Significance of shallow-marine and non-marine algae stable isotope (δ18O) compositions over long periods: Example from the Palaeogene of the Paris Basin

Damien Huyghe, Laurent Emmanuel, Maurice Renard, Franck Lartaud, Patrick Génot, Janine Riveline, Didier Merle

To cite this version:

Damien Huyghe, Laurent Emmanuel, Maurice Renard, Franck Lartaud, Patrick Génot, et al.. Significance of shallow-marine and non-marine algae stable isotope (δ18O) compositions over long periods: Example from the Palaeogene of the Paris Basin. Palaeogeography, Palaeoclimatology, Palaeoecology, 2017, 485, pp.247-259. 10.1016/j.palaeo.2017.06.017 . hal-01557354

HAL Id: hal-01557354

https://hal.sorbonne-universite.fr/hal-01557354v1

Submitted on 6 Jul 2017

Significance of shallow-marine and non-marine algae stable isotope (δ^{18}O) compositions over long periods: Example from the Palaeogene of the Paris Basin

Damien Huyghe[1,2], **Laurent Emmanuel**[1], **Maurice Renard**[1], **Franck Lartaud**[3], **Patrick Génot**[4], **Janine Riveline**[1], **Didier Merle**[5]

[1] Sorbonne Universités, UPMC-Paris 06, UMR CNRS 7193, ISTeP, F-75005, Paris, France

[2] Géosciences Environnement Toulouse, Université Paul Sabatier Toulouse 3, 14 Avenue Edouard Belin, 31400 Toulouse, France

[3] Sorbonne Universités, UPMC-Paris 06, UMR 8222, Lab. Ecogéochimie des environnements benthiques (LECOB), Observatoire Océanologique, F-66650, Banyuls-sur-mer, France

[4] Département des Sciences de la Terre, Université de Nantes, 2 rue de la Houssinière, 44072 Nantes

[5] Sorbonne Universités, UMR CNRS 7207 (MNHN, CNRS, UPMC) Muséum national d'Histoire naturelle. CP 38, 8, rue Buffon, 75005 Paris

Abstract

In this study, we test the potentiality of using dasycladales and charophytes, calcareous shallow-marine and non-marine algae respectively as palaeoclimatic recorders. These algae mineralize their carbonate during short periods in summer. Throughout the Palaeogene, we compare the $\delta^{18}O$ variation of these two taxa to identify a possible common factor influencing their isotopic composition, i.e. temperatures variations, from a local environmental signal. We sampled and isotopically analyzed eight species of charophytes and seven species of dasycladales from 23 formations ranging from the Palaeocene to the Oligocene series of the Paris Basin. By comparing the $\delta^{18}O$ of these two groups living in different environment with that of shallow-marine mollusks from a previous study, we show that temperature variations are the main factor influencing their $\delta^{18}O$ compositions and that local environmental effects does not screen the global thermal signal. Maximum annual palaeotemperatures are calculated from the $\delta^{18}O$ of the dasycladales and indicate by comparison with the data from mollusks previously analyzed that dasycladales species used probably mineralized their carbonate in equilibrium with sea-water. Dasycladales recorded the global climatic events already known for the Palaeogene, with high temperatures reached during the Early Eocene and Middle Eocene climatic optimums and relative cooling intervals during the Lutetian, the Priabonian and the Rupelian. Charophyte gyrogonites also recorded temperature variations in their $\delta^{18}O$ compositions but reconstituting reliable temperature values in non-marine environments is not directly possible and requires constraining $\delta^{18}O$ of local continental water using other proxies. These promising results show that carbonates mineralized from algae constitute a reliable support for palaeoclimatic information and should be more widely used in the fossil record.

Keywords: carbonates; dasycladales; charophytes; biomineralizations; palaeotemperatures

1. Introduction

Determining how temperatures fluctuated in the past is a key to understanding future climatic changes. This has been extensively investigated for the Palaeocene Eocene Thermal Maximum (PETM, ~ 55 Ma), which is considered as an analogue of modern global warming. For methodological reasons, especially the good preservation of the biogenic material, the chemical stability of the open ocean and the restricted diagenesis, Cenozoic palaeoclimatic reconstructions based on isotopic studies have focused on deep-sea marine biogenic material provided by the various ocean-drilling programs. Thus, Cenozoic palaeoclimatic data come mainly from the $\delta^{18}O$ of deep-sea benthic foraminifers and to a lesser extent from planktonic foraminifers (Shackleton and Kennett, 1975; Miller et al., 1987; Zachos et al., 2001), even if various attempts were carried out on bulk carbonate (Renard, 1986; Shackelton et al., 1993). These works have successfully documented that the Palaeogene experienced a long-term and discontinuous cooling from the greenhouse Early Eocene Climatic Optimum (EECO) to a permanent icehouse world since the Eocene - Oligocene boundary (~ 34 Ma). This long-term cooling was interrupted by a major transient hyperthermal event (warming of ~ 4 °C of the deep ocean) at ~ 40 Ma, the Middle Eocene Climatic Optimum (MECO; Bohaty and Zachos, 2003).

However, the deep-sea record presents some limitations because only mean annual temperatures can be estimated from these proxies and important climate parameters like the seasonal gradient of temperatures cannot be documented. Moreover, oceanic environments are less sensitive to short duration and low intensity climatic events, giving a mean vision of the climate. Furthermore, it is particularly important to characterize how other environments like coastal and non-marine domains were impacted by such temperature fluctuations during this major climatic transition. Following the pioneer works of Tivollier and Letolle (1968) and Buchardt (1978), this has led more and more researchers to focus on shallow-marine environments and especially on the measurement of the $\delta^{18}O$ in mollusk shells (Andreasson and Schmitz, 1996; Ivany et al., 2008; Huyghe et al., 2015; Walliser et al., 2016). In the best cases, these measurements reveal the amplitude of seasonal temperature changes (Andreasson and Schmitz, 1996; Lartaud et al., 2010). However, because of the wide environmental variability of the near-shore realm, mollusks are not always available and sufficiently preserved to yield a pristine signal, and it appears important to diversify both the approaches and kinds of materials used for palaeoclimatic investigations. Moreover, even if marine mollusks are used to document seasonal variations of temperatures, many species do not mineralize their shell throughout the year, making it difficult to reconstruct the seasonal extremes (Goodwin et al., 2003). Thus, it is necessary to diversify fossil proxies that can be used as a record of the palaeoclimatic information.

The Palaeogene is also a recommended period to investigate the relationships between greenhouse gas concentrations, temperature variations and marine biodiversity fluctuations (Merle, 2008; Huyghe et al., 2012a; Sanders et al., 2015). This period exhibits a long-term cooling and a decrease in greenhouse gas concentrations (Zachos et al., 2008), which are also contemporaneous with wide fluctuations in the biodiversity of marine invertebrates including mollusks, benthic macro-foraminifers and planktonic foraminifers (Hallock et al., 1991; Merle, 2008). Their specific richness first increased from the K/P Boundary to the Lutetian and then decreased from the Bartonian to the end of the Eocene. The peak of biodiversity was thus surprisingly reached during the Lutetian, concomitant with a relative cooling between the climatic optimums of the Early Eocene (~53-50 Ma) and Middle Eocene (40 Ma) (Huyghe et al., 2012a). Coupling between temperature variations, greenhouse gas concentrations and biodiversity is thus not easy to understand and new proxies have to be found to explore these questions more in detail.

In the continental domain, the Palaeogene climate has mostly been studied using floral and palynologic analyses (e.g. Châteauneuf, 1980; Mosbrugger et al., 2005) but geochemical proxies has rarely been used and data remains scarce (Grimes et al., 2003, 2005; Sheldon et al., 2016). It is linked on one hand to the discontinuity of the stratigraphic record, and on the other hand to the complexity of interpretation of the isotopic signal in this realm due to greater environmental fluctuations.

Dasycladales and charophytes are common marine and non-marine shallow-water green algae respectively. They produce biogenic carbonate during the warmer months of the year (Génot, 1991; Jones et al., 1996) and their $\delta^{18}O$ compositions could thus provide an effective proxy for maximum temperatures in their living environments. The aim of this work is to investigate the parameters that govern the $\delta^{18}O$ trends of these algae over an interval of ~25 Ma and to determine if a climatic signal can be identified. We focus on the Palaeogene series from the Paris Basin where it is possible to sample both well-preserved dasycladales and charophytes in many outcrops through time (Génot, 1987; Riveline, 1984). The Paris Basin also provides the possibility to compare these isotopic data from algae with previous data from mollusks sampled in the same or contemporaneous sites and where palaeoclimatic data were reconstructed (Andreason and Schmitz, 1996; Huyghe et al., 2012a, 2015). Studying both shallow-marine and non-marine algae $\delta^{18}O$ composition is a suitable way to extract climatic information relative to an environmental signal related to their living conditions.

2. Use of calcareous algae as palaeoclimatic proxies: state of the art and limitations

2.1. Dasycladales

Dasycladales are shallow marine unicellular green macroalgae existing since the Palaeozoic (Fig. 1A). Modern specimens are found in tropical and subtropical, low-energy, shallow-marine (> 10 m) and brackish water environments (Génot, 1991; Granier, 2012). Modern specimens from the Mediterranean Sea like Acetabularia occur within an isocryme of 13°C and some ones like Neomeris and Bornetella at 20°C, which is important for palaeoclimatic studies (Elliott, 1977, 1984). Dasycladales prefer higher and more stable salinities (Jaffrezo and Renard, 1979; Elliott, 1984; Biber and Irlandi, 2006) but can tolerate relatively broad salinity ranges (+20 to +45 ‰). Some modern species can also be found in more open marine conditions, but only a few species have been detected in closed lagoons with extremely high salinity due to water evaporation, or low salinity due to freshwater supply (Berger and Kaever 1992). Cenozoic dasycladales include about 43 genera and 200 species. The richest Cenozoic assemblages have been found in the Palaeocene of Sardinia and in the Palaeocene and Eocene of the Paris Basin (Génot, 1987, 2009). Calcification occurs mostly in aragonite, but some traces of low-magnesian calcite have also been identified in modern specimens (Granier, 2012). The calcified parts enclose sterile and fertile organs to a varying degree, according to genera, species, and individuals. Consequently, fossil preservation depends mainly on the extent of the initial calcification around the thallus. The processes that govern the mineralization of dasycladales remain poorly understood, but they seem to mineralize their carbonate during the warmer months of the year during short periods of a few weeks (Génot, 1991).

The use of $\delta^{18}O$ measurements of marine calcareous algae as a climate proxy was developed in very different ways depending on taxonomic groups. Isotopic studies on red algae and especially on coralline algae have been considerably developed leading to high-resolution reconstructions of climate and palaeoceanography from modern or recent samples

(Halfar et al., 2008). On the contrary, climate reconstructions, based on isotope analyses of green algae like dasycladales remain rare. Only a few research papers deal with isotopic studies of modern dasycladales, and the presence of a vital effect for those organisms is not clearly understood. Wefer and Berger (1991) showed that modern dasycladales from Bermuda exhibit disequilibrium of about +1 ‰ with sea-water. On the contrary, Lee and Carpenter (2001) conducted isotopic measurements on the different components of the organism and found that the difference in isotopic $\delta^{18}O$ values was a maximum of +0.3 ‰. However, they conclude that dasycladales are close to equilibrium with sea-water and constitute good recorders of the climatic conditions of their living environments.

2.2. Charophytes

Charophytes are small macrophyte green algae living entirely submerged in fresh and brackish waters (Fig. 1B). They are represented by six modern genera (Wood and Imahori, 1965). These algae are able to produce calcite during their ontogeny (Leitch, 1991), and fossil remains usually consist of the calcified female fructifications, i.e. gyrogonites, even if the thallus can also be well preserved (Pelechaty et al., 2013). Gyrogonites correspond to the oosporangium surrounding the oospore, and constitute the most usable parts for geochemical analysis (Fig. 1B). Anadón et al. (2002) observed that the mineralogy of the gyrogonites is related to environmental conditions with a polymineral calcification (calcite, high-magnesian calcite, aragonite) in relation to the Mg / Ca ratio of the water in which specimens lived. The calcification occurs over one month at the end of the growing season, which corresponds to the warmer months of the year (Jones et al., 1996). For the Palaeogene, they have been successfully used as palaeoclimatic proxies, combined with other fossils (mammals), at the reduced scale of a local formation (Grimes et al., 2003, 2005; Sheldon et al., 2016) but the signification of their δ^{18}O variation over long periods has never been investigated.

Charophytes never occur in marine habitats or in water bodies with permanently high salinity (Soulié-Marsche, 1991). Nevertheless, some species present a relative salinity tolerance and can be found in brackish water (Corillon, 1957; Renard and Riveline, 1973; Soulié-Marsche, 2008). For example, the genus *Chara* withstands salinity up to +1 to +3 ‰, and the genus *Nitella* up to +1 to +5 ‰. For the species *Chara aspera*, in the laboratory, the fertility seems to decrease at higher salinity (Corillion, 1957). Halophilous species can also be observed in modern environments, but it does not concern the specimens analyzed here from the Palaeogene of the Paris Basin.

Relative to our geochemical investigation, these ecological data should be used with caution. The fact that some of these taxa can be found in saline water pools does not mean that fructification and calcification were carried out in such conditions, because this type of pond has extremely large salinity variations throughout the year. Indeed, salinity limits the fructification and calcification of the oospores of brackish and saline water charophytes. Thus, the salinity of the water in which gyrogonites grow should be narrower than the range where the plants are able to stay alive (Soulié-Marsche, 2008). Thus, according to the facies and fossil associations determined in the sedimentary formations where charophytes were sampled in this study, we can argue that the main part of the gyrogonites were collected in freshwater deposits (< +0.5 ‰). But salinity fluctuations reaching the domain of brackish waters (+0.5 to +30 ‰) cannot be excluded in some time intervals, especially during the Late Eocene, which concentrates many evaporitic deposits, and which could disturb the relationship between δ^{18}O and temperature (Riveline, 1984).

From a geochemical point of view, the relevance of charophyte calcite oxygen isotopes as palaeoenvironmental indicators has been debated question. Jones et al. (1996), Becker et al. (2002) or Grimes et al. (2003) suggested that the δ^{18}O of recent and fossil gyrogonites is in equilibrium with the $\delta^{18}O$ of water. However, cases of significant disequilibrium were observed in lacustrine carbonates (Fronval et al., 1995) and especially on modern specimens of the species *Chara globularis* (Huon and Mojon, 1994). Additionally, Andrews et al. (2004) demonstrated the role of the water mixing as a parameter controlling the $\delta^{18}O$ of charophytes. In well-mixed waters, the isotope composition of charophytes is closer to equilibrium than in shallow lakes without mixing. Pentecost et al. (2006) emphasize the influence of the highly alkaline pH resulting from photosynthesis on the strong disequilibrium between $\delta^{18}O$ carbonate of charophytes and the $\delta^{18}O$ of the parent water ($\delta^{18}O_w$) of ponds and shallow lakes. Additionally, Becker et al. (2002) demonstrated from Oligocene - Miocene gyrogonites that there is no significant variation of the $\delta^{18}O$ in one sample, nor within different samples of the species *Nitellopsis meriani*. On the contrary, a difference of +0.8 ‰ is observed in different specimens of a given species that exhibit different sizes. Moreover, a large inter-specific variability, possibly due to metabolic or environmental effects, has been identified (Becker et al., 2002). In a modern lake in Poland, Apolinarska et al., (2016) also found an isotopic disequilibrium in charophyte calcifications caused by fast mineralization during intense photosynthesis activity. In the same way, Apolinarska and Hammarlund (2009) outlined the influence of the coupling of temperatures and photosynthetic activity during warm intervals on the isotope composition of Quaternary charophytes. Thus, the use of modern or fossil charophytes as palaeoclimatic recorders is subject to debated.

