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Vincent Girard, Simona Saint Martin, Eric Buffetaut, Jean-Paul Saint Martin, Didier Néraudeau, et al.. Thai amber: insights into early diatom history?. Bulletin de la Société Géologique de France, 2020, L'ambre (special issue), 191, pp.23. 10.1051/bsgf/2020028 . insu-02890787v2

HAL Id: insu-02890787

<https://insu.hal.science/insu-02890787v2>

Submitted on 20 Jan 2021

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Thai amber: insights into early diatom history?

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Received: 29 August 2019 / Accepted: 28 June 2020

Abstract – The origin of the diatoms still remains enigmatic. Their fossil record is scarce until the Late Cretaceous and great divergences exist between molecular data and the earliest fossil evidence. While molecular data indicate an origin during the Triassic or Early Jurassic, early fossil evidence is only from the Late Jurassic-Early Cretaceous. The discovery of diatoms in French mid-Cretaceous amber by the end of the 2000s already suggested a potential bias in the diatom fossil record as it made older many diatom lineages, the record of which hitherto began at the end of the Cretaceous. The Jurassic/Early Cretaceous fossil record of diatoms is extremely sparse and any new occurrence is important for retracing the evolutionary, palaeogeographical and palaeoenvironmental history of diatoms. Thai amber has yielded a new diatom specimen that has been attributed to the genus *Hemiaulus*. Fossil assemblages and sedimentological data indicate that Thai amber and its *Hemiaulus* specimen are Late Jurassic in age. This discovery represents the oldest hitherto known specimen of *Hemiaulus* and so extends the fossil record of the bipolar diatoms and of the genus *Hemiaulus* by several dozens of millions of years and brings closer the fossil evidence and molecular data (that estimated an origin of the bipolar diatoms about 150 Ma ago). It reinforces the hypothesis of a pre-Cretaceous fossil diatom records and also supports an origin of the diatoms in shallow coastal environments.

Keywords: Fossil resin / Mesozoic / Bacillariophyta / Origin / Shallow marine environments

Résumé – **L'ambre de Thaïlande : une fenêtre sur l'histoire des premières diatomées ?** L'origine des diatomées reste toujours énigmatique. Leur registre fossile est rare jusqu'au Crétacé supérieur et il existe de grandes différences entre les données moléculaires et les premières évidences fossiles du groupe. Tandis que les données moléculaires indiquent une origine durant le Trias ou le Jurassique inférieur, les plus anciennes traces fossiles sont seulement de la fin du Jurassique, début du Crétacé. La découverte de diatomées dans l'ambre médio-crétacé français à la fin des années 2000 avait déjà suggéré un potentiel biais dans le registre fossile des diatomées car cela vieillissait plusieurs lignées précédemment connues uniquement à partir du Crétacé supérieur. Le registre fossile des diatomées du Jurassique et du Crétacé inférieur est extrêmement limité et toute nouvelle occurrence est importante pour retracer l'histoire évolutive, paléogéographique et paléoenvironnementale des diatomées. L'ambre de Thaïlande a permis la découverte d'un nouveau spécimen de diatomée attribué au genre *Hemiaulus*. Les données paléontologiques et sédimentologiques attestent que l'ambre thaïlandais et la diatomée qu'il contient sont d'âge Jurassique supérieur. Cette

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découverte représente le plus ancien spécimen du genre *Hemiaulus* connu à présent et étend donc le registre fossile des diatomées bipolaires et du genre *Hemiaulus* de plusieurs dizaines de millions d'années et rapproche ainsi le registre fossile des données moléculaires (qui estimaient l'origine des diatomées bipolaires à environ 150 millions d'années). Cela renforce l'hypothèse d'un registre fossile pré-crétacé et soutient une origine des diatomées au sein d'environnements marins néritiques.

Mots clés : Résine fossile / Mésozoïque / Bacillariophyceae / Origine / Environnements marins peu profonds

1 Introduction

Diatoms (Bacillariophyta) represent an extremely diverse and successful lineage of photosynthetic Stramenopiles (Chromalveolates) with a siliceous cell wall. They are one of the most important groups of primary producers in modern ecosystems (Kooistra *et al.*, 2007); they have colonized both marine and freshwater environments and are important agents in the global biosynthesis of organic matter (Kooistra *et al.*, 2007). They have a great impact on carbon cycling (Smetacek, 1999; Falkowski *et al.*, 2004) and play a key role in the biogeochemical cycle of silica (Tréguer *et al.*, 1995). Apart from their significance for modern ecosystems, the origin of diatoms is still enigmatic (Falkowski *et al.*, 2004). Molecular clock estimates suggest an origin at *ca.* 240 Ma, during the Triassic (Sorhannus, 2007) or, following Medlin (2011), a root of the diatom lineage is constrained between 250 and 190 Ma. Recently, Nakov *et al.* (2018) estimated the diatom crown age at 190.4 Ma and thus placed the origin of diatoms near the Triassic-Jurassic boundary.

The oldest available estimates are based on a 19th century record from the Early Jurassic of Germany (Rothpletz, 1896). However Rothpletz's material has been lost and thus cannot be studied again to verify its position within the Bacillariophyta (Harwood *et al.*, 2007). Serious doubts exist also about the age of Rothpletz's material. Some microfossils from the German diatomaceous sediments were studied by Rüst (1885). Kemper *et al.* (1975) reviewed Rüst's illustrations and referred the sediments (and therefore the diatoms) to the Early Cretaceous. In fact the known biostratigraphic distribution of diatoms indicates that their fossil record is very scarce until the Late Cretaceous (Harwood *et al.*, 2007). Diatom resting spores have been found in the Lower Cretaceous of Korea (Harwood *et al.*, 2007; Chang *et al.*, 2007), but the first well-preserved fossils of unequivocal vegetative cells and resting spores are known from Lower Cretaceous marine deposits of Antarctica; they were originally dated as late Aptian-early Albian (Gersonde and Harwood, 1990; Harwood and Gersonde, 1990), but they were recently reconsidered to be early to mid-Albian in age (McCartney *et al.*, 2014). Coeval fossils from Australia and Germany suggest that diatoms had already a broad distribution in marine environments by the end of the Early Cretaceous (Harwood *et al.*, 2007). This is confirmed by Albian and later fossil records of diatoms. During and after the Albian, deposits with fossil diatoms become more numerous, from Russia (Jousé, 1949; Strel'Nikova and Martirosjan, 1981), Canada (Wall, 1975), Germany (Forti and Schulz, 1932; Georgi, 1976) and Italy (Foucault *et al.*, 1986). These findings show that diatoms already had a worldwide distribution by the Albian.

