depicted, but it shows no sulcus, its lateral side is straighter than that of *D. isoclina* and the suture with the xiphiplastron is perpendicular to the antero-posterior axis, whereas it is slightly oblique in the holotype of *D. isoclina*, this posterior xiphiplastron could also be related to *Batagur* sp.

Family Trionychidae Fitzinger, 1826
Genus ***Amyda*** Saint-Hilaire, 1809

Amyda cartilaginea (Boddaert 1770)

Trionyx trinilensis was established on plastral and cervical material, pectoral girdle and limb bones, and was synonymized with *Amyda cartilaginea* by Karl (1987) on the basis of similarities to the living species. This was followed by Georgalis and Joyce (2017) and by the Turtle Extinctions Working Group (2015).

Genus ***Chitra*** Gray, 1844

Chitra chitra Nutphand, 1986

Chitra selenkae is known from an almost complete carapace, a xiphiplastron, a scapula, an entoplastron, and an epiplastron. The name was suppressed in favor of the living *Chitra chitra* (McCord and Pritchard, 2003). To end with, *Chitra minor* was described by Jaekel (1911) on the basis of an epiplastron and a hypoplastron. The material was later referred to a possible *Pelochelys cantorii* on geographical grounds (McCord and Pritchard, 2002), and was finally considered as uncertain in terms of generic affinities by Georgalis and Joyce (2017). The xiphiplastron is indistinguishable from that of *C. selenkae*. The size of the sculptural elements on the plastron tends to be less homogeneous and more variable, as in *Chitra* (whereas the sculpturing is finer, more regular and more homogeneous in *Pelochelys*). We therefore consider this material to belong to *Chitra* instead of *Pelochelys*.

In summary, there are at least five species in Trinil (late Early Pleistocene to early Middle Pleistocene): *Duboisemys isoclina*, *Batagur* sp.,*? Orlitia or Siebenrockiella*, *Chitra chitra*, and *Amyda cartilaginea*. *Duboisemys isoclina* is the only extinct taxon and no tortoise has been reported.

3.3.2. Middle Pleistocene of the Philippines

Fossil turtles are known from deposits of supposed early Middle Pleistocene age in Cagayan province were collected and present at the National Museum of the Philippines since the 70's but were not described. The fossils listed correspond giant tortoises represented by fragmentary material in San Juan, Tuao and in Espinosa ranch sites in Kalinga and by a trionychid at Solana (de Vos and Bautista, 2003). The recent excavation in the early Middle Pleistocene site of Kalinga in the Awidon Mesa Formation of the Philippines has yielded a vertebrate fauna associated with several mammals, a monitor lizard, and a turtle (Ingicco et al., 2020; Antoine et al., 2022). This turtle, initially reported as a tortoise, is a freshwater geoemydid instead. The description is provided below.

Family Geoemydidae Theobald, 1868
Genus ***Cuora*** Gray, 1856

Cuora amboinensis species complex (Riche in Daudin, 1801)
? Cuora philippinensis Blanck, Gaillard, Protiva, Wheatley, Shi, Liu, Chandra-Ray, Anders, 2023
(Fig. 4 A–C)

Description: II-2014-J1-349 (Fig. 4A) is an almost complete left hypoplastron, only the posterolateral margin is missing. Anteriorly, the abdominopectoral sulcus and the hyo-hypoplastral suture have the same position. The anterior margin of the plate showed an articulated hinge between the hyoplastron and hypoplastron. Laterally, the contact with the carapace is ligamentous and the inguinal buttress is considerably reduced and anteriorly placed. The hypoplastron shows a thickening in the middle of the plate at their midline contact. The sutural contact with the xiphiplastron is straight. The abdominofemoral sulcus is oblique on the hypoplastron, with the femoral scute covering only a small portion of the midline compared to the lateral side.