3. Geological setting and stratigraphy

3.1. Main geologic features of the Paris Basin

The Paris Basin is a historical reference area for sedimentary geology and the stratigraphy of the Cenozoic formations has been well studied since many decades from numerous approaches in all environments (Châteauneuf 1980; Mégnien and Mégnien 1980; Riveline, 1984; Aubry, 1986; Gély and Lorenz, 1991; Aubry et al., 2005).

The intracratonic Paris Basin recorded thin sedimentary deposits during the Cenozoic (Fig. 2). The sedimentary succession consists of an alternation of shallow-marine facies and continental facies (Mégnien and Mégnien, 1980; Gély and Lorenz, 1991) related to the subsidense intensity and the global sea level variations (Cavelier and Pomerol, 1979). A summary of facies variations in the Paris Basin can be found in Mégnien and Mégnien (1980) and Huyghe et al. (2015). Tectonic activity was restricted to the rise of local or more regional folds that governed the facies distribution such as the Bray, Meudon and Remarde anticlines (Cavelier and Pomerol, 1979; Lacombe and Obert, 2000), but the basin was not really affected by the main orogenies and can be considered as a stable climatic recorder, free from orographic effects (Huyghe et al., 2012b, 2015). Thus, in response to these local vertical movements, the Paris Basin was connected to different oceanic water masses during the Palaeogene, i.e. Atlantic or North Sea, and the extent of the successive transgressions was variable through time.

3.2. Palaeoenvironmental and stratigraphic settings of the sampling sites

We describe here after the stratigraphic, palaeoenvironmental and palaeoecological settings of the formations where the dasycladales and charophytes were sampled. The stratigraphic setting is mostly based on the syntheses of Mégnien and Mégnien (1980) and Gély and Lorenz (1991) for the names of the formations, the fossil associations and the facies of the formations; Riveline (1986), Riveline et al. (1996) and Girbau (2013) for the charophytes zones; Châteauneuf and Gruas-Cavagnetto (1978) for the dinoflagellate cyst stratigraphy and Aubry (1986) for the calcareous nannofossil zones. Figure 3 summarizes this information.

3.2.1. Dasycladales

Dasycladales are abundant in the near-shore Palaeogene deposits of the Paris Basin and exhibit an exceptional preservation in sandy deposits (Génot, 2009). These samples are regrouped in seven genera and 15 species coming from eight different stratigraphic intervals distributed in each stage from the Thanetian to the Rupelian (Fig. 3). The precise location of the outcrops, their detailed description and the representations of the analyzed species can be found in Génot (1987, 2009) and Génot and Granier (2011). Samples were separated from the rest of the sediment under a binocular magnifier.

The oldest dasycladales studied are attributed to the Thanetian and come from both the western and eastern part of the Paris Basin. They are assigned to the Sables de Bracheux Fm that belong to the terminal Palaeocene (zone NP9; Aubry 1986). These sands were deposited in near shore environments. In this formation, Wyns et al. (1981) reported 70 mollusk species (e.g. *Ostrea (Bellostrea) bellovacina*, *Phacoides scalaris*, *Haustator bellovacinus, Popenoeum primum, Athleta (Athleta) depressus*), many benthic foraminifers (27 species), ostracods (nine species) and green algae or dasycladacean (five species). These assemblages indicate open marine condition.

For the Ypresian, fossils come from the Cuisian and are assigned to the Sables d'Hérouval, sables de Pierrefonds and Sables de Cuise Fms (zone NP12). Open marine conditions are attested in the Hérouval Fm by the presence of ecologically specific fossils like

Haustator solanderi and *Nummulites planulatus* (Feugueur 1963; Le Calvez 1970) and by a rich assemblage of stenohaline mollusks (Feugueur 1963). At Cuise-la-Motte, the fossil fauna from the Sables de Cuise Fm is well known for its rich assemblage comprising 300 marine species, among which normal range to salinity fluctuations, such as turritellids and volutids (Feugueur 1963). However, the input of fresh water specified by brackish mollusks (e.g. *Eotympanotonus*, *Corbicula* and paralic muricids, such as *Nucellopsis;* Merle 2005) associated with wood remains, crocodile and turtle bones indicate changes in palaeoenvironmental conditions during the deposition of this formation. This fossil mix is evidence of significantly fluctuating salinities with an overall trend of decreasing salinity and this must be taken into account when interpreting $\delta^{18}O$ of dasycladales in terms of palaeotemperatures.

For the Middle Lutetian, fossils come from the Calcaire à Orbitolites Fm assigned to zone NP15. The fossil associations, containing many foraminifers like *Orbitolites*, echinids, corals, shark teeth and very diversified ostracod associations (Guernet et al. 2012) argue for full marine conditions. Our material comes from various localities in the western (Grignon and La Ferme de l'Orme) northern (Fercourt) and eastern (Damery) part of the basin. Previous palaeoclimatic reconstructions from Grignon mollusks support this normal palaeosalinity and warm regional subtropical conditions with Mean Annual Sea-Surface Temperatures (MASST) of ~ 20-22 °C and summer temperatures of ~ 28-30 °C (Andreasson and Schmitz 1996; Huyghe et al. 2012a).

Due to the scarcity of Late Lutetian outcrops in the central part of the Paris Basin (Faluns Foulangues) we sampled this time interval in the Cotentin (Calcaires de Fresville Fm, Hauteville and Gourbesville), which was well-connected with the Paris Basin during this period. These formations contain bioclastic calcareous sands with many benthic foraminifers like *Orbitolites* and *Alveolina*. They are attributed to the base of zone NP16.

The Sables d'Auvers Fm and the Sables de Mortefontaine Fm belong to the lower Bartonian (Auversian local stage). The Sables d'Auvers Fm deposited in a near shore environment belongs to zone NP 16 (Aubry, 1986) and contains many species with strictly marine preferences like benthic foraminifers (miliolids and nummulitids) and a highly diversified assemblage of approximately 600 mollusks species (Dolin et al., 1980). The Mortefontaine Fm begins with sands containing the species *Bithinella pulchra* and is then composed of fine white sands with euryhaline species able to tolerate transient brackish waters like *Pteria (Electroma) defrancei*, *Editharus copolygonus*, *Pugilina palissyi* or *Potamides* (*Potamidopsis) tricarinatus crispiacensis* (Lorenz and Pomerol, 1965).

For the Priabonian, fossils were sampled in the Marnes à *Pholadomya ludensis* Fm, which constitutes the first transgressive marine deposits of this stage in the Paris Basin (Gély and Lorenz, 1991). The Le Vouast (Oise) outcrop was located in the littoral domain of this formation. It consists of silty marls containing a mixed assemblage indicating fluctuating salinities represented by euryhaline species like *Potamides* (*Potamidopsis) tricarinatus vouastensis*, *Batillaria (Vicinocerithium) rustica* or *Hexacorbula aulacophora* and by other marine mollusks such as *Pteria (Electroma) boussaci*, *Gibbolucina (s. str.) incomposita, Saxolucina saxorum, Asaphinella (s. str.) vouastensis, Abra vouastensis, Lutetia ovalis, Conomitra vouastensis* and *C. anderidensis* (Pacaud and Ledon, 2007).

Fossils assigned to the Oligocene come from the Vauroux-Saint-Antoine Fm dated from the Late Rupelian (zone NP 23). It consists of sands with a faunal association containing shallow marine species like *Lentidium nitidum*, *L. donaciformis*, *Glvcymerita angusticostata*, *Glycymeris subterebratularis*, *Ostrea cyathula* and laguno-marine species like *Granulolabium plicatum*, *Potamides lamarcki*, *Hydrobia* and *Potamidopsis* (Gély and Lorenz, 1991, Plaziat et al., 2012).

3.2.2. Charophytes

We analyzed 28 samples of gyrogonites, representing eight genera and nine species. They come from 15 stratigraphic levels distributed throughout all stages from the Thanetian to the Rupelian. The location of the sampled outcrops, the listing of analyzed species, the stratigraphic ages with the correspondence between international stages and the historical local stages and formations of the Paris Basin can be found in Fig. 3. The precise location of the outcrops, their detailed description and the representations of the analyzed species can be found in Riveline (1984). The zonal attribution is relative to Riveline (1996) and Girbau (2013). Like for the dasycladales, gyrogonites were separated from the rest of the sediment under a binocular magnifier.

The oldest charophytes were sampled in the Calcaire de Rilly Fm at Montchenot in the eastern Paris Basin and assigned to the Thanetian. This formation was deposited in a non-stagnant freshwater environment and includes an abundant terrestrial assemblage including the species *Aplexa gigantea, Rillya rillyensis* and *Grandipatula rigaulti* (Barta et al., 1980). It is attributed to the *Sphaerochara edda* charophyte zone (Riveline, 1996; Girbau, 2013).

For the Sparnacian, fossils were sampled in the Marnes à Rognons, Calcaire d'Ailly, Cendrier and Mortemer Fms, which belong to pollen zone W1, and to the *Peckichara disermas* charophyte zone. The Calcaire d'Ailly Fm was deposited to the west of the basin in a lacustrine environment (Bignot, 1965) and contains many charophytes (*Nitellopsis* (*Tectochara) helicteres*) and mollusks species (*Aplexa* cf. *heberti, Viviparus desnoyerii* or *Eupera* cf. *subaevigata*). The Marnes à Rognons is contemporaneous with the Calcaire d'Ailly Fm (Aubry et al., 2005). It consists of white marls with calcareous nodules. The base of the formation corresponds to a brackish environment and evolves toward a lacustrine and then a continental environment at the top. This formation contains brackish species like

Melanopsis briarti, *Briartia velaini*, *Batillaria (Vicinocerithium) inopinata* (Bignot et al., 1980). The Cendrier Fm, consisting of dark-coloured clay was deposited in fluvio-lacustrine environment (Feugueur, 1963) and contains many freshwater mollusks (sphearids (*Cyclas*), unionids, lymneids, planorbids, crocodilian remains, fern marks (*Asplenium*, *Anostichum*), charophytes (*Nitellopsis* (*Tectochara) helicteres*) and mammals (*Coryphodon oweni*, *Hyracotherium* or *Pachyaena gigantea*) (Bignot et al., 1980). The Mortemer Fm is a fine limestone with oysters near its base, evolving toward a micritic limestone with high proportion of ostracods and some charophytes. It was deposited in laguno-lacustrine environment with temporary communications with the sea (Pomerol et al., 1977; Gély and Lorenz, 1991).

The Cuisian is represented by the Argiles à lignites d'Epernay Fm, corresponding to coastal laguno-lacustrine environments (mangrove type) containing the species *Corbicula (Loxoptychodon) cuneiformis* and *Eotympanotonos funatus* (Ducreux et al., 1984). They belong to pollen zone W6 and to the *Peckichara piveteaui* charophyte zone.

The Lutetian is represented by the Banc Vert Fm, attributed to the Late Lutetian (zone NP15). It consists of limestones containing brackish fossils (Blondeau, 1965; Gély and Lorenz, 1991). Our material comes from the locality Guitrancourt which containing a rich vertebrate fauna like turtles, crocodiles, mammals and many pollens and palm trees (de Lapparent et al. 1993).

For the Auversian, fossils come from the top of the Sables du Guépelle Fm and the Calcaire de Jaignes Fm. The latter is a part of a regressive unit, which ends with the establishment of a laguno-lacustrine environment containing the species *Dissostomia mumia*, hydrobids and planorbids (Perreau, 1980; Gély and Lorenz, 1991). It was attributed to pollen zone W10 and the *Raskyella pecki* charophyte zone.

For the Marinesian, charophyte gyrogonites were sampled in the Calcaire de Ducy and Calcaire de Saint-Ouen inférieurs Fms. The Calcaire de Ducy is the laguno-lacustrine border of the Marinesian transgression (Lorenz and Pomerol, 1965). Its relatively poor faunal assemblage contains *Lymnea arenularia*, *Hydrobia (Polycirsus) tuba* and *Discorbis bractifera* (Gély and Lorenz, 1991). It is attributed to pollen zone W11 and the *Raskyella pecki* charophyte zone. The Calcaire de Saint-Ouen inférieur Fm (pollen zone W11, the *Chara friteli* charophyte zone) was deposited in a lacustrine environment (Lorenz and Pomerol, 1965; Gély and Lorenz, 1991). The faunal assemblage is dominated by the species *Galba longiscata*, *Biomphalaria similis* and *Dissostoma mumia* (Cavelier et al., 1980a).

For the Ludian, the Calcaire de Ludes Fm, Calcaire de Château-Landon Fm and the Marnes bleues d'Argenteuil Fm provided the analyzed fossils. The Calcaire de Ludes Fm was deposited in the eastern part of the basin (pollen zone W12 and *Gyrogona tuberosa* charophyte zone) and constitutes the non-marine lateral equivalent of the Marnes à *Pholadomya ludensis* Fm (zone NP 18) (Gély and Lorenz, 1991). Furon and Soyer (1947) record around 20 marine species and among them *Pholadomya ludensis*. In the southern part of the basin, the Calcaire de Château-Landon Fm is a white micritic limestone deposited in a lacustrine environment. It contains many freshwater gastropods and charophytes (Cavelier et al., 1980a) and belongs to pollen zones W12-13 and to the *Gyrogona tuberculosa* charophyte zone. The Marnes Bleues d'Argenteuil Fm (central part of the basin) belongs to the charophyte zone *Lychthamnus vectensis* that corresponds to the late Priabonian. This formation was deposited in a lagoon with local occasional marine influences and where gypsum deposits could have occurred (Cavelier 1965). This formation contains some mammals (*Plagiolophus* sp., *Paleotherium medium*) and ostracods (Cytheridae) that confirm the non-marine deposition environment (Cavelier et al., 1980a).

Charophytes attributed to the Rupelian were sampled in the upper part of the marine Argiles Vertes de Romainville Fm and correspond to the Bande Blanche Fm deposited in a lacustrine environment (Cavelier, 1965). This formation was attributed to pollen zone W14 (Gély and Lorenz, 1991) and contains many lymneids and charophytes (Cavelier et al., 1980b). The last formation sampled was the Ormoy Fm at Itteville (Essonne). It contains freshwater mollusks (*Pomatias antiquum*, *Lymnea* and *Planorbarius*), crocodiles (*Diplocynodon*) and mammals (*Bachitherium* and *Ronsotherium*) (Ginsburg and Hugueney 1987).