One drawback of the Cretaceous fossil record of diatoms is their pyritized preservation, which obscures morphological

features (Girard *et al.*, 2009b). Diatoms were rare in non-marine environments before the Maastrichtian (Chacón-Baca *et al.*, 2002) and they did not become abundant until the Eocene (Sims *et al.*, 2006).

Here we report a unique diatom specimen preserved in amber from the Upper Jurassic of Thailand. This specimen provides a new case of diatom preservation in amber and new insights into early diatom history, both in terms of evolutionary history and palaeogeographical origin.

2 Material and Methods

2.1 Geological and palaeoenvironmental settings

The amber originates from the Khlong Min Formation, in Southern Peninsular Thailand (Philippe *et al.*, 2005). It is found in non-marine sediments, the stratigraphy of which has been reviewed by Teerarungsigul *et al.* (1999). The Khlong Min Formation is the basal part of the Trang Group that corresponds to clastic sediments (Philippe *et al.*, 2005). Philippe *et al.* (2005) indicated that the amber site does not provide marine fossils. These authors described the stratigraphy of the amber site as follows, from bottom to top:

- Layer 1: calcareous sandstones in which large lignitic trunks are preserved. Other plant debris are rarer, even though smaller woody axes (branches and roots) have been found in these sandstones. Philippe *et al.* (2005) interpreted these sediments as fluvial deposits.
- Layer 2: lenticular clayey silts that contain abundant amber nodules, conifer leafy twigs, lignite and charcoal. On the basis of the taphonomic characteristics of the fossils, Philippe *et al.* (2005) interpreted this assemblage as parautochthonous and deposited on a lake margin.
- Layer 3: calcareous conglomerate that contains a few plant remains such as rounded charcoal pieces, very small amber fragments and calcitised wood pebbles. Philippe *et al.* (2005) interpreted it as high-energy fluvial deposits.

Philippe *et al.* (2005) analysed the fossil wood specimens from the amber site. All correspond to conifers and the most interesting finding was the discovery of a 5-cm-long amber nodule filling a crack within wood of *Agathoxylon* Hartig. It suggests that Auracariaceae and/or Cheroledipidiaceae have produced Thai amber.

2.2 Age of the Khlong Min Formation

Asama *et al.* (1981) were the first to date the Khlong Mon Formation and they suggest an Early Cretaceous age on the basis of the study of the palaeoflora, especially because of the presence of the conifer *Frenelopsis* only known from the

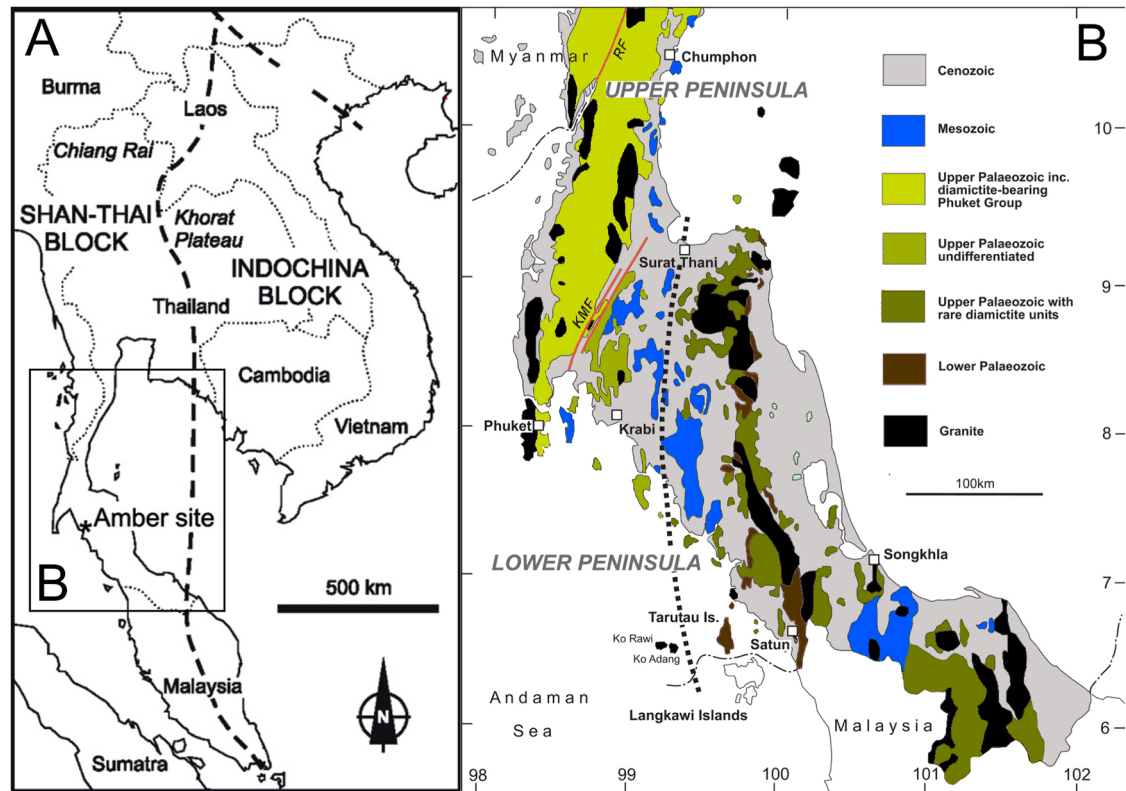


Fig. 1. Location map of Late Jurassic/Early Cretaceous amber outcrop of Thailand.

Cretaceous. However [Philippe *et al.* \(2005\)](#), reviewing the illustrations given by [Asama *et al.* \(1981\)](#), noticed that the fossils look more like the genus *Cupressinocladus* that is known from the Jurassic to the Cretaceous.

On the basis of a palynological study, [Lei \(1993\)](#) attributed a Jurassic age to the formation. More precisely, he suggested a Late Jurassic age because of the high percentage of *Classopollis*, although [Vakhrameev \(1987\)](#) had demonstrated that the percentage of *Classopollis* is an inverse factor of latitude and cannot be used for dating. [Racey and Goodall \(2009\)](#) revised the data of [Lei \(1993\)](#) and they suggested that the age of the Khlong Min Formation was not younger than Cenomanian. However these authors did not clearly indicate which part of the Khlong Min Formation their samples came from.