II-2014-J1-351 is a complete left epiplastron. The free margin is broadly rounded but has a very short anteromedial section perpendicular to the anteroposterior axis. The epiplastron widens posteriorly. The contact with the hypoplastron is longer than the medial contact between the epiplastra. The gulo-humeral sulcus

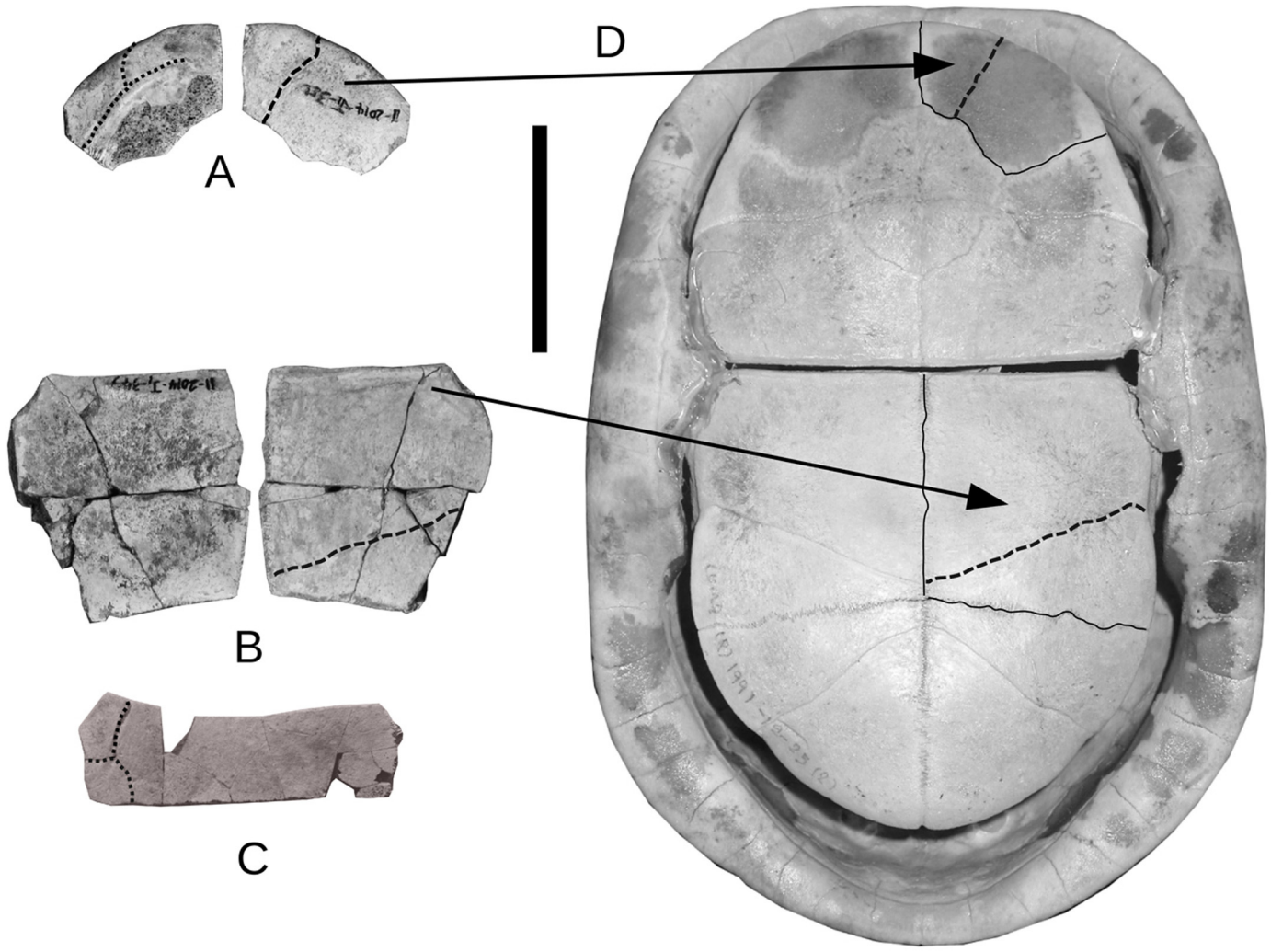

Fig. 4. A, B, C: *Cuora amboinensis* from Kalinga in the Philippines; A, epiplastron (II-2014-J1-351) in visceral and ventral views; B, hypoplastron (II-2014-J1-349) in visceral and ventral views; C, Costal 3 (II-2014-J1-547, 548) in dorsal view; *D, Cuora couro kamaroma* from Thailand, ventral view.
A, B, C : Cuora amboinensis *du site de Kalinga aux Philippines; A, épiplastron (II-2014-J1-351) en vues viscérale et ventrale; B, hypoplastron (II-2014-J1-349) en vues viscérale et ventrale; C, Costal 3 (II-2014-J1-547, 548) en vue dorsale; D,* Cuora couro kamaroma *de Thaïlande, vue ventrale.*

runs posteriorly and was likely forming an acute angle with the midline sulcus on the entoplastron (not preserved). The gular scute is relatively narrow and long and triangular in shape. The sulcus formed a small obtuse angle anteriorly (4 mm anterior to the anterior margin). On the visceral side, the gular and humeral sulcus can be seen, showing that the scute covered the plate dorsally on at least 7 mm in the midline to nearly 10 mm at the level of the humeral scute. The portion of the epiplastron covered by the humeral scute is approximately three times that covered by the gular scute.