5. Analytical method

Geochemical analyses of biogenic carbonates can be used for palaeoenvironmental reconstructions only if their primary mineralogy is well preserved. Diagenetic imprint was examined (after crushing the gyrogonites and dasycladales), first under a binocular magnifier to eliminate samples containing infilling matrix or recrystallization. Samples were then analyzed with X-Ray diffraction and SEM observations to confirm a pristine preservation. Samples were ultrasonically cleaned to remove any residual sediment. Charophyte gyrogonites and dasycladales articles were completely crushed to a powder and one measurement corresponds to a combination of five individual samples.

From each sample, 2 to 3 mg of carbonate powder was reacted during 15 minutes with 100 % anhydrous orthophosphoric acid in a coupled on-line carbonate preparation device at 50 °C. The resulting CO_2 was analyzed using a VG MM903 isotope ratio mass spectrometer at the ISTeP laboratory of Pierre et Marie Curie University (Paris, France). Oxygen isotope values ($\delta^{18}O$) are reported as per mil (‰) deviation in the isotope ratio ($^{18}O/^{16}O$) standardized to the Vienna Peedee belemnite (V-PDB) scale using an in-house standard (Marceau marble: mean $\delta^{18}O$ = –1.83 ‰ V-PDB) calibrated against the international calcite material NBS-19. Long-term analytical precision on replicate standard analyses was better than 0.1 ‰ for $\delta^{18}O$.

6. Results

Figure 4 presents the $\delta^{18}O$ variations in charophytes and dasycladales during the Palaeogene in the Paris Basin. All these values are reported in Appendix 1. Genera are individualized for each fossil group. The isotopic signal varies widely for each group, as well as for a given stratigraphic level than over the considered period but the general trend is similar for the two groups.

For the charophytes, the lowest values are recorded during the Late Palaeocene (–7.5 ‰) and then increase during the Ypresian, with $\delta^{18}O$ ranging between ~ –7 and –5 ‰. The Late Ypresian and Early Lutetian are not represented here but the Middle Lutetian exhibits relatively high values, ranging between –2.3 and –1 ‰. Values are lower at the beginning of the Bartonian (–3.9 ‰) before increasing during the Middle Bartonian (–2.7 ‰). Then, a long and nearly continuous decrease of the $\delta^{18}O$ occurs with values ranging from –1.3 to –2.8 ‰ during the Late Bartonian to –4.2 to –5.8 ‰ during the Late Priabonian. Then the $\delta^{18}O$ rises to its highest value just after the Eocene – Oligocene boundary with values comprised between –1.3 and +0.4 ‰ and remains high (+0.3 ‰) at the end of the Rupelian.

For the dasycladales, the $\delta^{18}O$ variation is relatively similar. The lowest values are recorded during the Late Palaeocene with a large isotopic range from –7.3 to –3.6 ‰. The $\delta^{18}O$ increases slightly during the Ypresian, but the isotopic range remains elevated, from –5.7 to –2.6 ‰. As for the charophytes, values keep increasing during the Middle and Late Lutetian and the isotopic range decreases with values comprised between –3.5 and –2.5 ‰

and –1.9 and –1.5 ‰ respectively. δ^{18}O values are low during the Bartonian (from –6.1 to –3.9 ‰) and then increase during the Priabonian (–2.2 ‰). No samples were available around the Eocene – Oligocene boundary, but values remain relatively high during the Rupelian and reach –2.7 ‰.

Maximum and minimum isotopic values inside each formation are thus variable over the studied interval and range between +2.1 ‰ and +0.5 ‰ for the charophytes and +3.6 ‰ and +1 ‰ for the dasycladales. Thus, the isotopic variability is large for a given group of algae, as well as through time and for a given formation.

7. Significance of the δ^{18}O signal

Many factors influence the δ^{18}O of calcareous biomineralizations. For marine organisms like dasycladales, they are mainly environmental factors such as the climate, water depth at which the algae live and factors influencing the δ^{18}O of the sea-water ($\delta^{18}O_w$) which mostly relate to the evaporation/precipitation ratio, i.e. salinity and glacial effect (Epstein et al., 1951). For limnic organisms like charophytes, environmental parameters are more intricate. Physical and chemical characteristics of waters will depend on the type of lake, i.e. permanent vs. temporary, open with an outlet vs. close, the proximity of the sea (lagoon close to the sea vs. continental lake and ponds) and the climate zone (evaporation vs. precipitation). Biological factors also have to be considered and include the vital effect (metabolically induced fractionation with the parent solution from which the carbonate was mineralized), the period of the year at which carbonate mineralization occurs (continuously for several years or only during a part of the year) and mineralogy (calcite or aragonite) (Tarutani et al., 1969; Wefer and Berger, 1991).

7.1. Intra-group variations

Here we first consider how to explain the isotopic variability within a given group of algae. As dasycladales and charophytes occur in different environments, the degree to which vital effects and environmental factors influence their $\delta^{18}O$ is likely to be different.

Isotopic disequilibrium of the carbonates compared to the parent solution has been debated, especially concerning charophytes (Huon and Mojon, 1994; Jones et al., 1996; Becker et al., 2002; Grimes et al., 2003; Pentecost et al., 2006). However, it is difficult to determine from fossil material if a vital effect has occurred or not. Nevertheless, for the charophytes, monospecific levels exhibit the same isotopic range (~ +1.4 ‰) as those of an assemblage of different species. Vital effect of one species compared to another is thus not obvious for the charophytes, even if the influence of biases due to the variability of the kinetic of carbonate precipitation cannot be ruled out.

This isotopic variability of the charophytes could also reflect environmental variations. Andrews et al. (2004) and Pentecost et al. (2006) have shown the role of water mixing and of pH variations as factors influencing $\delta^{18}O$ isotopic disequilibrium. Our samples come from formations that could have been deposited over long periods and thus, these environmental parameters could have changed during these intervals generating the observed isotopic variations.

The understanding of the geochemical signal of dasycladales has been less investigated than for charophytes and to our knowledge, only a few works deal with this question, with contradictory results (Wefer and Berger, 1991; Lee and Carpenter, 2001). There are no monospecific levels in our samples that could allow for an intra-species comparison like we did for the charophytes. Isotopic ranges are higher for these algae, with a maximum of +3.6 ‰ during the late Thanetian and +3.1 ‰ during the Lower Eocene. In these two stratigraphic levels, the species *Jodotella veslensis* and *Utetia encrinella* have significantly lower values than the two species *Neomeris craniphora* and *Belzungia borneti* (Fig. 3). Then, from the Lutetian to the Rupelian, the isotopic range decreases to reach similar to lower values than for the charophytes (+0.4 to +2.4 ‰). Here, other parameters than vital effect likely affect the $\delta^{18}O$ because during the Lutetian the genus *Neomeris* has lower values than *Acicularia* or *Belzungia* and the opposite is observed during the Bartonian. Thus, we cannot exclude a possible vital effect for some of the species sampled in the Palaeocene – Early Eocene interval, but it is difficult to assign a precise value to such a deviation for fossil species.

Also, environmental parameters have to be taken into account, because as for the charophytes, the deposition of each formation where the dasycladales were sampled lasted several thousands of years and influencing factors like salinity could have changed.

Another criterion that is important to consider is the duration of the mineralization of these carbonates and the representativeness of their $\delta^{18}O$ values. Both charophytes and dasycladales produce their carbonate over short periods (a few weeks) and they thus only record a time window of climatic conditions and temperature variations in a given year. These algae were sampled in formations that could accumulate thousands of years of sedimentation, with varying environmental conditions. Thus, maximum temperatures might have fluctuated from year to year due to varying meteorological conditions, without huge climatic reorganization, inducing the observed $\delta^{18}O$ variability. This short period of carbonate production might also have generated the record of seasonally fluctuating $\delta^{18}O_w$ values, also responsible for the intra-taxa isotopic variability. This point highlights the problem of the representativeness of a mixing several samples from a given formation. However, due to the scarcity and the small size of these algae in the fossil record, this approach constitutes the best way to obtain paleoenvironmental information. Moreover, we observe that during intervals when the $\delta^{18}O$ reaches the most negative values, i.e. the Early Eocene and the beginning of the Bartonian, which could be interpreted in first approach as warm intervals (Zachos et al., 2001; Huyghe et al., 2015), that the isotopic variability is the highest for dasycladales. Fructification and mineralization processes remain still poorly uninvestigated for these algae, but one can imagine that these warmer temperatures could induce germination earlier in the season than during colder periods like the Lutetian or the Oligocene, thus integrating a wider temperature range in their $\delta^{18}O$.

7.2. Inter-group and temporal variations

To compare the $\delta^{18}O$ of dasycladales and charophytes in the Paris Basin during the Palaeogene, we have reported on Fig. 5 the mean values of all samples of each formation. These groups are compared to the mean $\delta^{18}O$ of marine mollusks from the Paris Basin (Huyghe et al., 2015), composed of an assemblage of four families: Turritellidae, Cerithiidae and Volutidae (aragonitic gastropods) and Ostreidae (calcitic bivalves). These mollusks were sampled in formations where marine conditions are documented. We made this comparison between three different taxa that occur in different environments to distinguish a possible common signal, i.e. temperature variations from the imprint of a local environmental signal.

Among the possible factors that can explain the isotopic shift between these different fossil groups, the mineralogical effect is the most obvious one. Charophytes and dasycladales exhibit calcite and aragonite mineralogies respectively. Experiments on synthetic carbonates identified an offset of +0.6 ‰ between aragonite and calcite for $\delta^{18}O$ (Tarutani et al., 1969).

Thus, we have normalized all aragonite values in Fig. 4 by correcting charophytes and calcitic mollusks (i.e. oysters) $\delta^{18}O$ values by +0.6 ‰.

We observe that all three groups follow the same general trend for $\delta^{18}O$ over time, except a decrease of their $\delta^{18}O$ for charophytes during the Priabonian. Charophytes and dasycladales isotopic values are similar for a given formation after applying the mineralogical correction and are consistently higher than the corresponding values for mollusks. During the Palaeocene and the Early Eocene charophytes values are lower than the dasycladales values and this relationship is reversed during the Lutetian and Early Bartonian (Fig. 5).

The period of the year at which the carbonate is mineralized has an influence on the isotopic signature of fossils, in response to the seasonal temperature fluctuations. Thus, mean $\delta^{18}O$ values of a fossil that mineralizes its carbonate throughout the year like the mollusks analyzed here will be higher than for fossils that mineralizes only during summer (Goodwin et al., 2003; Huyghe et al., 2012a). The isotopic shift between the algae and the mollusks should reflect this different duration of mineralization.

Despite living in different environments, non-marine and shallow-marine algae have a similar isotopic signature. This similarity requires that a common factor influences the $\delta^{18}O$ of these fossils. Temperature and $\delta^{18}O_w$ could generate discrepancies between these two fossil groups living in different environments. As these algae were sampled in the same basin, we assume that climatic conditions were similar for contemporaneous fossils. Despite coming from different environments, the $\delta^{18}O$ for charophytes and dasycladales evolve in the same way and exhibit similar values, meaning that the influence of $\delta^{18}O_w$ is not dominant and that $\delta^{18}O$ changes can be attributed to temperature variations.

To test this assumption we plotted in Fig. 6 the $\delta^{18}O$ of mollusks against charophytes of the same age and mollusks vs. contemporaneous dasycladales. Mollusks are supposed to record temperature variations and occur in formations were salinity and hence $\delta^{18}O_w$

variations are low (Huyghe et al., 2015). This comparison concerns three different taxa that live in different environments: the non-marine (charophytes), the shallow-water marine up to 10 m depth (dasycladales) and the shallow-water marine up to 30-40 m depth (mollusks). A good correlation coefficient between mollusks and each group of algae will attest to similar temperature conditions for a given stratigraphic interval. We selected six formations where charophytes occur contemporaneously with mollusks and seven for the dasycladales (Appendix 2). This comparison shows that the correlation coefficients are good for the two groups ($R^2 = 0.89$ for the dasycladales and $R^2 = 0.95$ for the charophytes) with a statistic intercept of –1.75 ± 0.37 ‰ for the charophytes and –1.37 ± 0.35 ‰ for the dasycladales (Fig. 6) and with similar slope of +1.26 and +1.23 respectively. It shows that a common parameter is recorded very similarly by the three taxa, despite their occurrence in different environments. This means that temperature variations have the highest influence on the $\delta^{18}O$ of these fossils compared to local environmental forcings. However, the fact that the statistic intercept is not zero means that the algae and the mollusks did not record the same temperatures. As these three groups should have recorded the same climatic conditions for contemporaneous levels, we consider that this shift reflects the different duration of carbonate mineralization between the mollusks and the algae and hence the temperatures recorded, i.e. mean annual temperatures (MAT) for the mollusks and temperatures of the warmer months for the algae (TWM).

Thus, considering on the one hand the good correlations between the $\delta^{18}O$ values for mollusks and algae and on the other hand the very similar trends in $\delta^{18}O$ values for the two groups of algae living in different environments, it seems that a climatic signal is reliably recorded in the $\delta^{18}O$ compositions of these algae and that the influence of local environmental fluctuations resulted in the $\delta^{18}O_w$ is low. Moreover, we can argue that the algae $\delta^{18}O$ values observed through time (Fig. 5) correspond to first order temperature variations. The main difference between the three groups is observed during the Priabonian for the charophytes, which exhibit more negative values than the mollusks and the dasycladales. However, these samples come from formations where evaporitic conditions occurred with the deposition of gypsum, which could explain this isotopic shift (Cavelier et al., 1980a).

8. Shallow marine palaeotemperatures

8.1. Palaeotemperature reconstruction

Considering that temperature is the main factor influencing the $\delta^{18}O$ values of dasycladales, it is possible to reconstruct palaeotemperature values for these algae. Palaeotemperatures from charophytes isotopic compositions are more difficult to constrain because reliable $\delta^{18}O_w$ values are nearly impossible to estimate in non-marine environments without using other proxies like remains of homoeothermic mammals (Grimes et al., 2003). Dasycladales are mineralized in aragonite and to our knowledge there are no equations of transfer for these organisms. Thus, we have chosen to reconstruct palaeotemperatures from the equation of Kobashi and Grossman (2003) used for gastropod shells:

$$T\ (°C) = 20.6 - 4.34\ (\delta^{18}O_a - \delta^{18}O_w) \qquad (1)$$

where $\delta^{18}O_a$ represents the $\delta^{18}O$ of aragonite, i.e. dasycladales and $\delta^{18}O_w$ the $\delta^{18}O$ of the water where the algae lived.