From a palaeontological point of view, all other authors considered the Khlong Min Formation as Jurassic in age. [Chonglakmani and Duan \(1990\)](#), on the basis of conchostreans suppose a late Middle Jurassic age. The presence of a sauropod originally referred to the Euhelopodidae ([Buffetaut *et al.*, 2005](#)) and now placed in the Mamenchisauridae ([Suteethorn *et al.*, 2012](#)) suggests a probable Late Jurassic age. Similarly, according to [Philippe *et al.* \(2005\)](#) the presence of *Asteracanthus* teeth is consistent with a Jurassic age because this genus is regionally known from Late Jurassic deposits ([Fontaine, 1990](#)). [Cuny *et al.* \(2009\)](#) indicated that the elasmobranch assemblage indicates a late Middle Jurassic age for the lower part of the Khlong Min Formation. [Saengsrichan *et al.* \(2011\)](#) mentioned the presence of *Parvamussium donaiense* Mansuy, 1914, a Jurassic bivalve, that is found up to the top of the Khlong Min Formation, suggesting that it is

really Jurassic in age. According to [Cuny *et al.* \(2014\)](#) concerning the shark faunas of northeastern Thailand, a Bathonian-Callovian age is considered for the Khlong Min Formation. Focused on thalattosuchian crocodylomorphs, recent works assign the Khlong Min Formation to the Late Jurassic ([Martin *et al.*, 2016](#)) and more precisely to the Bathonian-Callovian ([Martin *et al.*, 2019](#)).

From a geological point of view, the Khlong Min Formation is part of the Late Jurassic sedimentary series. [Meesook and Saengsrichan \(2011\)](#), in their synthesis of the Mesozoic of Thailand, attributed the Khlong Min Formation to the Middle Jurassic and they interpreted it as a gradual change from lagoonal to lacustrine deposits. According to [Kanjana-payont \(2014\)](#) the regressive trend continues during the Jurassic up to the upper Khlong Min Formation ([Fig. 1](#)).

It is clear from all this that the Khlong Min Formation is better considered as Jurassic in age, with some authors even specifying a Bathonian-Callovian age. Such an assumption is accepted in the recent review by [Seyfullah *et al.* \(2018\)](#) that indicates a Mid-Late Jurassic age for the amber of the Khlong Min Formation.

2.3 The amber

According to [Philippe *et al.* \(2005\)](#) the Thai amber is represented by abundant flattened nodules, that can reach 3 cm in diameter, occurring within clays (Layer 2 described above). The amber pieces are clear and exhibit a yellow-brown colour. [Philippe *et al.* \(2005\)](#) indicated that Thai amber is straw-coloured and not oxidised. The general aspect of Thai amber suggests that amber was not modified by any tectonic and/or

volcanic activities and remains in its primary shape, contrary to amber pieces that suffered metamorphic and/or volcanic alteration such as the amber piece described by Girard *et al.* (2014).

2.4 Optical observations

Amber samples were initially investigated under a standard stereomicroscope. Possible contamination was ruled out following the three-step chemical protocol described in Girard *et al.* (2009a). Samples were broken in order to obtain smaller pieces in which different characteristics of the fossils were easily visible. This step was done several times to obtain the smallest fragments that were then mounted on a slide with Canada balsam and observed. The amber samples were then investigated and photographed under a Leica DMLP microscope.

2.5 Thermal analysis

Thermogravimetric analysis of Thai amber was performed according to a previously described method (Ragazzi *et al.*, 2003). The thermogravimetric (Differential Thermo-Gravimetric, DTG) curves were obtained from three samples from Thai amber. According to published data (see Ragazzi *et al.*, 2003, 2009 for more details), a progressive change of the major thermal event is correlated to the age of the sample. The thermal analysis can therefore be used to estimate the age of the resin, in addition to other dating methods. Linear regressions through main thermal peak data available in our laboratory (for more information, contact two of us: GR and ER) and obtained from resins of different geological ages and origin (Ragazzi *et al.*, 2003, 2009) permitted to compare the thermal behavior data of the Thai amber samples. Different linear regression models were used to estimate the age of our samples.

3 Results

3.1 The diatom Thai specimen (Fig. 2)

A single specimen of bipolar diatom has been found in the amber sample KM01. Due to the presence of impurities in amber, the specimen is difficult to access. The characters present on the Thai diatom (such as a bipolar frustule, an elliptical valve with long polar elevations) indicate that the specimen belongs to the Hemiaulaceae Heiberg 1863 and more precisely to the genus *Hemiaulus* Heiberg 1863, according to generic characters from Hasle and Syvertsen (1997). The absence of more detailed features makes hazardous an assignment to the species level.

Here we present the description of the Thai diatom, using the classification presented by Guiry and Guiry (2020) from AlgaeBase.

Class Mediophyceae Medlin and Kaczmarek, 2004
 Subclass Chaetocerotophycidae Round and R.M. Crawford, 1990
 Order Hemiaulales Round and R.M. Crawford, 1990
 Family Hemiaulaceae Heiberg 1863
 Genus *Hemiaulus* Heiberg 1863
Hemiaulus sp.

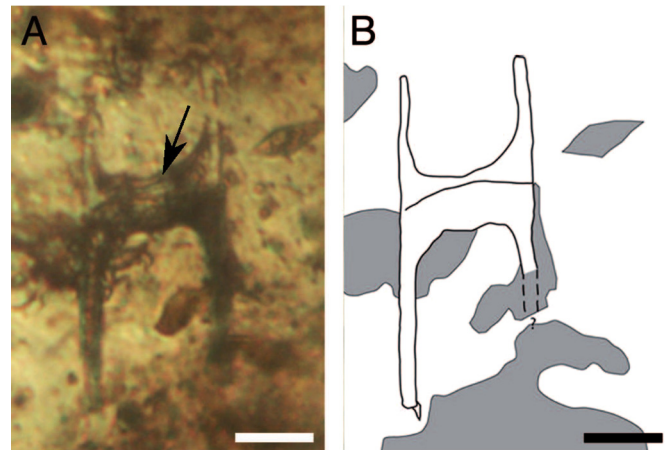


Fig. 2. The *Hemiaulus* diatom found in Late Jurassic-Early Cretaceous amber from Thailand. A. Photograph of specimen within dark amber matrix. B. Interpretative drawing of the photograph. Scale bar represents 10 μm . We can clearly distinguish the central parts of the frustule and its typical elevations. They end with spines corresponding to the linking apparatus of the frustule. The black arrow on A indicates the hyaline marginal ridge.

The specimen has subrectangular valves in girdle view with two long straight elevations (34 μm long) parallel to the pervalvar axis at the ends of the apical axis. Elevations exceed the valve length. Elevations seem to become very slightly narrower in their upper part. The ends of the elevations are not all visible. One of these polar elevations exhibits an apical spine (3 μm long) that represents the linking apparatus of the diatom. The girdle view allows to distinguish the hypovalve (the upper part of the specimen) and the epivalve (the lower part of the specimen). Thanks to small variations in the orientation of the microscopic slide and in the depth of observations within the amber, it seems that the specimen has an elliptical valve outline even though it has never been possible to confirm it with a clear observation of the valve view. Due to the mode of preservation, only the valve length along the apical axis was measured (45 μm long). The curvature of the valve face was not possible to be determined. It seems that two transapical pseudoseptae delimit a central segment. Unfortunately we were not able to observe whether there is a labiate process in the centre of the central segment. The valve mantle is not deep. Areolae are visible on the valve mantle and on the polar elevations. However due to the mode of preservation of the specimen, it has not been possible to clearly access this character. No clear pattern in the organization of the areolae is visible. A hyaline marginal ridge mostly visible on the hypovalve surrounds the valve face and seems to connect the two elevations.