II-2014-J1-547 and II-2014-J1-548 (same plate in two pieces) is an almost complete third right costal plate. It has almost parallel anterior and posterior sides, but the plate narrows slightly in the middle. It was in medial contact with two neural plates 3 and 2. These neural plates (not preserved) were hexagonal with posterior shortest sides. The antero-lateral border of vertebral 3 is rounded, whereas the posterior border of vertebral 2 forms an obtuse angle. The second vertebral scute extends slightly more than the third vertebral scute on the plate. The bone is covered laterally by the second pleural scute.

Comparison: The gular extending well to the dorsal surface of the epiplastron is diagnostic of the testudinoid superfamily. Neurals with posterior shortest sides are found in the family Geoemydidae in the genera *Rhinoclemmys*, *Cuora*, *Geoemyda*, *Vijayachelys*, *Melanochelys*, *Cyclemys*, *Leucocephalon*, *Notochelys*, and *Heosemys*. Only *Cyclemys*, *Notochelys*, and *Cuora* have mobile hinges. The hinge is much more developed in *Cuora* than in the other two genera. The fossil shows the condition of *Cuora*. Furthermore, the gular scute covers a smaller part of the dorsal surface of the epiplastron as in *Cuora*. Finally, the oblique abdominofemoral sulcus is a feature found only in some species of *Cuora*. In this group, its shape is straight and closer to that observed in "*C. amboinensis*" or *C. pani* (Naksri et al., 2013). The obliqueness of the sulcus is more comparable to that observed in the *C. amboinensis* complex, as is the shape of the V2/V3 contact on costal 3, although this may be subject to some variation. Within the *Cuora* genus, only the "*C. amboinensis*" species complex extends its range into insular Southeast Asia, including the Philippines, so we assign the specimen to the "*C. amboinensis*" species complex based on both its morphology and biogeographic context.

Discussion: Until 2023, it was recognized that *Cuora amboinensis* could be divided into four subspecies: *Cuora a. kamarona* in mainland Asia from eastern India to Cambodia and in Borneo, *C. a. lineata* in Myanmar, *C. a. couro* in Indonesia (Sumatra, Java, Timor and the Lesser Sunda), and *C. a. amboinensis* in the Philippines and Indonesia (Moluccas and Sulawesi) (Turtle Taxonomy Working Group, 2021). More recently, Blanck et al. (2023) have proposed to

split the *Cuora amboinensis* species complex into five species with *Cuora lineata* from Myanmar and India, *Cuora praschagi* from India, Bhutan and Bangladesh, *Cuora amboinensis* restricted to the Mollucas and Sulawesi (with *Cuora amboinensis amboinensis* from the Mollucas and Wallacean islands of Sulawesi and *Cuora amboinensis auriantae* from central Sulawesi), *Cuora philippinensis* in the Philippines (except Palawan and Sulu islands), and *Cuora couro* from the Sundashelf, Indochina and parts of the Philippines. The latter species would include two subpecies: *Cuora couro couro* in Malaysia, Southern Thailand, Borneo, Sumatra, Java, the Philippines (Palawan and Sulu and supposedly introduced in Luzon or Mindoro) and the Lesser Sunda islands, and *Cuora couro kamaroma* from Thailand, Laos, Vietnam, Cambodia and Nicobar islands (Blanck et al., 2023).