The most important limitation when interpreting $\delta^{18}O$ values as palaeotemperatures is the dependency on $\delta^{18}O_w$, which is a function of both local and global factors. First, the local $\delta^{18}O_w$ depends on the evaporation/precipitation ratio, i.e. salinity, which was estimated from the fossil associations described above. The $\delta^{18}O_w$ is calculated from the equation of Pierre

(1999) established for the modern Mediterranean Sea, which presents climatic and environmental conditions similar to those of the Paris Basin during the Palaeogene (Pomerol 1973; Guernet et al. 2012). In the previous equation the $\delta^{18}O_w$ is a function of the salinity (S):

$$\delta^{18}O_w \text{ (‰ SMOW)} = 0.25 \text{ S (‰)} - 8.2 + \delta^{18}O_{GW} \quad (2)$$

where $\delta^{18}O_w$ is the local $\delta^{18}O$ of the water, S is the salinity of the local water and $\delta^{18}O_{GW}$ is the global $\delta^{18}O$ of water. Salinity variation over time in the basin from the faunal associations described in each sampled level is summarized in Fig. 3. The $\delta^{18}O_w$ is also a function of global parameter corresponding to the glacial effect, i.e. the quantity of ice present on Earth. The mean global $\delta^{18}O_w$ value is generally considered as –1.2 ‰ during ice-free periods, like the lower Eocene (Shackleton and Kennett 1975). However, the Palaeogene is a transition from an ice-free world to an icehouse period (Zachos et al. 2001), which implies using a different global $\delta^{18}O_w$ depending on the period. Major controversies have existed about the age of the first ice-sheets on Earth during the Palaeogene (Lear et al. 2000; Dawber et al. 2011; Villa et al., 2014), but a consensus seems to have been adopted for the Middle Eocene. Here, we have chosen to use the work of Lear et al. (2000). They derived the values of global $\delta^{18}O_w$ from the $\delta^{18}O$ and the Mg/Ca ratio of deep-sea benthic foraminifers from the Pacific Ocean. The chosen global $\delta^{18}O_w$ values are reported on Fig. 3 for the levels sampled.

Figure 7 shows the variation of reconstructed mean temperature for the dasycladales and the marine mollusks from Huyghe et al. (2015). As it is unclear if dasycladales mineralize their carbonate in equilibrium (Lee and Carpenter, 2001) or not (Wefer and Berger, 1991) with seawater, we have calculated two distinct extreme temperatures for each formation, one without taking into account a vital effect and one with a maximum fractionation of +1‰ as observed in modern specimens (Wefer and Berger, 1991).

Highest temperatures calculated from dasycladales $\delta^{18}O$ values were recorded during the terminal Palaeocene and Early Eocene. Temperatures calculated without considering a vital effect reach 33-35 °C, whereas a vital effect of +1 ‰ generates temperatures 5 °C cooler (28 - 30 °C). Temperature then decreases during the Lutetian (31 - 27 °C without vital effect and 27 - 23 °C with an isotopic fractionation) followed by a substantial warming during the first part of the Bartonian (35 °C to 40 °C without fractionation and 31 °C to 35 °C with). A cooling is recorded during the Priabonian (24 °C to 19 °C) followed by another warming during the Rupelian (28 °C to 24 °C).

As explained above, dasycladales record the temperatures of the warmer months (TWM) of the year, during a very short time window (a few weeks), whereas mean mollusks temperature values reflect mean annual temperatures (MAT). Dasycladale-based temperatures should be higher than mollusk-derived temperatures. However, we observe that for most of the sampled layers, temperatures calculated with an isotopic fractionation of +1 ‰ with respect to seawater are lower or nearly equal to temperatures calculated for the marine mollusks, that should represent MAT. This observation suggests that the dasycladales analyzed in this work probably mineralize their carbonate with an isotopic fractionation less than +1 ‰ and that temperatures calculated without isotopic fractionation are more realistic. Consequently, we will consider temperatures calculated without vital effect in the following.

8.2. ***Palaeoclimatic and isotopic implications for the dasycladales***

The dasycladales-based palaeotemperatures are consistent with the overall climatic trend of the Palaeogene, both in the oceanic domain using the $\delta^{18}O$ compositions of deep-sea foraminifera (Zachos et al., 2001) and in the littoral domain in the Paris Basin using $\delta^{18}O$ of mollusk (Andreasson and Schmitz, 1996; Huyghe et al., 2015). The dasycladales-based palaeotemperatures also fit well with the continental domain from flora analyses (Châteauneuf, 1980; Grimes et al., 2003; Mosbbruger et al., 2005).

The elevated temperatures of the Late Palaeocene and Early Eocene (35 to 33 °C) fit well with the Early Eocene Climatic Optimum (EECO) which was the warmest period of the Cenozoic (Zachos et al., 2001). These temperatures are ~ 5 °C higher than the MAT calculated from mollusks δ^{18}O compositions. This implies a reduced seasonal temperature gradient, which is coherent with subtropical climatic conditions for this time interval (Pomerol, 1973).

The dasycladales-based palaeotemperatures decrease to the Lutetian also fits well with the global relative Lutetian cooling following the EECO. Here, maximum annual temperatures reach 31 to 27 °C. These temperatures agree with previous data obtained from shallow marine mollusks for the Paris Basin (Andreasson and Schmitz, 1996, 2000; Huyghe et al., 2012a, 2015) and the US Gulf Coast (Andreasson and Schmitz, 2000) located at the same latitude as the Paris Basin during the Lutetian. If we consider the maximum vital effect of +1 ‰, temperatures decrease to 27 to 23 °C, which is closer to the mean annual temperatures calculated for the mollusks (Andreasson and Schmitz, 1996; Huyghe et al., 2012a, 2015). This confirms that the temperatures calculated from the dasycladales δ^{18}O values are more consistent when a vital effect is ignored, as proposed by Lee and Carpenter (2001).

Also, these results confirm that the Kobashi and Grossman (2003) equation used to calculate palaeotemperatures seems to be suitable for the dasycladales. Moreover, the good fit between these two groups shows that despite a large isotopic variability for a given formation (~ 3 ‰), a mean of several samples (i.e. at least 5) allows the reconstruction of reliable temperatures in agreement with those from mollusks. These derived temperatures are consistent with the elevated seasonal temperature gradient for the Lutetian in the Paris Basin (~ 10 to 14 °C; Andreasson and Schmitz, 1996; Huyghe et al., 2012a).

The transient warming of the Bartonian, corresponding to the Middle Eocene Climatic Optimum (MECO), is also recorded in the $\delta^{18}O$ values for dasycladales in the Horizon de Mortefontaine Fm and for charophytes at the top of the Guépelle Fm. During the MECO, dasycladales-derived temperatures reached ~ 40 °C, i.e. higher than the temperatures of the EECO, whereas mollusks-based MAT were ~ 32 °C. Thus, the difference between MAT and TWM (Temperatures of the Warmer Months) were nearly the same during the Lutetian and the MECO. This result has strong implications concerning the temperature trends in shallow marine environments during greenhouse gas increases. It means that MAT exhibit nearly the same increase than the TWM during this hyperthermal event.

During the global cooling phase of the Priabonian until the glaciation of the Eocene – Oligocene boundary, TWM decreased to 24 °C. The difference between MAT and TWM (3 °C) is less compared to the previous stages of the Palaeogene.

In the Paris Basin, the Rupelian corresponds to a warming phase after the Eocene – Oligocene glaciation, what is expressed both in the MAT and in the TWM which reaches 28 °C. This warming is not well-represented in the $\delta^{18}O$ or Mg/Ca records of deep-sea benthic foraminifera (Zachos et al., 2001; Cramer et al., 2011) even if $p\mathrm{CO}_2$ levels and MAT were high (Hendriks and Pagani, 2008). Nevertheless, this warming could reflect a local palaeogeographic reorganization in the Paris Basin with the possible opening of the Ligerian Channel during the Rupelian, bringing warmer water from the Aquitaine Basin located to the southwest of the Paris Basin (Huyghe et al., 2015).

10. Conclusion

The $\delta^{18}O$ signal in dasycladales articles and in charophyte gyrogonites from the shallow-marine and non-marine deposits of the Paris Basin during the Palaeogene was studied to determine the parameters influencing their isotopic compositions over long periods. The comparison of the isotopic composition of these algae that are subject to various environmental forcing, with the $\delta^{18}O$ of shallow-marine mollusks previously analyzed shows that temperature variation is the main factor controlling the $\delta^{18}O$ of all these fossils. Even if the isotopic variability can be large for a given formation, the mean of at least 5 samples per level appears to be a reliable proxy to reconstruct climatic condition.

The conversion of dasycladales $\delta^{18}O$ values to temperatures values showed that these algae probably mineralized their carbonate in equilibrium with sea-water by comparing their isotopic signatures with those of marine mollusks. As dasycladales precipitate their carbonate during short periods of the warmer months of the year, the calculated temperatures reflect summer temperatures. These temperatures indicate that they recorded the global climatic events of the Palaeogene. The difference between the mean annual temperatures deduced from the mollusk isotopic compositions and maximum summer temperatures was small during the Late Palaeocene and Early Eocene and then increased during the Lutetian. The difference remained nearly the same during the MECO compared to the Lutetian, showing that summer temperatures were equally affected than mean annual temperatures during this hyperthermal event. The temperature gradient then decreased from the MECO to the Eocene – Oligocene boundary, followed by an increase in the Rupelian.

This palaeoclimatic investigation provides promising data that will allow a better understanding of the climatic events of the Palaeogene in near-shore and non-marine domains. It demonstrates that alternate fossil material can be used for palaeoclimatic investigations to densify the existing data and to document important climate parameters, such as seasonal temperature gradient and maximum annual temperatures. This study also demonstrated that the $\delta^{18}O$ of charophytes is primarily influenced by temperature variations when considering a representative mean of one formation. However, the calculation of reliable absolute temperatures requires more integrated studies as it is difficult to estimate non-marine $\delta^{18}O_w$ values.

Acknowledgements

We would like to thank Brian Mitchell for improving the English. DH thanks Jeremy Guignard for fruitful discussion. We would like to thank Editor T. Corrège and two anonymous reviewers for improving the manuscript.

Bibliography

Anadón, P., Utrilla, R., Vazquez, A., 2002. Mineralogy and Sr–Mg geochemistry of charophyte carbonates: a new tool for paleolimnological research. Earth and Planetary Science Letters 197(3), 205-214.

Andreasson, F.P., Schmitz, B., 1996. Winter and summer temperatures of the early middle Eocene of France from Turritella $\delta^{18}O$ profiles. Geology 24, 1067-1070.

Andreasson, F.P., Schmitz, B., 2000. Temperature seasonality in the early middle Eocene North Atlantic region: Evidence from stable isotope profiles of marine gastropod shells. Geological Society of America Bulletin 112, 628-640.

Andrews, J.E., Coletta, P., Pentecost A., Riding, R., Dennis, S., Dennis, P.F., Spiro, B., 2004. Equilibrium and disequilibrium stable isotope for palaeoenvironmental studies. Palaeogeography, Palaeoclimatology, Palaeoecology 204, 101-114.

Apolinarska, K., Hammarlund, D., 2009. Multi-component stable isotope records from Late Weichselian and early Holocene lake sediments at Imiolki, Poland: palaeoclimatic and methodological implications. Journal of Quaternary Science 24(8), 948-959.

Apolinarska, K., Pelechaty , M., Pronin, E., 2016. Discrepancies between the stable isotope compositions of water, macrophyte carbonates and organics, and mollusc shells in the littoral zone of a charophyte-dominated lake (Lake Lednica, Poland). Hydrobiologia 768, 1-17.

Aubry, M.P., 1986. Paleogene calcareous nannoplankton biostratigraphy of northwestern Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 55, 267-334.

Aubry, M.P., Thiry, M., Dupuis, C., Berggren, W.A., 2005. The Sparnacian deposits of the Paris Basin: A lithostratigraphic classification. Stratigraphy 2, 65-100.

Barta, L., Laurain, M., Leplat, J., Pomerol, B., Wyns, R., 1980. Paléocène. In Synthèse géologique du Bassin de Paris, Vol. 1 (ed. C. Mégnien and F. Mégnien), BRGM, pp. 337-350.

Becker, D., Picot, L., Berger, J.P., 2002. Stable isotopes (δ^{13}C and δ^{18}O) of charophytes gyrogonites: example from the Brochene Fluch section (Late Oligocene-Early Miocene, Switzerland). Geobios 35, 89-97.

Berger, S., Kaever, M.J., 1992. Dasycladales. Georg Thieme ed. Stuttgart. 247 pp.

Biber, P.D., Irlandi, E.A., 2006. Temporal and spatial dynamics of macroalgal communities along an anthropogenic salinity gradient in Biscayne Bay (Florida, USA). Aquatic Botany 85(1), 65-77.

Bignot, G., 1965. Le gisement Eocène du cap d'Ailly (près de Dieppe, Seine-Maritime). Bulletin de la Société Géologique de France 7, 273-283.

Bignot, G., Cavelier, C., Labourguigne, J., Laurain, M., Leplat, J., Mégnien, C., Mégnien, J., Perreau, M., Pomerol, B., Rasplus, L., Russel, D.E., Tourenq, J., 1980. Eocène Inférieur. In Synthèse géologique du Bassin de Paris, Vol. 1 (ed. C. Mégnien and F. Mégnien), BRGM, pp. 351-365.

Blondeau, A. 1965. Le Lutétien des Bassins de Paris, de Belgique et du Hampshire. PhD thesis, Université Pierre et Marie Curie, Paris.

Bohaty, S.M., Zachos, J.C., 2003. Significant Southern Ocean warming event in the late middle Eocene. Geology 31, 1017–1020.

Buchardt, B., 1978. Oxygen isotope palaeotemperatures from the Tertiary period in the North Sea area. Nature 275, 121-123.

Cavelier, C., 1965. Le Sannoisien de Sannois (S et O) dans le cadre du bassin de Paris et sa signification stratigraphique. Bulletin de la Société Géologique de France 7, 228-238.

Cavelier, C., Pomerol, C., 1979. Chronologie et interprétation des évènements tectoniques cénozoïques dans le Bassin de Paris. Bulletin de la Société Géologique de France 7, 33-48.

Cavelier, C., Labourguigne, J., Mégnien, C., Mégnien, F., Pomerol, C., Wyns, R., 1980a. Eocène supérieur. In Synthèse géologique du Bassin de Paris, Vol. 1 (ed. C. Mégnien and F. Mégnien), BRGM, pp. 379-399.

Cavelier, C., Ménillet F., Riveline J., Rasplus L., 1980b. Oligocène et Miocène basal. In Synthèse géologique du Bassin de Paris, Vol. 1 (ed. C. Mégnien and F. Mégnien), BRGM, pp. 401-413.

Châteauneuf, J.J., 1980. Palynostratigraphie et paléoclimatologe de l'Eocène supérieur et de l'Oligocène du Bassin de Paris. Mémoire du BRGM 116, 1-360.

Châteauneuf, J.J., Gruas-Cavagnetto, C., 1978. Les zones de Wetzeliellacea (Dinophyceae) du Bassin de Paris. Bulletin du BRGM IV, 2, 59-93.

Corillon, R., 1957. Les Charophycées de France et de l'Europe occidentale. Bulletin de la Société Scientifique de Bretagne 32(1-2), 1-499.

Dawber, C.F., Tripati, A.K., Gale, A.S., MacNiocaill, C., Hesselbo, S.P., 2011. Glacioeustasy during the middle Eocene? Insights from the stratigraphy of the Hampshire Basin, UK. Palaeogeography, Palaeoclimatology, Palaeoecology 300, 84-100.

Dolin, L., Dolin, C., Le Renard, J., 1980. Inventaire systématique des Mollusques de l'Auversien à « faciès charrié » de Baron (Oise) et remarques paléontologiques. Bulletin d'Information des Géologues du Bassin parisien 17(2), 26-48.

Ducreux, J.L., Michoux, D., Wyns, R., 1984. Contrôle climatique de la sédimentation yprésienne (Eocène inférieur) en Brie et en Champagne (Est du Bassin de Paris, France), Conséquences stratigraphiques. Comptes Rendus de l'Académie des Sciences, série II 299, 1283-1286.