Remarks: We attribute the Thai specimen to *Hemiaulus* since we observed typical characteristics of the genus that distinguish it from other similar looking genera with “hemiauloid” valves, such as *Cortinocornus* and *Riedelia*. The Thai specimen shows a general aspect of the valve similar to *Cortinocornus*, a genus common in Late Cretaceous assemblages from Devon Island, Canadian Arctic as mentioned by Tapia and Harwood (2002) and Witkowski *et al.* (2011) and also in the Upper Cretaceous of Saratov region (Oreshkina

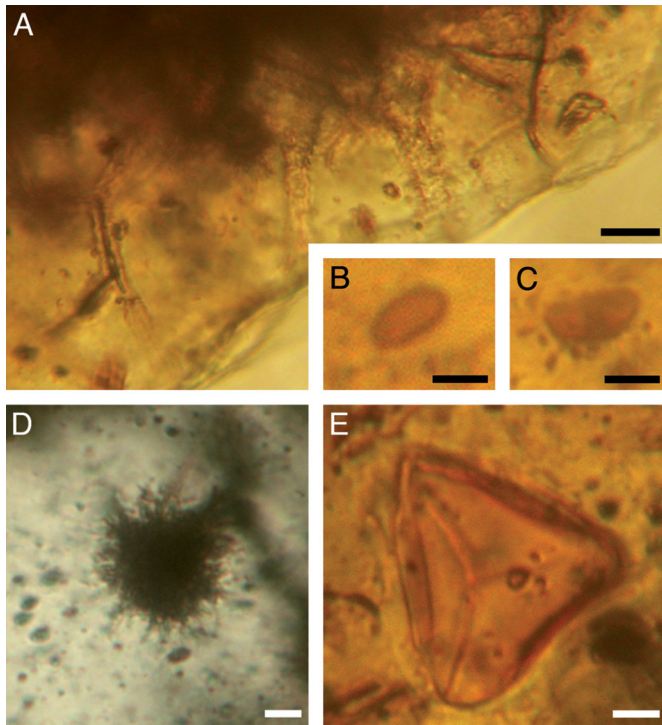


Fig. 3. Microfossils found in amber from Thailand. A. Sheathed prokaryotes. Scale bar: 20 μm . B. Single fungal spore. Scale bar: 5 μm . C. Fungal Didymospore. Scale bar: 5 μm . D. Colony of unidentified actinomycete. Scale bar: 10 μm . E. Spore of the pteridophyte genus *Gleicheniidites*. Scale bar: 10 μm .

et al., 2013) and the Paleogene of Central Russia, Transuralia (Oreshkina and Radionova, 2014). The main difference between the two genera consists in the presence of spines on elevations in *Hemiaulus*, while *Cortinocornus* does not possess this character.

Riedelia is a fossil genus containing species originally described under the genus *Hemiaulus* mainly from the DSDP Leg 38 (Schrader and Fenner, 1976). *Riedelia* valves are punctate with isolated punctae, while *Hemiaulus* has polygonal areolated valves. Moreover, *Riedelia* has two spines on each elevation, while *Hemiaulus* has only one. Also, the absence of any pseudoseptae is typical for *Riedelia*. In our specimen from Thai amber, the presence of areolae on the valve, a single spine on each elevation and transapical pseudoseptae supports the placement of the specimen in the genus *Hemiaulus*.

3.3 Amber syninclusions

The single specimen is in close proximity to fragments of either decayed organic matter or spherical to ovoid microinclusions in a very dark part of the amber.

The diatom was found with other syninclusions of which the most abundant are sheathed prokaryotes (Fig. 3A). They are composed of a trichome, 1 μm thick surrounded by a translucent sheath, 5–8 μm in diameter. These microinclusions are very similar to those described in many Cretaceous ambers (see review and discussion in Saint Martin and Saint Martin, 2018). Whatever their real nature, this is the oldest known

occurrence of this type of resinicolous microorganisms. Two different spores of fungi have also been identified. The first one consists of a single ovoid cell (Fig. 3B), the second corresponds to a didymospore (Fig. 3C). Colonies of unidentified actinomycetes were also observed (Fig. 3D). A spore belonging to the genus *Gleicheniidites* Ross ex Delcourt and Sprumont 1955 (Pteridophyta) was also found (Fig. 3E).

3.4 Thermal analysis

The main exothermal event (indicating the highest rate of weight loss under controlled heating) evidenced by a main thermal peak (MaTHEP), ranged between 425 and 435 $^{\circ}\text{C}$ (Fig. 4). Additional peaks, indicating further exothermal events, occurred at 470 $^{\circ}\text{C}$ and at 568–590 $^{\circ}\text{C}$.

Linear regressions through main thermal peak data provided the possibility to calculate a theoretical age for this amber (Tab. 1). Considering a first linear model (where x axis is MaTHEP in $^{\circ}\text{C}$, and y axis is age in Ma) it was possible to obtain, through a linear regression, an age estimate of the samples in the range 104–118 Ma (corresponding to the Lower Cretaceous–Albian) (Fig. 5A). Using another linear regression model (where x axis is age, and y axis is MaTHEP), a higher estimate was obtained, ranging 124–165 Ma (Fig. 5B). It may be noted that the slope of this line is mainly affected by the data apparently being outliers, and therefore the values obtained may be overestimated. The use of a robust linear regression however did not modify the values obtained with a regular linear model estimate. Moreover, the variability of thermal peaks observed in analysed Thai amber suggests that there is probably a different resin maturation profile among specimens, that can affect the age estimate. Thermal analysis of amber cannot be considered an unbiased method for amber estimation, but a complementary method to other age estimates, as suggested by the above cited palaeontological and geological investigations.

4 Discussion

4.1 Thai amber age

The thermal analysis was used to have a rough estimate of the age of the resin as described in Ragazzi *et al.* (2003), assuming a proportional relationship between the temperature of the main exothermal event and the age of the resin. Because of the different peaks and mathematical models, the analysis revealed contradictory estimated ages varying from 165 to 104 Ma. These new results however suggests that Khlong Min amber could be Late Jurassic–Early Cretaceous in age. Comparing it to all previous data published on the age of the Formation (see above), it is possible to suggest that Khlong Min amber is Late Jurassic in age.