As the material described here is fragmentary and no clear skeletal or scute differences have been reported in the living species, it is difficult to assign the specimens to a subspecies in the 2021 TTWG partition or to a species in the 2023 revision of Blanck and colleagues. The strongly oblique femoroabdominal sulcus is in better agreement with *C. amboinensis aurientae* or *C. philippinensis* and *C. couro kamaroma* rather than in *C. couro couro*, *C. lineata* or *C. praschagi*. The position of the sulcus between the second and third vertebral scutes is not consistent with the *C. couro kamarona* specimens we have examined (it is more anterior in the fossil) and may be more consistent with *C couro couro, C. amboinensis amboinensis, C. amboinensis aurientae* or *C. philippinensis.* The specimen would therefore match with *C. philippinensis*. However, as the sample of turtles we have seen is too small to assign it clearly to one of the different living taxa within the genus complex, we opted to assign it to? *C. philippinensis*. The fossil record of the *C. amboinensis* species complex is really scanty; pending a clearer identification of the remains found in Flores (Setiyabudi, 2016). The fossil from Kalinga might therefore represent the oldest clear occurrence of the complex and it is the oldest freshwater turtle known so far in the Philippines. *Cuora amboinensis sensu lato* is known in neither the continent nor the Sunda Shelf before the Late Pleistocene. If we consider the partition in *Cuora amboinensis sensu lato* prior to 2023, molecular data (Spinks et al., 2004) indicated that *C. a. amboinensis* from the Philippines, Moluccas and Sulawesi might have been the first split within the species. The part of the study of Blanck et al. (2023) on mitochondrial DNA for *C. amboinensis amboinensis* shows a comparable result with Spinks et al. (2004) (see Fig. 6–8 in Blanck et al., 2023) and shows that the Huxley line is important to understand the geographical evolution of the complex (with the exception of the lesser Sunda islands). These studies involve that the Eastern Malesian *Cuora* are not necessarily deriving lately from western populations but that Philippines, Sulawesi and the Moluccas could correspond to the initial range of the species derived either from an Indochinese, either from a Chinese stock, later dispersing and differentiating to the West. This therefore leaves a room for the Sino-Taiwanese colonization path to be active during the Miocene. Nevertheless, when nuclear and mitochondrial DNA are concatenated, Blanck et al. (2023) are recovering a West to East differentiation among groups suggesting that the Siva-Malayan route of dispersion might better explain the differentiation among taxonomic units (Fig. 5 in Blanck et al., 2023).

Although the fossil record of *C. amboinensis sensu lato* is scanty, *Cuora* is widely distributed in Southeast Asia and in China, and it also has a fossil record in mainland Asia since the Miocene and that record extends in Thailand, China, and Japan (Naksri, 2013) but no fossil in the Cenozoic of Malesia. As mitochondrial and nuclear genomic data are not in full agreement and as fossil data are too limited in Malesia, the hypotheses of dispersal and differentiation via the Siva- or Sino-Malayan path or the Sino-Taiwanese path should be kept in mind for understanding differentiation patterns in that species. In depth molecular study regarding recent and past introgressions and more palaeontological data could eventually help to prefer one of these scenarios.

3.3.3. Other localities

Hooijer (1971a, b) described several giant tortoise bones from different localities in Indonesian Timor, that represent several individuals. No complete material was found, but partial epiplastra show strong projections. Hooijer (1971a, 1971b) noted several similarities with *Megalochelys sivalensis* and suggested that the Timor material should be placed in *Megalochelys atlas* along with the Sulawesi material. Van der Geer et al. (2010) and Sondaar (1981) have suggested a Middle Pleistocene age for these remains; the age may correspond to the late Middle Pleistocene if the giant tortoises and *Stegodon* remains correspond to the same deposit (Louys et al., 2016). Storm (2012) reported *Batagur* sp. from the localities of Bangle and Kedung Brubus and *Chitra* from Kedung Brubus. Trionychid turtles occur at Sangiran (Bouteaux, 2008), but they are not described in detail. Finally, Setiyabudi et al. (2016) reported the first costal plate of *Orlitia borneensis* from a Middle Pleistocene deposit along the Solo River Cemeng in the Sambungmacan area. The plate described shows that the lateral vertebral sulcus reached the first neural as in the genera *Orlitia* or *Siebenrockiella*, but Setiyabudi et al. (2016) considered it closer to *Orlitia* based on the shape of the contact with the nuchal plate and the vertebral pattern.

3.4. Late Pleistocene (Fig. 1)

A few Late Pleistocene localities have been published with illustrated or described material. Niah Caves in Borneo seems to be the richest assemblage described so far. In this locality, turtles have been reported from the middle Late Pleistocene (Phase I) and from the latest Pleistocene (Phase II) (Pritchard et al., 2009; Barton et al., 2013; Reynolds et al., 2013). The middle Late Pleistocene chelonian fauna consists of *Amyda cartilaginea*, *Cuora ambinensis*, *Cyclemys dentata*, *Dogania subplana*, *Manouria emys*, *Notochelys platynota*, *Orlitia borneensis*. The latest Pleistocene includes *Amyda cartilaginea*, *Cyclemys dentata*, *Dogania subplana*, *Heosemys spinosa*, *Manouria emys*, and *Notochelys platynota*.