Elliott, G.F., 1977. Inferred isocrymal distribution of Jurassic dasycladacean Algae in Europe, north Africa and southwestern Asia. Journal of the Geological Society 133, 363-373.

Elliott, G.F., 1984. Climatic tolerance in some aragonitic green algae of the post-Palaeozoic. Palaeogeography, Palaeoclimatology, Palaeoecology 48(2-4), 163-169.

Epstein, S., Buchsbaum, R., Lowenstam, H., Urey, H.C., 1951. Carbonate-water isotopic temperature scale. Bulletin of the Geological Society of America 62, 417-426.

Feugueur, L., 1963. L'Yprésien du Bassin de Paris. Essai de monographie stratigraphique. Mémoire du Service de la Carte Géologique de France, Paris.

Fronval, T., Jensen, N.B., Buchardt, B., 1995. Oxygen isotope disequilibrium precipitation of calcite in Lake Arresø, Denmark. Geology 23, 463-466.

Furon, R., Soyer R., 1947. Catalogue des fossiles tertiaires du bassin de Paris. Lechevalier.

Gély, J.-P., Lorenz, C., 1991. Analyse séquentielle de l'Eocène et de l'Oligocène du Bassin parisien (France). Revue de l'institut Français du Pétrole 46, 713-747.

Génot, P., 1987. Les Chlorophycées calcaires du Paléogène d'Europe nord-occidentale (Bassin de Paris, Bretagne, Cotentin, Bassin de Mons). Thèse, Université de Nantes, 500p.

Génot, P., 1991. Cenozoic and recent dasycladales. In *Calcareous algae and stromatolites*, pp. 131-145, Springer Berlin Heidelberg.

Génot, P., 2009. Cenozoic Dasycladales. A photo-atlas of Lutetian species from French Cenozoic basins. Carnets de Géologie, Special Publication 1, 1-180.

Génot P., Granier B., 2011. Cenozoic Dasycladales. A photo-atlas of Thanetian, Ypresian and Bartonian species from the Paris basin. Notebooks on Geology, Special Paper 1, 1-44.

Ginsburg, L., Hugueney M., 1987. Les Mammifères terrestres des sables stampiens du Bassin de Paris. Annales de paléontologie 73(2), 83-134.

Girbau, J.S., 2013. Els Carofits del limit Eocè-Ologocé de la Conca de l'Ebre. Tesi doctoral Barcelona, 111p.

Goodwin, D.H., Schöne, B.R., Dettman, D.L., 2003. Resolution and fidelity of oxygen isotopes as paleotemperature proxies in bivalves mollusk shells: Models and Observations. Palaios 18, 110-125.

Granier, B., 2012. The contribution of calcareous green algae to the production of limestones: a review. Geodiversitas 34(1), 35-60.

Grimes, S.T., Mattey, D.P., Hooker, J.J., Collinson, M.E., 2003. Paleogene paleoclimate reconstruction using oxygen isotopes from land and freshwater organisms: the use of multiple paleoproxies. Geochimica et Cosmochimica Acta 67, 4033-4047.

Grimes S.T., Hooker J.J., Collinson M.E., Mattey D.P., 2005. Summer temperatures of late Eocene to early Oligocene freshwaters. Geology 33, 189-192.

Guernet, C., Huyghe, D., Lartaud, F., Merle, D., Emmanuel, L., Gély, J.-P., Michel, F., Pilet, O., 2012. La faune d'Ostracodes de la falunière de Grignon (Lutétien du bassin de Paris): implications stratigraphiques. Geodiversitas 34(4), 909-959.

Halfar, J., Steneck, R.S., Joachimski, M., Kronz, A., Wanamaker, A.D., 2008. Coralline red algae as high-resolution climate recorders. Geology 36(6), 463-466.

Hallock, P., Premoli Silva, I., Boersma, A., 1991. Similarities between planktonic and larger foraminiferal evolutionary trends through Paleogene paleoceanographic changes. Palaeogeography, Palaeoclimatology, Palaeoecology 83, 49-64.

Hendriks, J., Pagani, M., 2008. Coccolithophore cell size and the Paleogene decline in atmospheric CO2. Earth and Planetary Science Letters 269, 576–584.

Hottinger, L., Schaub, H., 1960. Zur Stufeneinteilung des Paleocaens und des Eocaens: Einfuhrung der Stufen Ilerdien und Biarritzien. Eclogae Geologicae Helvetiae 53, 453-480.

Huon, S., Mojon, P.-O., 1994. Déséquilibre isotopique entre eau et parties calcifées de Charophytes actuels (Chara globularis): résultats préliminaires. Comptes Rendus de l'Académie des Sciences, Série II 318, 205–210.

Huyghe, D., Merle, D., Lartaud, F., Cheype, E., Emmanuel, L., 2012a. Middle Lutetian climate in the Paris basin: implications for a marine hotspot of paleobiodiversity. Facies 58, 587-604.

Huyghe, D., Mouthereau, F., Emmanuel, L., 2012b. Oxygen isotopes of marine mollusc shells record Eocene elevation change in the Pyrenees. Earth and Planetary Science Letters 345-348, 131-141.

Huyghe, D., Lartaud, F. Emmanuel, L., Merle, D., Renard, M., 2015. Paleogene climate evolution during the Paleogene in the Paris Basin from marine molluscs oxygen stable isotope ($\delta^{18}O$) compositions. Journal of the Geological Society 172, 576-587.

Ivany, L.C., Lohmann K.C., Hasiuk, F., Blacke, D.B., Glass, A., Aronson, R.B., Moody, R.M., 2008. Eocene climate record of a high southern latitude continental shelf: Seymour Island, Antarctica. Geological Society of America Bulletin 120, 659-678.

Jaffrezo, M., Renard, M., 1979. Eléments en traces de calcaires à Dasycladales et Charophytes. Bull Centr Rech Elf-Aquitaine Expl-Product Mém 3, 639-649.

Jones, T.P., Fortier, S.M., Pentecost, A., Collinson, M.A., 1996. Stable carbon and oxygen isotope compositions of Recent charophyte oosporangia and water from Malham Tarn U.K.: palaeontological implications. Biogeochemistry 34, 99–112.

Kobashi, T., Grossman, E., 2003. The oxygen isotopic record of seasonality in Conus shells and its application to the understanding late middle Eocene (38 Ma) climate. Paleontological Research 7, 343-355.

Lacombe, O., Obert, D., 2000. Héritage structural et déformation de couverture : plissement et fracturation tertiaires dans l'Ouest du bassin de Paris. Compte Rendu de l'Académie des Sciences 330, 793-798.

Lapparent de Broin, F. (de), Merle, D., Fontana, M., Ginsburg, G., Hervat, P., Le Calvez, Y., Riveline, J., 1993. Une faune continentale à Vertébrés dans le Lutétien supérieur de Guitrancourt (Yvelines) et son environnement. Bulletin d'Informations des géologues du bassin de Paris 30(4), 3-16.

Lartaud, F., Emmanuel, L., de Rafelis, M., Ropert, M., Labourdette, N., Richarson, C.A., Renard, M. 2010. A latitudinal gradient of seasonal temperature variation recorded in oyster shells from the coastal waters of France and the Netherlands. Facies 56, 13-25.

Lear, C.H., Elderfield, H., Wilson, P.A., 2000. Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca in benthic foraminiferal calcite. Science 287, 269-272.

Le Calvez, Y., 1970. Contribution à l'étude des Foraminifères paléogènes du Bassin de Paris. Cahiers de Paléontologie, 326p.

Lee, D., Carpenter, S.J., 2001. Isotopic disequilibrium in marine calcareous algae. Chemical Geology 172, 307-329.

Leitch, A.R., 1991. Calcification of the charophyte oosporangium. In: R. Ridding (Ed.) Calcareous Algae and Stromatolites. Springer Verlag, Berlin, pp. 204-216.

Lorenz, J., Pomerol, C., 1965. Caractères sédimentologiques et micropaléontologiques des formations de Ducy, Mortefontaine, Saint-Ouen et des Marnes à Pholadomya ludensis dans le Bartonien du Bassin de Paris. Bulletin de la Société Géologique de France 7, 292-295.

Mégnien, C., Mégnien, F., 1980. Stratigraphie et Paléogéographie. In: Mégnien, C. (ed) Synthèse Géologique du bassin de Paris, Volume 1. Mémoire du BRGM, 101, 1-466.

Merle, D., 2005. Nucellopsis (Gastropoda, Muricidae), a new genus from the paralic domain of the European Palaeogene. Comptes Rendus de Paléoévolution 4, 177–189.

Merle, D. 2008. Le Lutétien du bassin de Paris: un exemple de point-chaud de la paléobiodiversité. In: Merle, D. (ed) Stratotype Lutétien. MNHN, Paris, Biotope, Mèze, BRGM, Orléans, 174-181.

Miller, K.G., Fairbanks, R.A., Mountain, G.S, 1987. Tertiary oxygen isotope synthesis, sea-level history and continental margin erosion. Paleoceanography 2, 1-19.

Mosbrugger, V., Utescher, T., Dilcher, D.L., 2005. Cenozoic continental climatic evolution of Central Europe. Proceeding of the National Academic Society 108, 14964–14969.

Pacaud, J.-M., Ledon, D., 2007. Sur les espèces de mollusques du Ludien (Priabonien, Eocène supérieur) du bassin de Paris introduites par Périer en 1941. Cossmanniana 11, 7-25.

Pelechaty, M., Pukacz, A., Apolinarska, K., Pelechata, A., Siepak, M., 2013. The significance of Chara vegetation in the precipitation of lacustrine calcium carbonate. Sedimentology 60, 1017-1035.

Pentecost, A., Andrews, J.E., Dennis, P.F., Marca-Bell, A., Dennis, S., 2006. Charophyte growth in small temperate water bodies: Extreme isotopic disequilibrium and implications for the palaeoecology of shallow marl lakes. Palaeogeography, Palaeoclimatology, Palaeoecology 240, 389-404.

Perreau, M., 1980. Malacofaune et paléoenvironnements dans les sables du Guépelle, les sables à Batillaria bouei, le calcaire de Jaignes, la formation d'Ermenonville et les sables de Beauchamp à Baron (Oise). Bulletin d’Information des Géologues du Bassin de Paris 17(2), 53-56.

Pierre, C., 1999. The oxygen and carbon isotope distribution in the Mediterranean water masses. Marine Geology 153, 41-55.

Plaziat, J.-C., Lozouet, P., Briot, D., 2012. Les dépôts du Stampien et leur interprétation du point de vue des paléoenvironnements. In: Lozouet (ed.) Stratotype Stampien. Biotope, MNHN, pp. 75-124.

Pomerol, C., 1973. Ere Cénozoïque. Doin, Paris.

Pomerol, B., Renard, M., Riveline, J., 1977. Données nouvelles sur le Thanétien supérieur du Nord du Bassin de Paris. La limite Paleocène-Eocène dans les bassins nordiques et sa corrélation avec les bassins mésogéens. Bulletin de la Société Géologique de France 7, 155-164.

Renard, M., 1986. Pelagic carbonate chemiostratigraphy (Sr, Mg, ^{18}O, ^{13}C). Marine Micropaleontology 10, 117-164.

Renard, M., Riveline J., 1973. Evolution géochimique et floristique (Characées) dans le calcaire de Saint-Ouen (Bartonien moyen = Marinésien) du Mont-Pagnotte (Oise). Comptes Rendus de l'Académie des Sciences 277, 557-560.

Riveline, J., 1984. Les gisements à Charophytes du Cénozoïque (Danien à Burdigalien): lithostratigraphie, biostratigraphie, chronostratigraphie. Bulletin d'Information des Géologues du Bassin de Paris, volume hors série 4, 523 p.

Riveline, J., 1986. Les charophytes du Paléogène et du Miocène inférieur d'Europe occidentale. Editions du CNRS, cahiers de Paléontologie, 227 p, 38 planches.

Riveline, J., Berger, JP., Feist, M., Martin-Closas, C., Schudack, M., Souie-Märsche, I., 1996. European Mesozoic-Cenozoic charophyte biozonation. Bulletin de la Société Géologique de France 167, 437-468.

Sanders, M.T., Merle, D., Villier, L., 2015. The molluscs of the "Falunière" of Grignon (Middle Lutetian, Yvelines, France): quantification of lithification bias and its impact on the biodiversity assessment of the Middle Eocene of Western Europe. Geodiversitas 37, 345-365.

Shackleton, N.J., Kennett, J.P., 1975. Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analyses in DSDP sites 277, 279 and 281. Initial Report of the Deep Sea Drilling Project 29, 743-755.

Shackleton, N.J., Hall, M.A., Pate, D., Meynadier, L., Valet, J.-P., 1993. High resolution stable isotope stratigraphy from bulk sediment. Paleoceanography 8, 141-148.

Sheldon, N.D., Grimes S.T., Hooker, J.J., Collinson, M.E., Bugler, M.J., Hren, M.T., Price, G.D., Sutton, P.A., 2016. Coupling of marine and continental oxygen isotope records during the Eocene-Oligocene transition. Geological Society of America Bulletin 128, 502-510.

Soulié-Marsche, I., 1991. Charophytes as lacustrine biomarkers during the quaternary in North Africa. Journal of African Earth Sciences 12, 341-351

Soulié-Marsche, I., 2008. Charophytes, indicators for low salinity phases in North African sebkhet. Journal of African Earth Sciences 51, 69-76.

Tarutani, T., Clayton, R.N., Mayeda, T.K., 1969. The effect of polymorphism and magnesium substitution on oxygen isotope fractionation between calcium carbonate and water. Geochimica et Cosmochimica Acta 33, 987-996.

Tivollier, J., Létolle, R., 1968. Résultats et interprétation d'analyses isotopiques de faunes malacologiques du Tertiaire parisien. In: BRGM (ed). Colloque sur l'Eocène. Mémoire du BRGM 58, 346-357.

Villa, G., Fioroni, C., Persico, D., Roberts, A.P., Florindo, F., 2014. Middle Eocene to Late Oligocene Antarctic glaciation/deglaciation and Southern Ocean productivity. Paleoceanography 29, 223-237.

Walliser, E.O., Lohmann, G., Niezgodzki, I., Tütken, T., Schöne, B.R., 2016. Response of Central European SST to atmospheric $p\mathrm{CO}_2$ forcing during the Oligocene – A combined proxy data and numerical climate model approach. Palaeogeography, Palaeoclimatology, Palaeoecology 459, 552-569.

Wefer, G., Berger, W.H., 1991. Isotope paleontology: growth and composition of extant calcareous species. Marine Geology 100, 207-248.

Wood, R.D., Imahori, K., 1965. A revision of the Characeae. I. Cramer, Weinheim, pp. 904.

Wyns, R., Perreau, M., Le Calvez, Y., Damotte, R., Génot, P., 1981. Le Thanétien supérieur de Bachivillers (Oise): paléoécologie et environnement paléogéographique. Bulletin de l'Association des Géologues du Bassin de Paris 18, 47-53.

Zachos, J.C., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, Rythm, and Aberrations in Global Climate 65 Ma to Present. Science 292, 686-693.

Zachos, J.C., Dickens, G.R., Zeebe, R.E., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451, 279-283.