4.2 Amber forest palaeoecology

The fragments of decayed organic matter and the spherical to ovoid microinclusions in the very dark parts of the amber are similar to some microinclusions described by Girard *et al.* (2011) in honey and yellow ambers from Charentes (France). Girard (2010) and Girard *et al.* (2011) interpreted such kinds of

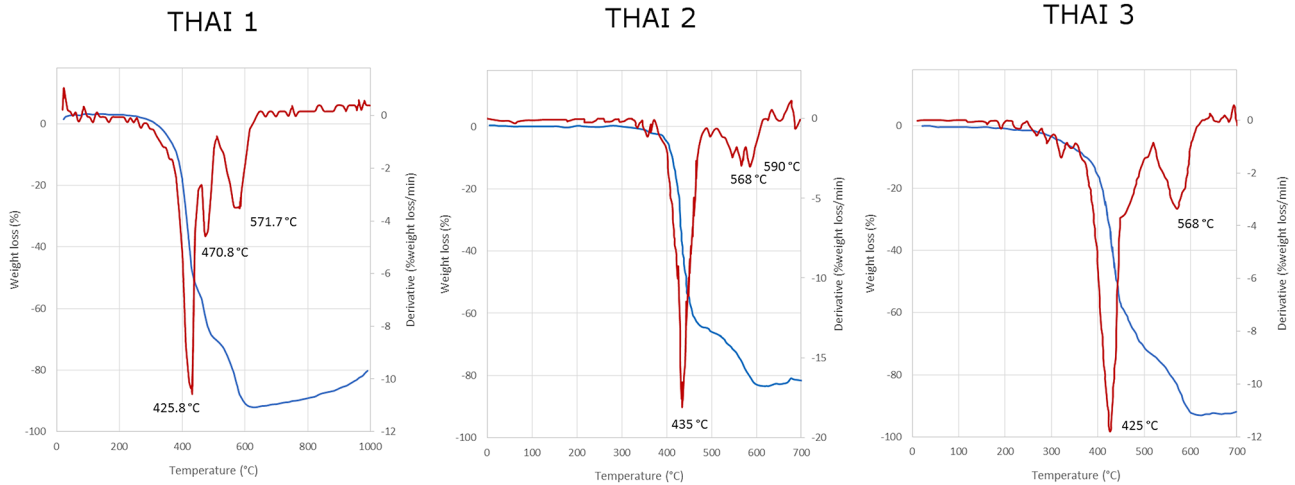


Fig. 4. Thermogravimetric curves obtained with three samples of Thailand amber. Thick line indicates the DTG profile; thin line is the TG profile (see Ragazzi *et al.*, 2003, 2009 for details).

Table 1. Age estimation of the Thai amber by thermogravimetric analyses.

Sample	Main DTG peak (MaTHEP, °C)	Age estimation (Ma), model 1	Age estimation (Ma), model 2
Thai1	425.8	105	127
Thai2	425	104	124
Thai3	435	118	165

SOM1: Full list of MaTHEP data of fossil resins used for the thermogravimetry method.

$$\text{Age (Ma)} = -464.361 + 1.338 \cdot \text{Main DTG peak (}^\circ\text{C)}$$

$$\text{Main DTG peak (}^\circ\text{C)} = 394.607 + 0.245 \cdot \text{Age (Ma)}$$

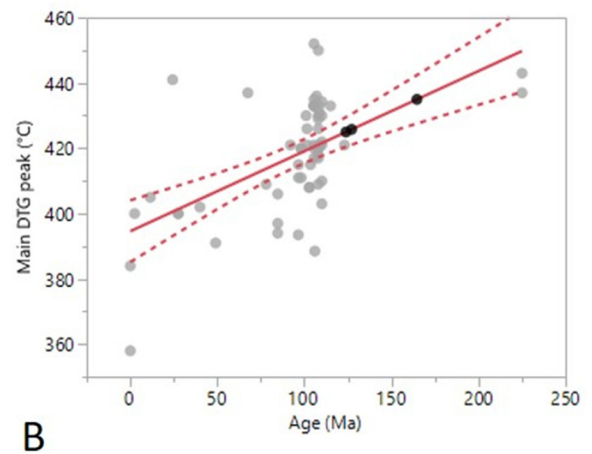
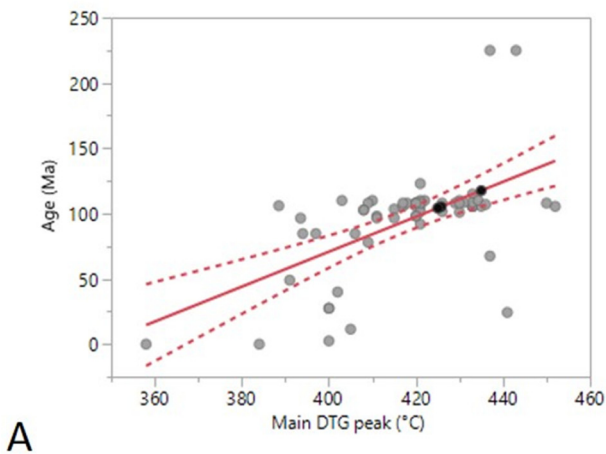


Fig. 5. Bivariate fit of Age *versus* MaTHEP (Main DTG peak, °C) for several data available in our database, obtained from samples of amber of different ages, indicated as grey circles. A significant correlation coefficient ($r = 0.5730$, $p < 0.0001$) was obtained throughout the overall dataset. Black points along the regression line indicate the three samples of Thai amber. As the dependent variable, MaTHEP was considered in panel on the left (A), and Age in the panel on the right (B); respective equations obtained with standard least squares method are indicated above each graph. Complete list of data for regression is provided as supplementary information.

amber as probable aerial secretions on the trunk and branches of the resiniferous trees.

The scarcity of syninclusions in Thai amber does not allow to reconstruct with much precision the amber forest ecology.

The presence of bacterial filaments in Thai amber, developed in some pieces of amber as dense networks of filaments, can indicate that Thai amber had been secreted in a humid environment. Such a hypothesis is in agreement with Philippe

et al. (2005) who interpreted the fossils from the amber-bearing clayey silts as parautochthonous and the depositional environment as the margin of a lake. The presence of a fern spore in Thai amber also supported this hypothesis. Its discovery is remarkable because pollen and spores are relatively rare in Mesozoic amber. *Gleicheniidites* spores were already found in Mesozoic Thai sediments (Racey and Goodall, 2009). The presence of a spore in Thai amber suggests that resiniferous conifers and Gleicheniaceae ferns grew together in the Jurassic vegetations. It is highly probable that ferns formed the undergrowth of the Thai conifer forests. The presence of fungal spores also corroborates the hypothesis of the resiniferous forests growing in a humid or close to a humid environment. The presence of a marine diatom in Thai amber indicates that the amber forests grew close to the sea. The interpretation of Philippe *et al.* (2005) considering the depositional environment as the margin of a lake can thus be revised: it was as a seashore rather a lakeshore.