Still in Sarawak region, Lydekker (1889) reported *Trionyx phayrei* (i.e. *Amyda cartilaginea*) from Paku flat (or Paken flat), probably from the collections of Everett HA. Georgalis and Joyce (2017) considered it as Trionychidae indet.

In Java, in the latest Pleistocene of Braholo cave, Amano et al. (2016) reported *Amyda cartilaginea*, *Cyclemys dentata* and *Cuora amboinensis* in the upper layers. Setiyabudi et al. (2021) reported and illustrated a hypoplastron fragment of *Cuora amboinensis* from the Wajak site in East Java. In Timor-Leste, Samper Carro et al. (2023) reported *Chelodina timorensis* in Late Pleistocene of Matja Kuru 2 site. An ulnar fragment of a small turtle from the Late Pleistocene is also reported from Laili cave in Timor-Leste (Hawkins et al., 2017). These different occurrences suggest that the Late Pleistocene turtle fauna was similar to the modern one.

4. Conclusion

This work makes it possible to establish dates for the earliest appearance of several taxa in Malesia during the Pleistocene: *Amyda cartilaginea*, *Chitra chitra*, *Cyclemys dentata*, *Cuora amboinensis*, *Dogania subplana*, *Heosemys spinosa*, *Manouria emys*, *Notochelys platynota*, and *Orlitia borneensis*. *Cuora amboinensis* certainly arrived in the Philippines during the earliest Middle Pleistocene or before, and its late Early Pleistocene presence in Flores needs to be confirmed. Molecular data or the fossil record for this species are insufficient to determine whether it arrived in the Philippines via the Sino-Taiwanese or the Sino-Malayan route. *Chitra chitra*, *Amyda cartilaginea*, and *Orlitia borneensis* were present in Java

in the Middle Pleistocene; *Amyda cartilaginea*, *Cyclemys dentata*, *Manouria emys*, *Notochelys platynota*, *Orlitia borneensis*, and *Dogania subplana* were already present in Borneo in the Late Pleistocene. The Pleistocene records of *Pelochelys* should be confirmed, and the identification of the Middle Pleistocene *Batagur* species from Java needs to be refined through shell material showing suture and sulcus. None of the living endemics has a fossil record yet in the continent or in Malesia, but the splits between geoemydid and testudinid endemics of Malesia with their continental counterpart — is are rather old (Oligocene to Early Miocene) according to molecular data (e.g., Thomson et al., 2021). For *Siebenrockiella leytensis* at least, it is likely that the separation of Palawan tectonic unit from mainland could explain its isolation and divergence from continental relatives (even if the fossil record of that species has not been yet documented in the Cenozoic of continental Southeast Asia). A better survey of Neogene sediments in Malesia and on the continent may, however, be needed to appraise whether Malesia promoted chelonian vicariance or was simply used as a refugium. The systematics of the "*Cuora amboinensis*" species complex should also retain a special attention to understand the role and timing of dispersal routes and the isolation of populations of Sulawesi, the Moluccas and the Philippines. Disagreement between messages recovered from nuclear and mitochondrial DNA found in Blanck et al. (2023) should receive an evolutionary interpretation and further investigation.

Giant tortoises, originating from South Asia and Indochina, flourished in Malesia from the Early Pleistocene and were probably extinct in the Middle Pleistocene. The most recent fossils come from Timor, where humans are thought to have arrived later than in Java and Flores. A clarification of the age of the last giant tortoises in the Philippines is needed to appraise their extinction in this archipelago. With the giant tortoises, *Duboisemys isoclina* is the second taxon to go completely extinct. *Batagur* became extinct in Java. Whether this extirpation occurred in the Holocene or earlier is difficult to assess with certainty, but the genus is not recorded in the Late Pleistocene, suggesting a possible ancient extinction as well.

Most turtles of Malesia have more affinities with the Indo-Burmese and Thai faunas than with the Chinese one, even for remote islands beyond the Wallace Line. This suggests that the turtles mostly colonized Malesia via the Siva or Sino-Malayan routes during a low sea-level stages. However, there is a clear need of additional Pliocene and early Pleistocene fossil material from the Sunda Shelf area to precisely date these events. On the other hand, new material from southern China or Taiwan could still challenge this scenario, especially for the fauna found in the Philippines, Sulawesi and the Moluccas.

Disclosure of interest

The authors declare that they have no competing interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.annpal.2024.102665.

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