Figure Captions:

Figure 1: Illustration of some fossils analyzed in this study. A: dasycladales. 1: Schematic reconstruction of the general shape of the thallus of the genius Neomeris, 2: Neomeris craniphora (Thanetian, Abbecourt); 3: Neomeris limbata (Lutetian, la Ferme de l'Orme), 4: *Dactylopora cylindracea* (Bartonian, Le Fayel). B: charophytes. 5: schematic illustration of the charophytes algae; 6: *Gyrogona medicaginula*; 7: *Psilochara repanda*; 8: *Peckichara disermas*; 9: *Sphaerochara edda*.

Figure 2: Geologic map of the Paris Basin and location of the sampled areas.

Figure 3: Stratigraphic setting of the formations where dasycladales and charophyte gyrogonites were sampled in the Paris Basin. We reported salinity estimations of the marine formations where dasycladales were sampled and corresponding global $\delta^{18}O_w$ values.

Figure 4: $\delta^{18}O$ variations in the charophytes and dasycladales during the Palaeogene in the Paris Basin.

Figure 5: Variation of the mean $\delta^{18}O$ values of each formation for the charophyte gyrogonites, dasycladales and marine mollusks (from Huyghe et al., 2015) in the Paris Basin during the Palaeogene. Because of a mineralogical effect of +0.6 ‰ between calcite and aragonite (Tarutani et al., 1969), all fossils that exhibit a calcitic primary mineralogy (i.e. charophytes and oysters) were corrected by +0.6 ‰ for a reliable comparison. See text for explanations.

Figure 6: Comparison of the δ^{18}O values of dasycladales and charophytes plotted against mollusk δ^{18}O values. To make reliable comparisons, we corrected for the mineralogical effect of +0.6 ‰ between calcite and aragonite (Tarutani et al., 1969). All calcitic mollusk (i.e. oysters) values plotted vs. dasycladales were corrected by +0.6 ‰ and all aragonitic mollusks (i.e. gastropods) values plotted vs. charophytes were corrected by –0.6 ‰. Isotopic values and stratigraphic levels selected for this comparison are reported in Appendix 2.

Figure 7: Variation of the sea-surface temperatures of the Paris Basin derived from mollusks (Huyghe et al., 2015) and from dasycladales δ^{18}O values. Two cases are considered for the dasycladales: without vital effect, i.e. without fractionation between aragonite and sea-water (black squares) and with a vital effect of +1 ‰ between aragonite and sea-water (grey squares) according to Wefer and Berger (1991). The "Neomeris line" represents the lowest temperature at which specimens of the genius Neomeris can occur (Elliott, 1977). Horizontal bars represent the 95% interval of confidence for each mean temperature.

Appendix 1: δ^{18}O values and stratigraphic context of the dasycladales and charophytes species analyzed in this study.

Appendix 2: Dasycladales and charophytes species used to compare δ^{18}O values with contemporaneous mollusks values.

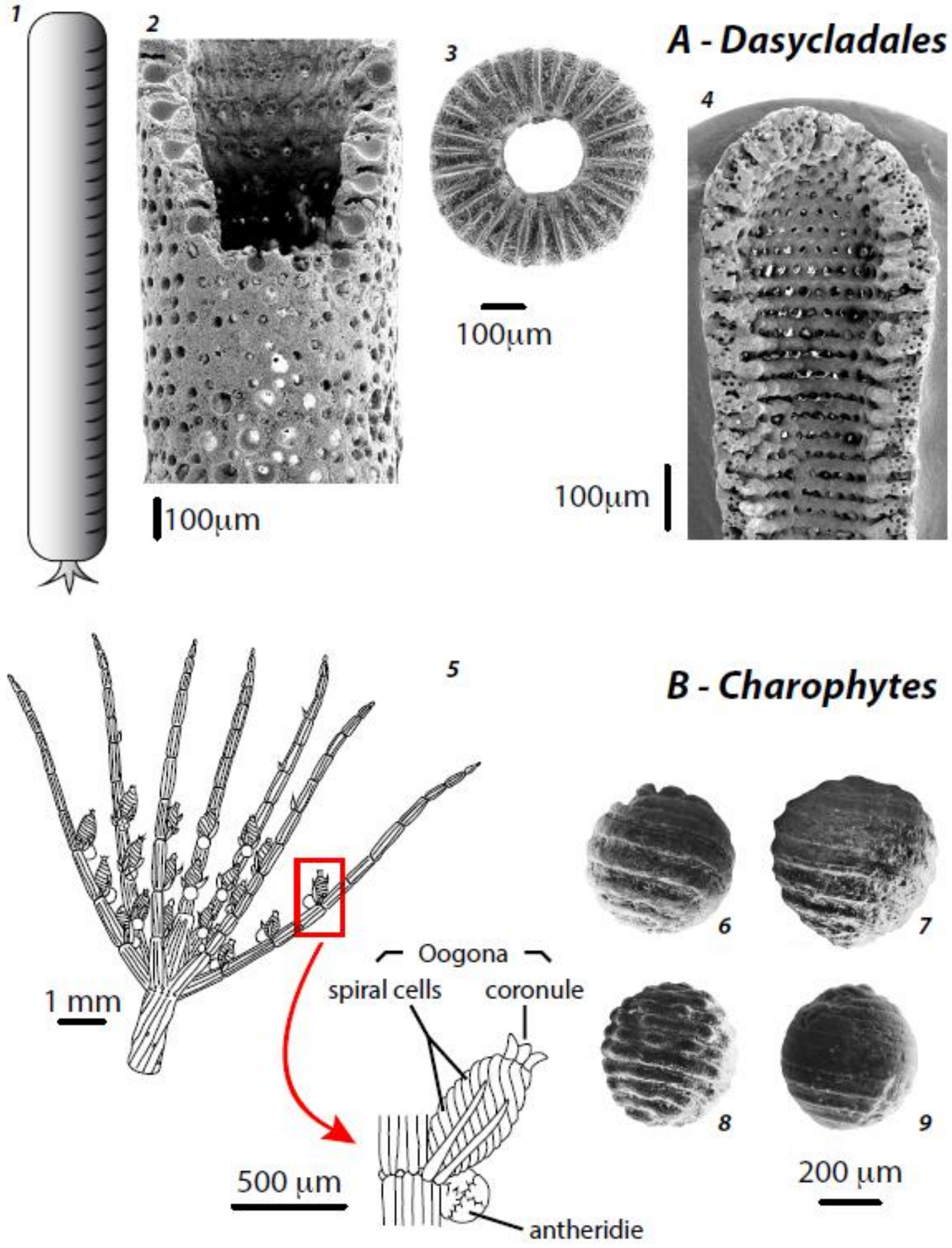
A - Dasycladales
1
2
3
4
100µm
100µm
100µm
B - Charophytes
5
1 mm
Oogona
spiral cells
coronule
500 µm
antheridie
6
7
8
9
200 µm

Fig. 1

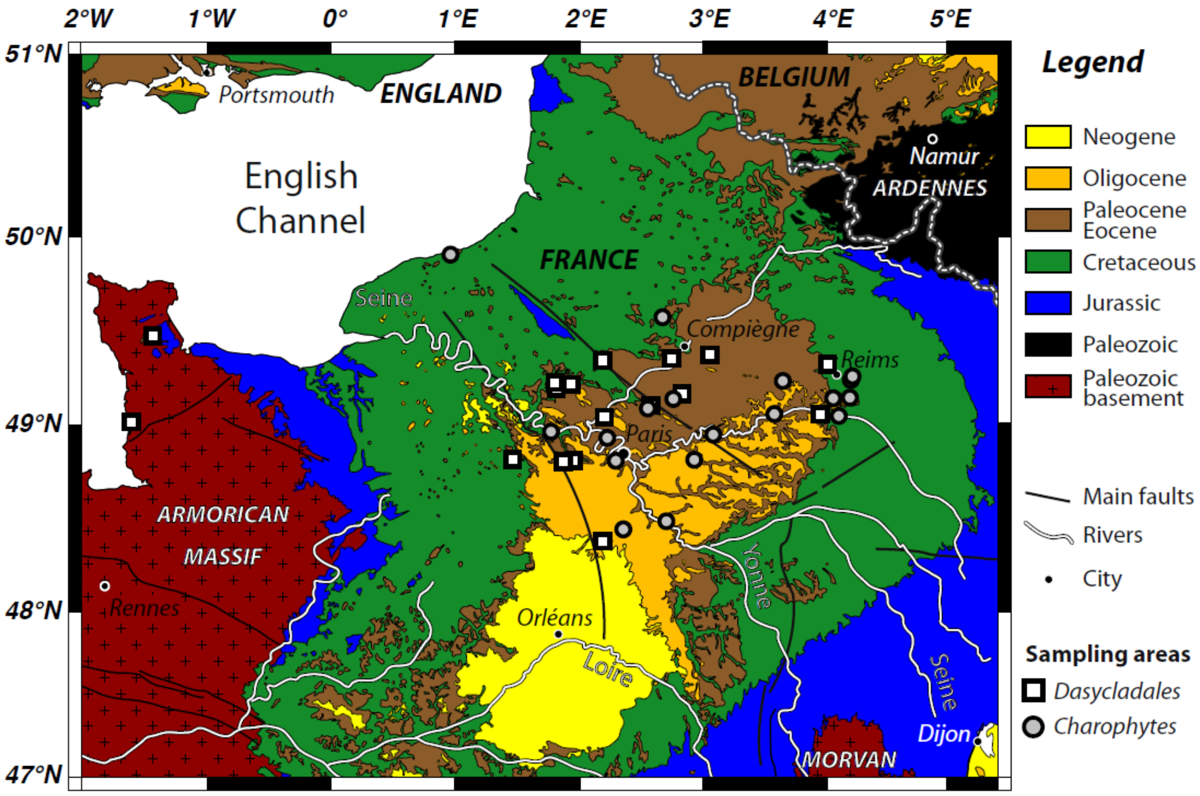
2°W
1°W
0°
1°E
2°E
3°E
4°E
5°E
51°N
50°N
49°N
48°N
47°N
Portsmouth
ENGLAND
English Channel
BELGIUM
Namur
ARDENNES
FRANCE
Seine
Compiegne
Reims
Paris
ARMORICAN MASSIF
Rennes
Orléans
Loire
Yonne
Seine
Dijon
MORVAN
Legend
Neogene
Oligocene
Paleocene Eocene
Cretaceous
Jurassic
Paleozoic
Paleozoic basement
Main faults
Rivers
City
Sampling areas
Dasycladales
Charophytes

Fig. 2

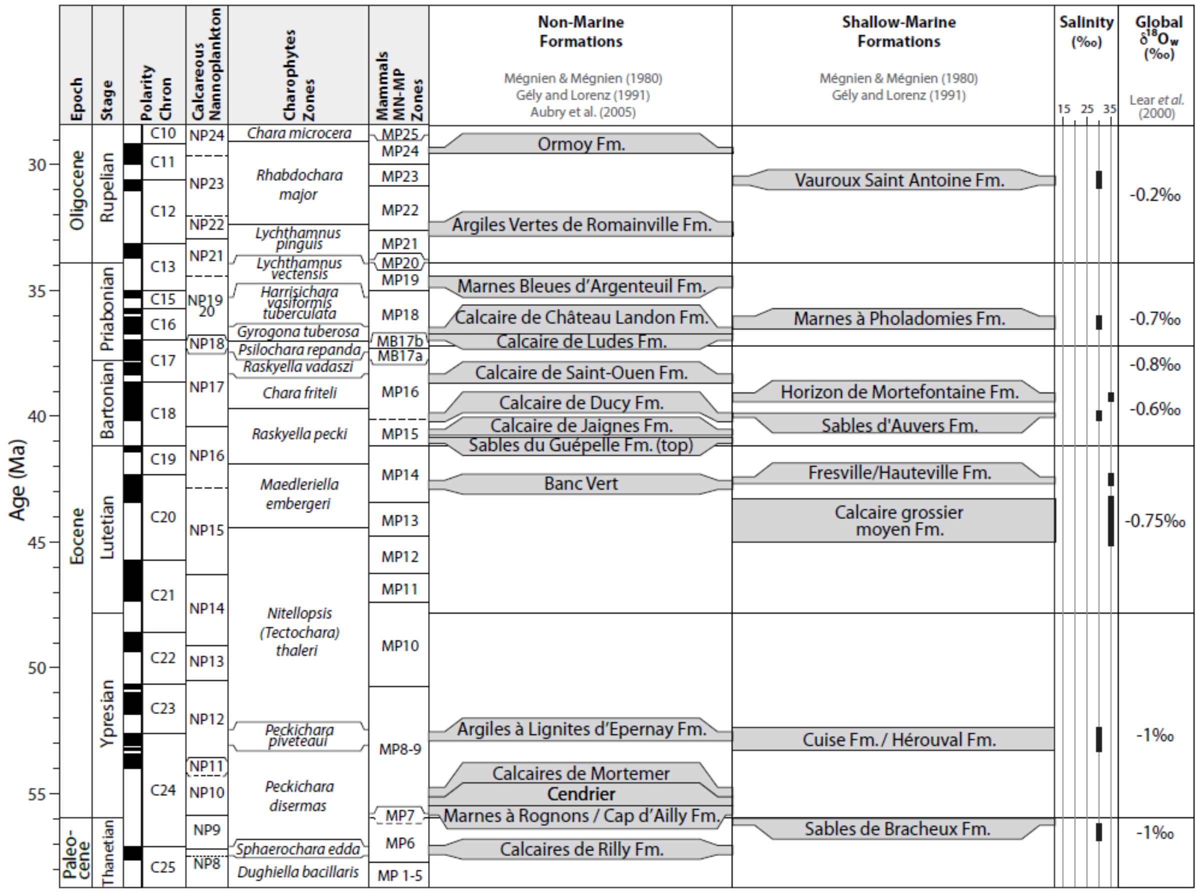
Epoch
Stage
Polarity Chron
Calcareous Nannoplankton
Charophytes Zones
Mammals MN-MP Zones
Non-Marine Formations
Mégnien & Mégnien (1980)
Gély and Lorenz (1991)
Aubry et al. (2005)
Shallow-Marine Formations
Mégnien & Mégnien (1980)
Gély and Lorenz (1991)
Salinity (‰)
15 25 35
Global δ18Ow (‰)
Lear et al. (2000)
Age (Ma)
30
35
40
45
50
55
Oligocene
Eocene
Paleo-cene
Rupelian
Priabonian
Bartonian
Lutetian
Ypresian
Thanetian
C10
C11
C12
C13
C15
C16
C17
C18
C19
C20
C21
C22
C23
C24
C25
NP24
NP23
NP22
NP21
NP19 20
NP18
NP17
NP16
NP15
NP14
NP13
NP12
NP11
NP10
NP9
NP8
Chara microcera
Rhabdochara major
Lychthamnus pinguis
Lychthamnus vectensis
Harrisichara vasiformis tuberculata
Gyrogona tuberosa
Psilochara repanda
Raskyella vadaszi
Chara friteli
Raskyella pecki
Maedleriella embergeri
Nitellopsis (Tectochara) thaleri
Peckichara piveteaui
Peckichara disermas
Sphaerochara edda
Dughiella bacillaris
MP25
MP24
MP23
MP22
MP21
MP20
MP19
MP18
MB17b
MB17a
MP16
MP15
MP14
MP13
MP12
MP11
MP10
MP8-9
MP7
MP6
MP 1-5
Ormoy Fm.
Argiles Vertes de Romainville Fm.
Marnes Bleues d'Argenteuil Fm.
Calcaire de Château Landon Fm.
Calcaire de Ludes Fm.
Calcaire de Saint-Ouen Fm.
Calcaire de Ducy Fm.
Calcaire de Jaignes Fm.
Sables du Guépelle Fm. (top)
Banc Vert
Argiles à Lignites d'Epernay Fm.
Calcaires de Mortemer
Cendrier
Marnes à Rognons / Cap d'Ailly Fm.
Calcaires de Rilly Fm.
Vauroux Saint Antoine Fm.
Marnes à Pholadomies Fm.
Horizon de Mortefontaine Fm.
Sables d'Auvers Fm.
Fresville/Hauteville Fm.
Calcaire grossier moyen Fm.
Cuise Fm. / Hérouval Fm.
Sables de Bracheux Fm.
-0.2‰
-0.7‰
-0.8‰
-0.6‰
-0.75‰
-1‰
-1‰