4.3 Stratigraphic range of bipolar diatoms and *Hemiaulus*

Based on molecular data supported by morphological and cytological characteristics, the Clade 1 and Clades 2a and 2b proposed by Medlin and Kaczmarek (2004) are recognized (Sims *et al.*, 2006; Medlin, 2011) at class level: Coscinodiscophyceae containing centric diatoms with radial symmetry of valve shape and structure; Mediophyceae containing the bi- or multipolar centrics and the radial Thalassiosirales; Bacillariophyceae containing the pennates.

The genus *Hemiaulus*, because of its bipolar shape in valve view, is included in Mediophyceae within the bipolar centrics.

Sorhannus (2007), based on nuclear-encoded SSU rRNA analyses, estimated the divergence of bipolar centric diatoms at 150 Ma ago. Medlin (2010) and Sato (2008) found much older divergence times for all the classes. Their clock suggests that the radial centrics, Class Coscinodiscophyceae, arose from 180 to 240 Ma ago and the bipolar centrics, Class Mediophyceae diverged from the Class Bacillariophyceae at 183–238 Ma (minimum to maximum, respectively). However, fossil records of bipolar diatoms still do not agree with this estimate. Up to know the oldest fossil evidence of bipolar diatoms came from Aptian/Albian sediments of the Weddell Sea (Antarctica) where Gersonde and Harwood (1990) found *Bilingua rossii* Gersonde and Harwood 1990 and *Kerkis bispinosa* Gersonde and Harwood 1990. Slightly younger (Late Albian) is the diverse assemblage of marine diatoms from the amber of Charentes (Girard *et al.*, 2008, 2009b). It comprises many specimens attributed to the genus *Hemiaulus* and one specimen of *Rutilaria*, named *Syndetocystis* in Girard *et al.* (2008) and revised by Witkowski *et al.* (2011). These assemblages testify to a very long stratigraphic range (100 million years) for *Hemiaulus*.

Before these discoveries, the divergences between molecular data and the fossil records of different families were greater. Indeed, the Hemialuceae, more precisely the genus *Hemiaulus*, were first found in Early Late Cretaceous marine sediments (Tapia and Harwood, 2002), before becoming more abundant and diverse into Upper Cretaceous deposits (Strel'Nikova, 1975; Jousé, 1978; Oreshkina *et al.*, 2013). During the Cenozoic, they become very abundant, with

some species such as some included in the genus *Hemiaulus* that have been used as stratigraphic markers (Barron and Baldauf, 1995). Extant *Hemiaulus* comprises only four species.

The Thai specimen extends the stratigraphic range of the genus *Hemiaulus* to the Late Jurassic, making *Hemiaulus* the diatom genus with the longest stratigraphic range ever found. According to molecular dating (Sorhannus, 2007), the Thai specimen provides geological evidence for the occurrence of *Hemiaulus* soon after the origin of bi- and multipolar diatoms. The recent time calibrated phylogeny of diatoms published by Nakov *et al.* (2018) indicates a minimum age for the emergence of *Hemiaulus* at ca. 130 Ma, and the age of the emergence of the clade containing *Hemiaulus* and *Chaetoceros* between 150 ~ 100 Ma. Our discovery of a *Hemiaulus* specimen in amber dated from the Late Jurassic agrees quite well with the results of this new diatom evolutionary tree. Therefore, the Thai specimen also extends the fossil record of the hemiauloids in particular and consequently that of bipolar diatoms.

Other bipolar diatoms, the Rutilariaceae, seem to originate from the Late Cretaceous (Witkowski *et al.*, 2011). Only the possible specimen of *Rutilaria* found in French amber (Girard *et al.*, 2008) makes this family older. *Hemiaulus* from Thai amber supports the supposition of Ross (1995) followed by Witkowski *et al.* (2011), who considers the Hemialuceae as ancestral to the Rutilariaceae.

The Thai diatom corroborates the estimation proposed by Sorhannus (2007) and confirms the hypothesis of an origin of the bi- and multipolar diatoms by the end of the Jurassic/beginning of the Cretaceous.

No other evidence of Jurassic diatoms is known, except the problematic Liassic German specimens of *Pyxidicula* (Rothpletz, 1896, 1900) as mentioned above.

The discovery of fossil diatoms in amber from Charentes (Girard *et al.*, 2008, 2009b) and Vendée (Saint Martin *et al.*, 2015) already showed that this specific preservation of diatoms provides important data that bring new insights into our knowledge of the early fossil record of diatoms. The Thai specimen reinforces the state of the art and should stimulate active researches on Jurassic to Early Cretaceous ambers. Mesozoic ambers from the Triassic of Italy (Roghi *et al.*, 2006, 2017), Jurassic amber localities in Lebanon (Nohra *et al.*, 2013) and mid Cretaceous Burmese amber (Yu *et al.*, 2019) could be good candidates.

4.4 Long ranging *Hemiaulus*: palaeogeographical and palaeoecological implications

As discussed above, the discovery of *Hemiaulus* in Late Jurassic Thai amber reveals the persistence of the genus from ca 145–160 million years ago to the present. Long morphological stases were already mentioned for some protists, especially based on amber inclusions (Martín-González *et al.*, 2008). These possible stases have been mostly observed in green algae and amoebae. For example the Cenomanian Schliersee amber preserved six different green algae, an euglena, two fungi and sixteen amoebae (Poinar *et al.*, 1993a, 1993b; Schönborn *et al.*, 1999; Dörfelt and Schäfer, 2000; Schmidt *et al.*, 2004). Among all these fossils, 19 taxa have

been related to modern genera, and in some cases, to modern species. A long stratigraphic range for the diatom genus *Hemiaulus* can appear remarkable for a group of organisms known to have rapid evolutionary rates (Bowler *et al.*, 2008). However, Wornardt (1972) and Jousé (1978) already mentioned 11 and respectively 7 genera including *Hemiaulus* that are known from the Cretaceous to the Present Day.

Thus the genus *Hemiaulus* has been present since the beginning of the Mediophyceae, survived different extinction events such as that of the Cenomanian/Turonian boundary (Harwood *et al.*, 2007) and experienced several major periods of floral turnover during the Cenozoic, such as that of the Middle Eocene-early Oligocene (Baldauf, 1992).