Fig. 3

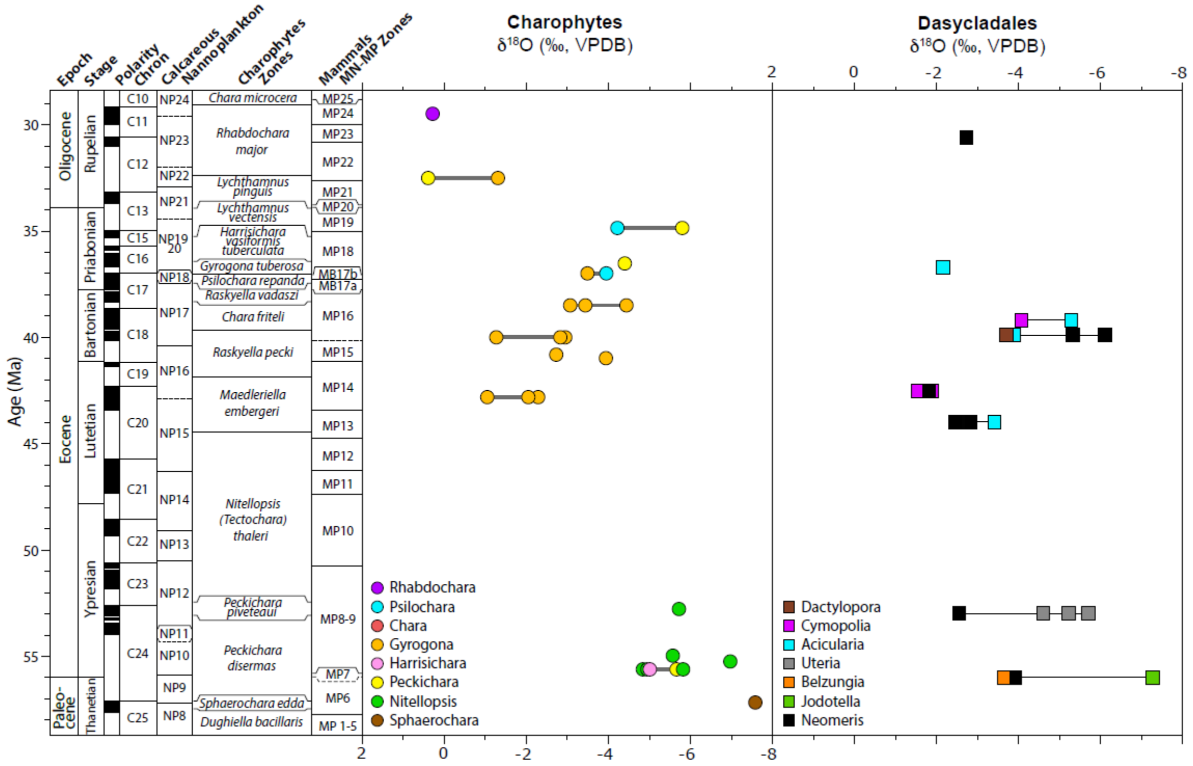
Epoch
Stage
Polarity Chron
Calcareous Nannoplankton
Charophytes Zones
Mammals MN-MP Zones
Charophytes
δ18O (‰, VPDB)
Dasycladales
δ18O (‰, VPDB)
Age (Ma)
Oligocene
Eocene
Paleo-cene
Rupelian
Priabonian
Bartonian
Lutetian
Ypresian
Thanetian
Chara microcera
Rhabdochara major
Lychthamnus pinguis
Lychthamnus vectensis
Harrisichara vasiformis tuberculata
Gyrogona tuberosa
Psilochara repanda
Raskyella vadaszi
Chara friteli
Raskyella pecki
Maedleriella embergeri
Nitellopsis (Tectochara) thaleri
Peckichara piveteaui
Peckichara disermas
Sphaerochara edda
Dughiella bacillaris
Rhabdochara
Psilochara
Chara
Gyrogona
Harrisichara
Peckichara
Nitellopsis
Sphaerochara
Dactylopora
Cymopolia
Acicularia
Uteria
Belzungia
Jodotella
Neomeris

Fig. 4

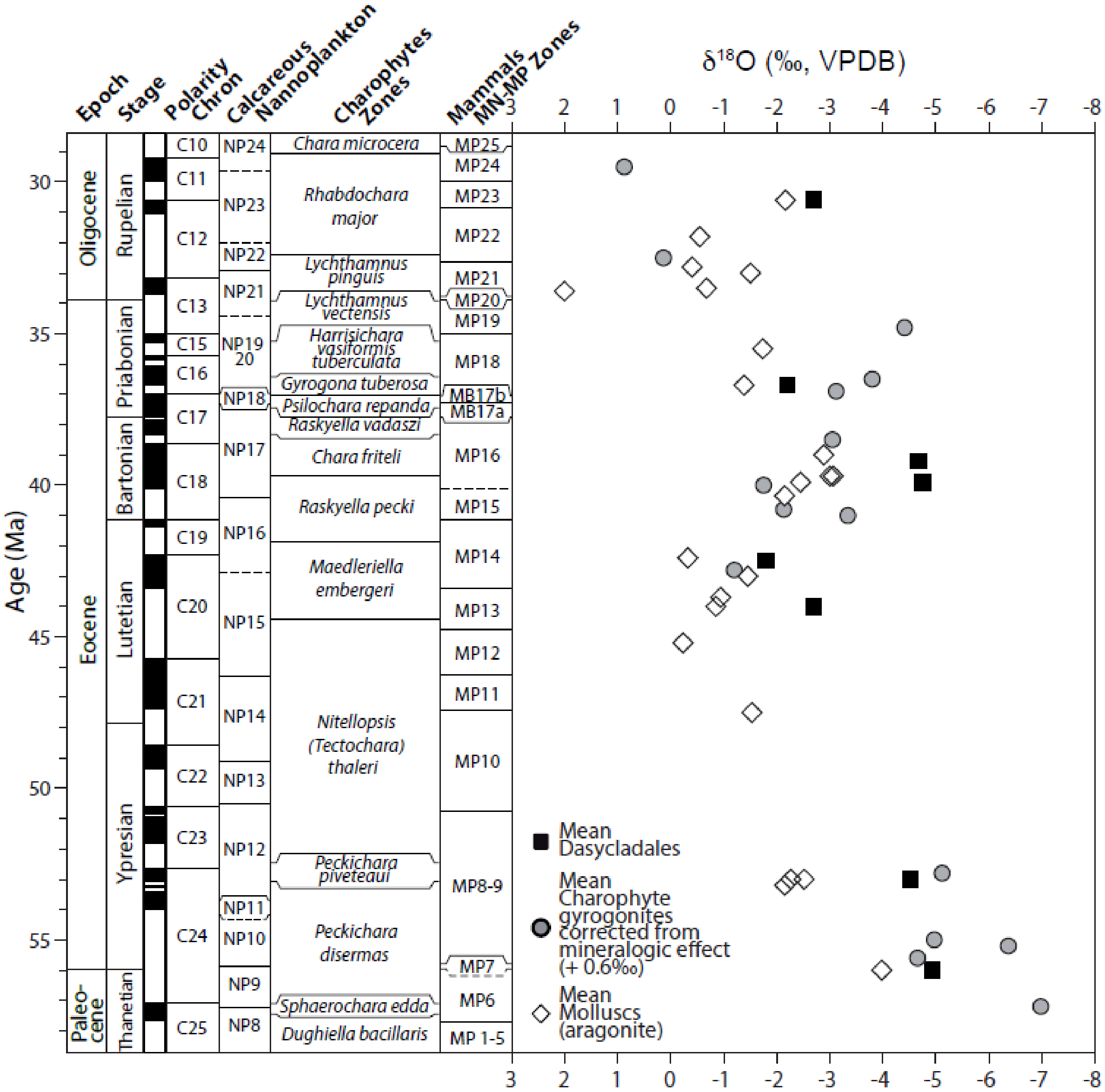
Epoch
Stage
Polarity Chron
Calcareous Nannoplankton
Charophytes Zones
Mammals MN-MP Zones
δ18O (‰, VPDB)
3 2 1 0 -1 -2 -3 -4 -5 -6 -7 -8
Age (Ma)
30
35
40
45
50
55
Oligocene
Eocene
Paleo-cene
Rupelian
Priabonian
Bartonian
Lutetian
Ypresian
Thanetian
C10
C11
C12
C13
C15
C16
C17
C18
C19
C20
C21
C22
C23
C24
C25
NP24
NP23
NP22
NP21
NP19 20
NP18
NP17
NP16
NP15
NP14
NP13
NP12
NP11
NP10
NP9
NP8
Chara microcera
Rhabdochara major
Lychthamnus pinguis
Lychthamnus vectensis
Harrisichara vasiformis tuberculata
Gyrogona tuberosa
Psilochara repanda
Raskyella vadaszi
Chara friteli
Raskyella pecki
Maedleriella embergeri
Nitellopsis (Tectochara) thaleri
Peckichara piveteaui
Peckichara disermas
Sphaerochara edda
Dughiella bacillaris
MP25
MP24
MP23
MP22
MP21
MP20
MP19
MP18
MB17b
MB17a
MP16
MP15
MP14
MP13
MP12
MP11
MP10
MP8-9
MP7
MP6
MP 1-5
■ Mean Dasycladales
● Mean Charophyte gyrogonites corrected from mineralogic effect (+ 0.6‰)
◇ Mean Molluscs (aragonite)

Fig. 5

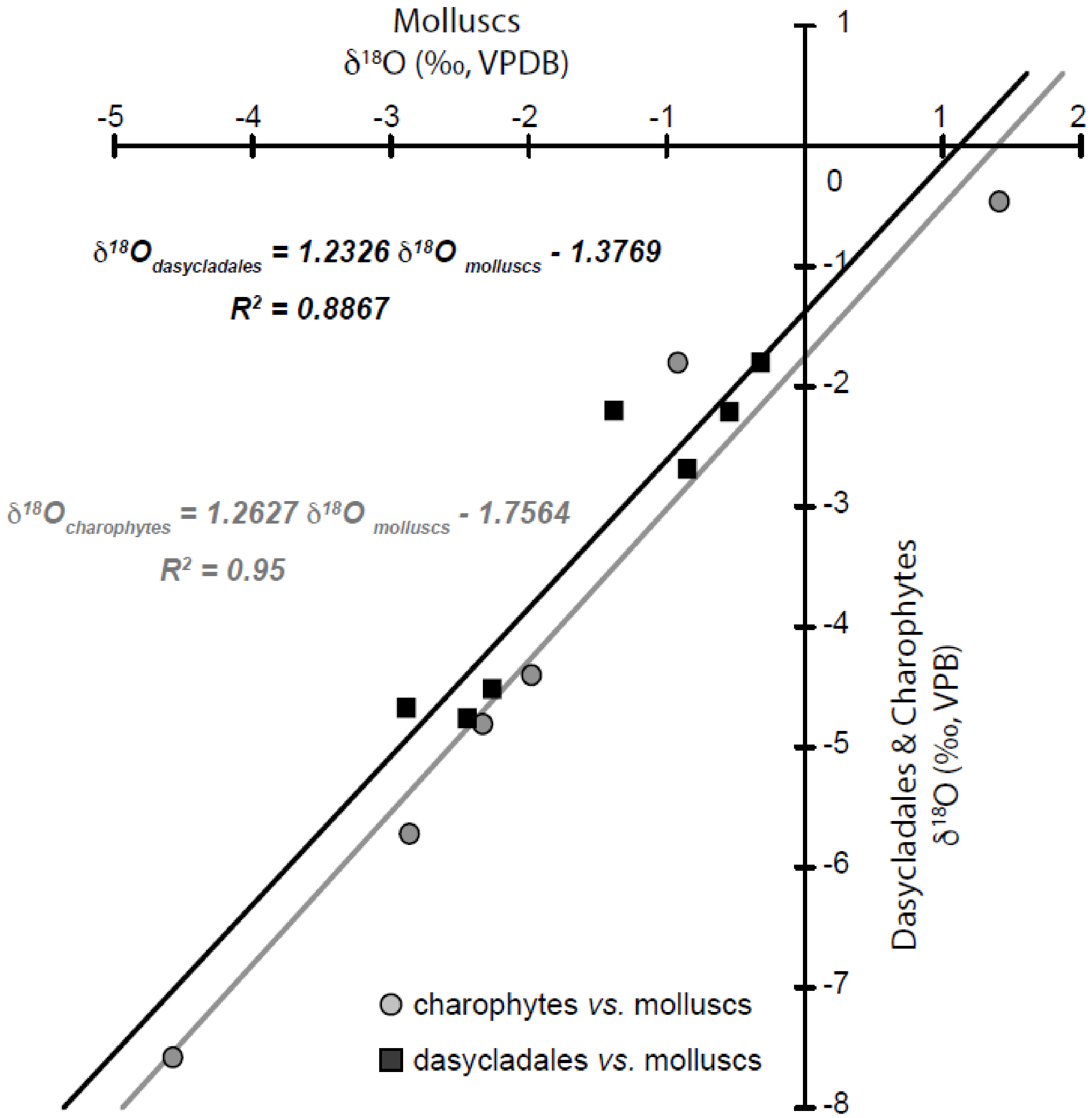
Molluscs
δ18O (‰, VPDB)
-5
-4
-3
-2
-1
1
2
1
0
-1
-2
-3
-4
-5
-6
-7
-8
δ18O dasycladales = 1.2326 δ18O molluscs - 1.3769
R2 = 0.8867
δ18O charophytes = 1.2627 δ18O molluscs - 1.7564
R2 = 0.95
Dasycladales & Charophytes
δ18O (‰, VPB)
● charophytes vs. molluscs
■ dasycladales vs. molluscs

Fig. 6

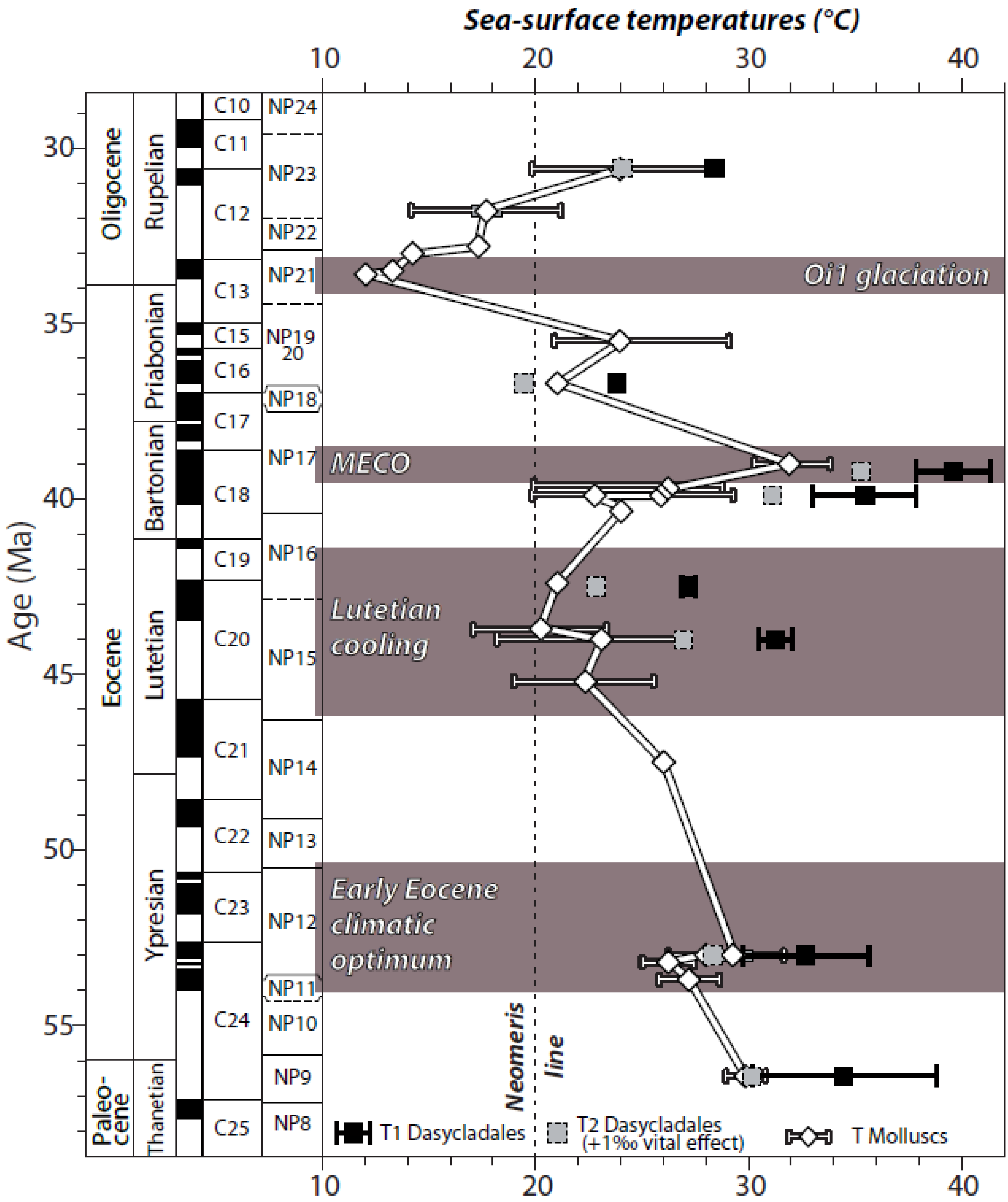
Sea-surface temperatures (°C)
10
20
30
40
Age (Ma)
30
35
40
45
50
55
Oligocene
Eocene
Paleo-cene
Rupelian
Priabonian
Bartonian
Lutetian
Ypresian
Thanetian
C10
C11
C12
C13
C15
C16
C17
C18
C19
C20
C21
C22
C23
C24
C25
NP24
NP23
NP22
NP21
NP19 20
NP18
NP17
NP16
NP15
NP14
NP13
NP12
NP11
NP10
NP9
NP8
Oi1 glaciation
MECO
Lutetian cooling
Early Eocene climatic optimum
Neomeris line
T1 Dasycladales
T2 Dasycladales (+1‰ vital effect)
T Molluscs

Fig. 7

Appendix 1

strati	Species	outcrop	Formation	NP	age	∂18O	∂18O mean	Salinity	∂18Ow global	∂18Ow	T1	T moy	age	∂18O + 1%	T2 +1% ∂18O	T moy2
Oligo	*Néomméris courtyi*	St Antoine (91)	Sables de Vauroux-St Antoine Formation	NP 23	30.6	-2.7	-2.7	30	-0.2	-0.93	28.4	28.4	30.6	-1.7	24.1	24.1
Priab	*Acicularia parvula*	Le Vouast (60)	Marnes à Pholadomyes Formation	NP 18	36.7	-2.2	-2.2	30	-0.7	-1.43	23.8	23.8	36.7	-1.2	19.5	19.5
Bartonien	*Acicularia pavantina*	La Chapelle-en-Serval (60)	Horizon de Mortefontaine Formation	NP 17	39.2	-5.3	-4.7	30	-0.8	-1.53	36.9	34.2	39.2	-4.3	32.5	29.9
	Cymopolia elongata	Roziéres (60)	Horizon de Mortefontaine Formation	NP 17	39.2	-4.1		30	-0.8	-1.53	31.6			-3.1	27.3	
	Neomeris auversiensis	Auvers-sur-Oise (95)	Auvers Formation	NP 16	39.9	-5.3	-4.8	30	-0.6	-1.33	38.0	35.5	39.9	-4.3	33.6	31.1
	Neomeris arenularia	Le Fayel (60)	Auvers Formatio	NP 16	39.9	-6.1		30	-0.6	-1.33	41.3			-5.1	37.0	

			n													
	Acicularia pavantina	Le Guépelle (95)	Auvers Formation	NP 16	39.9	-3.9		30	-0.6	-1.33	31.7			-2.9	27.3	
	Dactylopora cylindracea	Auvers-sur-Oise (95)	Auvers Formation	NP 16	39.9	-3.7		30	-0.6	-1.33	30.9			-2.7	26.6	
Lutétien	*Cymopolia elongata*	Hauteville (50)	Fresville Formation	NP 16	42.5	-1.5	-1.8	35	-0.75	-0.23	26.3	27.2	42.5	-0.5	21.9	22.9
	Néoméris sp.	Gourbesville (50)	Gourbesville Formation	NP 16	42.5	-1.8		35	-0.75	-0.23	27.5			-0.8	23.2	
	Cymopolia elongata	Gourbesville (50)	Gourbesville Formation	NP 16	42.5	-1.9		35	-0.75	-0.23	27.8			-0.9	23.5	
	Acicularia pavantina	Ferme de l'Orme (78)	Zone IVa	NP 16	44	-3.4	-2.7	35	-0.75	-0.23	34.4	31.3	44.0	-2.4	30.1	26.9
	Neomeris limbata	Ferme de l'Orme (78)	Zone IVa	NP 16	44	-2.8		35	-0.75	-0.23	31.9			-1.8	27.5	
	Neomeris limbata	Grignon (78)	Zone IVa	NP 16	44	-2.5		35	-0.75	-0.23	30.3			-1.5	26.0	
	Neomeris limbata	Fercourt (60)	Zone IVa	NP 16	44	-2.5		35	-0.75	-0.23	30.2			-1.5	25.9	
	Neomeris limbata	Damery (51)	Zone IVa	NP 16	44	-2.5		35	-0.75	-0.23	30.4			-1.5	26.0	
	Belzugia Terquemi	Gourbesville (50)	Zone IVa	NP 16	44	-2.5		35	-0.75	-0.23	30.3			-1.5	26.0	
Yprésien	*Uteria encrinella*	Hérouval (60)	Hérouval Formation	NP 12	53	-5.2	-4.5	30	-1	-1.73	35.7	32.7	53.0	-4.2	31.4	28.3
	Neomeris herouvalensis	Hérouval (60)	Hérouval Formation	NP 12	53	-2.6		30	-1	-1.73	24.2			-1.6	19.8	

	Uteria encrinella	Cuise-la-Motte (60)	Cuise Formation	NP 12	53	-5.7		30	-1	-1.73	37.8			-4.7	33.4	
	Uteria encrinella	Liancourt-St-Pierre (60)	Hérouval Formation	NP 12	53	-4.6		30	-1	-1.73	33.1			-3.6	28.7	
Thané	*Belzugia borneti*	Abbecourt (60)	Sables de Bracheux	NP 10	56	-3.6	-4.93	30	-1	-1.73	28.9	34.5	56.0	-2.6	24.5	30.2
	Jodotella veslensis	Villers Franqueux (51)	Sables de Bracheux	NP 10	56	-7.3		30	-1	-1.73	44.6			-6.3	40.3	
	Neomeris craniphora	Boncourt (60)	Sables de Bracheux	NP 10	56	-3.9		30	-1	-1.73	30.0			-2.9	25.7	

equation T : Kobashi & Grosman (2003)

Strati	**Species**	**Outcrop**	**Formations**	**Stage**	**Age**	**∂18O**	**Mean ∂18O**	**∂18O corr + 0,6**
Oligo	Rhabdochara major	Itteville (91)	intecallation lacustre au dessus des Sables de Fontainebleau	Stampien supérieur	29.5	0.28	0.28	0.9
	Harrisichara tuberculata	Cormeilles (95)	Argile Verte de Romainville (bande blanche)	Stampien basal	32.5	0.39	-0.46	0.1
	Gyrogona wrighti	Cormeilles (95)	Argile Verte de Romainville (bande blanche)	Stampien basal	32.5	-1.31		
Priabonian	Psilochara repanda	Les Loges (77)	Marnes bleues d'Argenteuil	Ludien supérieur	34.8	-4.22	-5.01	-4.4
	Harrisichara tuberculata	Les Loges (77)	Marnes bleues d'Argenteuil	Ludien supérieur	34.8	-5.8		
	Harrisichara tuberculata	Le Coudray (77)	Calcaire de Chateau-Landon (sommet)	Ludien supérieur	36.5	-4.4	-4.4	-3.8
	Gyrogona	Verzenay (51)	Calcaire de Ludes	Ludien	36	-	-3.72	-3.1

	wrighti			inférieur	.9	3.49		
	Psilochara repanda	Verzenay (51)	Calcaire de Ludes	Ludien inférieur	36.9	-3.95		
Bartonian	Gyrogona wrighti	Verzenay (51)	Calcaire de Saint-Ouen inférieurs	Marinesien moyen	38.5	-3.44		
	Gyrogona wrighti	Chery-Chartreuve (02)	Calcaire de Saint-Ouen inférieurs	Marinesien moyen	38.5	-3.07	-3.65	-3.1
	Gyrogona wrighti	Chery-Chartreuve (02)	Calcaire de Saint-Ouen inférieurs	Marinesien moyen	38.5	-4.44		
	Gyrogona lemani	Chery-Chartreuve (02)	Calcaire de Ducy	Marinesien inférieur	40	-2.83		
	Gyrogona wrighti	Chery-Chartreuve (02)	Calcaire de Ducy	Marinesien inférieur	40	-2.95	-2.35	-1.8
	Gyrogona lemani	La Chapelle en Serval (95)	Calcaire de Ducy	Marinesien inférieur	40	-1.27		
	Gyrogona lemani cap.	Jaignes (77)	Calcaire de Jaignes	Auversien	40.8	-2.73	-2.73	-2.1
	Gyrogona sp.	Baron (60)	Sommet de l'horizon du Guépelle	Auversien	41	-3.94	-3.94	-3.3
Lut	Gyrogona lemani cap.	Jaulgonne (02)	équivalent "banc vert" ?	Lutetien moyen	42.8	-1.05	-1.80	-1.2
	Gyrogona lemani cap.	Guitrancourt (78)	Base "banc vert"	Lutetien moyen	42.8	-2.05		
	Gyrogona lemani	Guitrancourt (78)	Base "banc vert"	Lutetien	42	-		

	cap.			moyen	.8	2.29		
Ypresian	Nitellopsis helicteres	Avenay-Vaal-d'Or (51)	Argile à lignite d'Epernay	Infracuisien	52.8	-5.72	-5.72	-5.1
	Nitellopsis helicteres	Rollot (80)	Calcaire de Mortemer	Sparnacien basal	55	-5.57	-5.57	-4.97
	Nitellopsis helicteres	Passy (75)	Cendrier	Sparnacien basal	55.2	-6.97	-6.97	-6.37
	Harrisichara leptoceras	Nogent L'Abbesse (51)	Marnes à rognons	Sparnacien inférieur	55.6	-5.82		
	Peckichara disermas	Nogent L'Abbesse (51)	Marnes à rognons	Sparnacien inférieur	55.6	-4.95		
	Nitellopsis helicteres	Berru (51)	Marnes à rognons	Sparnacien inférieur	55.6	-5.01	-5.26	-4.7
	Nitellopsis dutemplei	Berru (51)	Marnes à rognons	Sparnacien inférieur	55.6	-5.66		
	Nitellopsis helicteres	Ste Marguerite (76)	Calcaire du Cap d'Ailly	Sparnacien basal	55.6	-4.84		
Pal	Sphaerochara edda	Mont Chenot (51)	Calcaire de Rilly	Thanétien	57.2	-7.58	-7.58	-7.0

Appendix 2

stage	Formation Dasycladales	δ18O Dasycladales	Formation Molluscs	δ18O Molluscs
Stampian	Sables de Vauroux-St Antoine Fm	-2.2	Falun de Jeurre	-0.55
Priabonian	Marnes à Pholadomyes Fm	-2.2	Marnes à Pholadomya Fm	-1.38
Bartonian	Horizon de Mortefontaine Fm	-4.7	Sables de Cresnes	-2.89
Bartonian	Auvers Fm	-4.8	Auvers Fm	-2.45
Lutetian	Gourbesville Fm	-1.8	Facies de Pacy / Eure	-0.32
Lutetian	Calcaire Grossier Fm	-2.7	Calcaire Grossier Fm	-0.85
Cuisian	Sables de Cuise / Hérouval Fm	-4.5	Sables de Cuise Fm	-2.26

stage	Formation Charrophytes	δ18O Charophytes	Formation Molluscs	δ18O Molluscs
Stampian	Argiles Vertes de Romainville Fm	-0.46	Argiles à Corbules Fm	1.41
Priabonian	Marnes Bleues d'Argenteuil Fm	-4.81	Headon Hill Fm	-2.33
Priabonian	Calcaire de Château Landon Fm	-4.40	Marnes à Pholadomya Fm	-1.98
Lutetian	Banc Vert Fm	-1.8	Facies de Pacy sur Eure Fm	-0.92
Cuisian	Argile à lignite d'Epernay Fm	-5.72	Sables de Cuise Fm	-2.86
Thanetian	Calcaire de Rilly Fm	-7.58	Sables de Bracheux Fm	-4.58

Highlights

We test the use of dasycladales and charophytes as paleoclimatic recorders

We show that dasycladales and charophytes $\delta^{18}O$ reflects mostly temperature variations

We reconstruct summer temperatures from dasycladales $\delta^{18}O$ compositions