The oldest known occurrence of *Hemiaulus* (present study) comes from a low latitude neritic coastal context. Early Late Cretaceous *Hemiaulus* from French amber (Charentes) corresponds to mid-latitude coastal environments (Girard *et al.*, 2008, Girard *et al.*, 2009a, 2009b; Girard, 2010). This is consistent with the observation of Jewson and Harwood (2017), who suggested that Early Cretaceous diatoms were restricted to continental margins. Late Cretaceous diatom assemblages (including *Hemiaulus*) are known from extensive diatomites developed in different geographical zones: the eastern Urals and north-western Siberia (e.g. Strel'Nikova, 1975), the Marca Shale, Moreno Formation in California (e.g. Hanna, 1927; Nikolaev *et al.*, 2001) and also in sediments from Antarctica (Harwood, 1988), Arctic Canada (Tapia and Harwood, 2002; Witkowski *et al.*, 2011) associated with a deposition in a shallow nearshore habitat. Other occurrences come from diatomaceous sediments recorded in the Pacific Ocean deep-sea drilling core Site 275 (Hajos and Stradner, 1975), Indian Ocean, site 758 (Fournanier 1991a), Arctic Ocean, Core FI-437 Alpha Ridge (Dell'Agnesse and Clark, 1994), CESAR core 6, Arctic Ocean (Barron, 1985). In Arctic sites *Hemiaulus* was found in associations with resting spores, benthic and neritic species suggesting a shallow water environment (Harwood, 1988). Poor diatom occurrences or with pyritized diatoms are also known from the Lower and Upper Cretaceous (see list in Tapia and Harwood, 2002).

Paleocene occurrences of *Hemiaulus* come from extensive biosiliceous sediments in land section and also from profiles recovered by successive Deep Sea Drilling Projects. Diatom assemblages including *Hemiaulus* are known mainly from the Russian Platform in a context of epicontinental shallow sea basins (for reviews of the sites see Jousé, 1978, Oreshkina and Radionova, 2014), from the Fur Formation, Denmark (Homann, 1991; Fenner, 1994) and Seymour Island, Antarctica (Harwood, 1988). *Hemiaulus* is recorded from several deep-sea drilling cores from the Atlantic, Pacific and Indian Oceans (for lists of sites see Fournanier, 1991b; Renaudie *et al.*, 2018). During the Paleocene *Hemiaulus* was represented by a plethora of species and had a geographic distribution in both the southern and northern hemispheres, both in epicontinental seas and in more open oceanic environments.

Eocene *Hemiaulus* occurrences are documented in onshore sections of the Fur Formation (Moler Formation) in Denmark (Benda, 1972; Fenner, 1988), in the Urals, western Siberia, the Volga basin, Ukraine, south Kazakhstan (see review in Oreshkina and Radionova 2014), the Kellog Shale, California (Barron *et al.*, 1984), lower part of Oceanic formation of

Barbados and Oamaru, New Zealand (Edwards, 1991) and also from deep-sea drilling cores from the Atlantic, Pacific and Indian Oceans, the Norwegian Sea (for lists of sites see Fournanier, 1991b; Barron *et al.*, 2015). Distinct latitudinal diatom assemblages with distinct *Hemiaulus* species were identified for high and middle low latitudes and for low latitudes respectively together with cosmopolitan species (Fenner, 1985). As in the Paleocene, *Hemiaulus* persists among the dominant genera within diatom assemblages corresponding either to epicontinental seas, or more open oceanic environments.

Oligocene *Hemiaulus* is documented from different deep-sea drilling cores both at high (e.g. Schrader and Fenner, 1976; Monjanel, 1987; Scherer *et al.*, 2000) and low latitudes (e.g. Barron, 1985; Fenner, 1985). A major change concerning *Hemiaulus* diversity begins with the middle Oligocene when most of the typical Eocene diatom species have disappeared (Fenner, 1985). In the Late Oligocene high-latitude *Hemiaulus* species spread far toward the equator (Fenner, 1984) corresponding to a reorganization of oceanic circulations.

Neogene diatom deposits were investigated all over the world both in land outcrops and in many deep-sea drilling cores in different oceans at low, middle and high latitudes. Therefore it is difficult to list here *Hemiaulus* occurrences from all around the world. It should be noted that *Hemiaulus* diversity continuously dropped through the Miocene and Pliocene, as already shown by Jousé (1978) in a diagram of evolutionary changes in the generic composition of marine diatoms. During the Neogene, *Hemiaulus* is listed among other genera related to littoral or neritic areas (e.g. Jousé, 1978; Monjanel, 1987; Pestrea *et al.*, 2002).

There are only four extant species: *Hemiaulus hauckii* Grunow ex Van Heurck 1882 and *H. sinensis* Greville 1875 reported from warm to temperate waters and *H. indicus* Karsten 1907, and *H. membranaceous* Cleve 1873 from warm waters (Hasle and Syvertsen, 1997). Recent and present day *Hemiaulus* are known both from neritic (Hendey, 1964; Cupp, 1977; Guo, 1994; Sá *et al.*, 2013) and pelagic open marine ecosystems (Villareal, 1991; Rivera *et al.*, 2003; Kemp and Villareal, 2013; Anderson *et al.*, 2018).

It should be noted that the genus *Hemiaulus* was not reassessed recently as was the case for instance for the genus *Triceratium* that was split into several genera. Further taxonomic studies might reveal that what currently is still referred to *Hemiaulus* might be in fact a group of several similar looking genera.

It seems that during a long geological time span *Hemiaulus* experienced some ecological changes implying the passage from neritic to more open oceanic environments. Adaptation to pelagic open marine ecosystems was possible for diatoms thanks to specificities such as symbioses with N₂-fixing cyanobacteria (Foster *et al.*, 2011). The presence of such a symbiosis, clearly identified for modern *Hemiaulus* (Villareal, 1991), has been interpreted as an adaptation of the diatoms to low-nutrient waters of the open ocean (Foster *et al.*, 2011; Kemp and Villareal, 2013). This adaptation seems to have already been acquired in the Late Cretaceous since *Hemiaulus* blooms were identified by Davies and Kemp (2016) in Upper Cretaceous sequences from Alpha Ridge (Arctic Ocean, core CESAR 6) and Marca Shale (Moreno Formation, California) corresponding to summer stratified conditions. Their obser-

rvations are supported indirectly by isotopic evidence for N-fixation (Meyers *et al.*, 2009) and biomarker evidence for the presence of cyanobacteria (Kuypers *et al.*, 2004; Wagner *et al.*, 2004).

The long ranging *Hemiaulus* was witness to several steps in the long and complex diatom history. Some events are thought to be responses to environmental changes related to global palaeoceanographic conditions driven by global climate changes and tectonics (e.g. Barron and Baldauf, 1989; Sims *et al.*, 2006; Harwood *et al.*, 2007; Kooistra *et al.*, 2007; Egan *et al.*, 2013; Lazarus *et al.*, 2014). *Hemiaulus* crossed the crucial boundary Cretaceous-Paleogene boundary being among the 84% of diatoms (estimation in Harwood, 1988) that did not suffer a major extinction. According to its species occurrences (see Strel'Nikova, 1975), *Hemiaulus* testifies to a latitudinal zonation of diatoms since the Late Cretaceous. *Hemiaulus* is among the genera that suffered a major shift in diversity that happened during the Oligocene. Indeed, many lineages known since the Cretaceous disappeared or became less common, whereas new taxa emerged or became more common (Kooistra *et al.*, 2007). This new picture in diatom diversity is correlative with global changes (Sims *et al.*, 2006). Beginning with the Cenozoic, the reorganization of the oceanic masses became more evident with the onset of Antarctic glaciations and deep-water cooling in the earliest Oligocene (Fenner, 1985; Scherer *et al.*, 2000) and intensified during the Miocene and Pliocene, punctuated by several high-latitude cooling steps (Barron and Baldauf, 1989; Lazarus *et al.*, 2014; Barron *et al.*, 2015). So, *Hemiaulus* experienced life in a changing world, from a Cretaceous “green house” with a thermospheric circulation to a gradual development of the cryosphere with a thermohaline circulation reflecting the continuously installation of ice on Antarctica (Berggren and Prothero, 1992). The decline of the diversity of *Hemiaulus* from over 40 species in the Late Cretaceous (Harwood and Nikolaev, 1995) to only four extant species *via* an important drop in the Oligocene might be explained at least partially by a more global trend of lowering of water temperatures. Late Cretaceous global sea surface temperatures were estimated to be around 10 °C warmer than today (De Conto *et al.*, 2000). The Thai specimen shows that some long ranging genera registered in the early history of diatoms such as *Hemiaulus* were able to acclimatize and/or adapt through geological time to various conditions in the marine environment.

The discovery of *Hemiaulus* in Thai amber also raises questions about the initial palaeogeographic distribution of diatoms. Indeed, during the Jurassic-Early Cretaceous, all sites recording diatoms, including *Hemiaulus*, were situated on the southern coast of Laurasia. It is possible that early diatoms originated from the northern shore of the Tethys on which diatoms lived in shallow coastal waters. Such a hypothesis could be verified only with the discovery of new fossil diatoms from the Jurassic/Early Cretaceous (including amber deposits that demonstrated their potential for diatom preservation; Girard *et al.*, 2009b).

Another palaeoecological implication related to the discovery of the oldest known occurrence of *Hemiaulus* from Thai amber concerns the hypothesis about the ancient habitats of early diatoms. According to Harwood *et al.* (2007) diatoms found in the Korean earliest Cretaceous would extend the confirmed presence of diatoms and suggest a continental

habitat for early diatoms. The occurrence of the marine genus *Hemiaulus* from the Late Jurassic in the same geographical area obviously raises questions. It should be noted that no subsequent fossil record attests the occurrence of freshwater diatoms until the Late Cretaceous. The co-occurrence of marine and freshwater diatoms at the same time would therefore need to be confirmed. The record of Thai *Hemiaulus* is in agreement with the molecular data indicating that most of the extant basal lineages of diatoms are marine (Medlin and Kaczmarska, 2004). The discovery of the Thai specimen may revive the ever-recurring question of whether the first diatoms were marine or freshwater. *Hemiaulus* is a typical marine genus and no species is known from brackish or freshwater environments, either in the fossil record or in present-day assemblages. The hypothesis of the invasions of freshwater environments by marine diatoms was invoked to explain the evolution of the diatom flora from marine taxa based on the record of fossil marine diatoms extending before those of freshwater forms (see citations in Sims *et al.*, 2006). Among centric diatoms the example of *Actinocyclus* should be noted: it originated in marine environments that experienced a large diversification before moving into freshwaters (Bradbury and Krebs, 1995). The occurrence of *Hemiaulus* only in marine environments since its earliest known record from Thai amber (present work) agrees with the observation of Strel'Nikova and Lastivka (1999) that older centric diatom lineages failed to adapt to the lower salinity of inland waters, apart from the Early Cretaceous marine *Archeopyrgus* that is considered by Harwood and Nikolaev (1995) as the ancestor of freshwater *Aulacoseira*.

Finally, any discovery of Pre-Cretaceous diatoms could potentially help to answer crucial questions about the palaeobiogeographical and environmental conditions in which diatoms emerge.

5 Conclusions

As for the angiosperms, Darwin could have described the origin of diatoms as “an abominable mystery”. Although Thai amber does not solve this problem, it does provide new evidences about the early fossil record of diatoms and highlights that a probable pre-Cretaceous fossil record should exist. To judge from the oldest known diatom fossils, this fossil record should come from neritic shallow environments that developed along the northern shore of the Tethys. The fact that the oldest known diatom occurrence corresponds to *Hemiaulus*, a still extant genus, raises questions concerning diatom evolution: a) morphology of the frustules that is supposed to show evolutionary innovations already in the Late Jurassic allowing this genus to cross critical boundaries while other Early Cretaceous genera disappeared; b) insights on the early history of bipolar diatoms; c) information about the roots of “oldest” and “modern” lineage histories; d) adaptation/acclimatization to changing marine environments (e.g. water stratification and anoxia, eutropic upwelling systems, diazotrophic conditions). *Hemiaulus* might be regarded as opening a path into the very long history of a marine genus: from the origin of diatoms in the marine environment marine to geographical expansion, high species diversification and then gradual decline.

Supplementary Material

SOM Thermogravimetry.

The Supplementary Material is available at <http://www.bsgf.fr/10.1051/bsgf/2020028/olm>.

Acknowledgement. We thank M. Philippe and J. Le Loeuff for constructive discussion about the age of the material and N. Rowe for checking the usage of English. We thank also A. Giaretta (Padua, Italy) for thermal analysis of amber. We thank J. Witkowski for its kindly suggestions and a anonymous reviewer for its constructive comments. Material is housed in the collection of the Palaeontological Research and Education Centre, Maha Sarakham University (Thailand). For more information, please contact V. Suteethorn. This is publication n° ISEM 2020-175 SUD of the Institut des Sciences de l'Evolution de Montpellier (France).

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Cite this article as: Girard V, Saint Martin S, Buffetaut E, Saint Martin J-P, Néraudeau D, Peyrot D, Roghi G, Ragazzi E, Suteethorn V. 2020. Thai amber: insights into early diatom history? *BSGF - Earth Sciences Bulletin* 191: 23.