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Fossil record of the Icacinaceae and its paleogeographic implications

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Abstract

In the past decades, the concept of Icacinaceae has been refined greatly, as morphological and molecular data have led to a narrower circumscription of a monophyletic Icacinaceae family with only 23 genera (vs 58 sensu Sleumer, 1942). This family possesses an extensive fossil record, important to the biogeographic history of the Northern Hemisphere, but the reported fossils need to be carefully evaluated in the current phylogenetic framework. We evaluated 183 fossil reports of Icacinaceae from the literature but considered only 92 as reliably belonging to this family. Most of the accepted records are from endocarp remains. With this sampling, we show an increase of the species richness during the Paleocene. A great increase of diversity in terms of genera, species, and morphological range is shown through the Paleocene-Eocene interval and during the Early Eocene (Ypresian). Exchanges occurred between North America and Europe near the PETM in both directions. During the middle and late Eocene, several of the modern genera appear first in the fossil record such as *Natsiatum*, *Phytocrene*, and *Pyrenacantha*. Decreased diversity of post-Eocene records might be explained by cooling during and subsequent to the Oligocene, which was less favourable to climbers. We observe the same pattern in other megathermal families showing the global dynamic of megathermal groups of the North Hemisphere forest (boreotropical sensu. Wolfe, 1975) during the Paleogene.

Keywords: Icacinaceae, endocarp, leaves, pollen, biogeography, palaeobotany

1. Introduction

In the past decades, the concept of Icacinaceae has been revised considerably with the results of new molecular and morphological data that show that the former Icacinaceae family concept with about 400 species and 58 genera (from Sleumer, 1942) was polyphyletic (Kårehed, 2001). That phylogenetic study defined the Icacinaceae s.s. as belonging to the Garryales order and placed some genera in the Aquifoliales and Apiales orders. In particular, Kårehed described a new family, Stemonuraceae, and added some species to the Cardiopteridaceae family. The resulting circumscription of Icacinaceae included only 36 genera divided in four informal groups: Icacina, Cassinopsis, Emmotum, and Apodytes. Later, another study showed that this new circumscription of Icacinaceae corresponds to a basal lamiid group (Lens et al., 2008). According to Lens et al. (2008), the Icacinaceae have simple perforation plates in vessels (except for *Cassinopsis*), which is not the case for other excluded former Icacinaceae. However, the Icacinaceae (sensu Lens et al., 2008) was still considered as a polyphyletic group (Byng et al., 2014). More recently, a new Icacinaceae s.s. family was delimited with only the Icacina group sensu Kårehed (2001) accepted, using a new molecular data set (Stull et al., 2015). Icacinaceae s.s. (sensu Stull et al. 2015) contains only 23 genera, with about 160 species, and is a basal lamiid group close to the Oncothecaceae family. Both families are in the newly defined Icacinales order. Those taxonomic assignments are accepted and used in the APG IV (APG, 2016). Thus, the Icacinaceae family s.l. belongs now to four indirectly related orders in Asterids group (Fig.1).

This family possesses an extensive fossil record that extends geographically and geologically. The record is mainly composed of endocarps (e.g., Reid and Chandler, 1933; Manchester, 1994; Collinson et al., 2012) but there are also reports of wood (e.g., Greguss, 1969), pollen (e.g., Kedves, 1970; Krutzsch & Vanhoorne, 1977; Cavagnetto, 2000), a flower

(Del Rio et al., 2017) and leaf remains (e.g., Wolfe, 1977; Tanai, 1990). However, most of the paleobotanical discoveries and descriptions on Icacinaceae family were made before the twenty first century. Therefore, assignments to Icacinaceae were done before the recent modifications of the phylogenetic framework and some characters used to define Icacinaceae can be in fact been simply apomorphic for Asterids (Fig. 1).

Some fossil species (e.g., *Icacinoxylon alternipuncata*, *Icacinicarya papillaris*, and *Iodes germanica*), were used to calibrate an angiosperm phylogeny (Magallón et al., 2015). In addition, the Icacinaceae fossil remains have been used as a paleoclimatic clue and contributed to the characterization of the Boreotropical forest definition, a vegetation type that was widespread across middle latitudes in Northern Hemisphere during the Eocene (Wolfe, 1975). The Icacinaceae fossils also played an important role in the understanding of the dispersion between Europe and North America during the early-middle Eocene (Manchester, 1994; Stull et al., 2011; Allen et al., 2015). Thus, it is crucial to evaluate the Icacinaceae fossil record within a phylogenetic framework. Two reviews of the fossil record including the asteridae were made (Martínez-Millán, 2010; Manchester, 2015), highlighting a Maastrichtian minimum age for the Icacinaceae family. However, neither of these reviews embraces all the Icacinaceae fossils described until now.

In this study, we reviewed previously published reports of fossils attributed to the Icacinaceae. Our main questions are: (1) what is the fossil diversity of Icacinaceae s.s. following the new circumscription of the family and (2) what is the paleogeography and biogeographic history of this family based on this new circumscription?

2. Material and methods

We compiled all the occurrences of Icacinaceae in the literature to the extent of our knowledge (Table 1.). The fossil record depends on available outcrops, search efforts, and findings. Here we took into consideration a majority of species from North America and Europe. This distribution is probably due to a more thorough search effort in this area than others in palaeobotanical history (Morley & Dick, 2003). Indeed, Icacinaceae fossils were recently found from Paleocene-Miocene range in South America (Stull et al., 2012). The palaeobotanical studies of South-America have been increased during the last ten years (Herrera et al., 2011, 2014; Jud et al., 2016; Pérez-Consuegra et al., 2017, 2018), and reveal a new diversity and new biogeographical hypotheses, including for Icacinaceae. We tabulated 183 fossil occurrences according to the age, locality, country and the concerned organs, among them 105 (81 species) were represented by fossil of endocarps divided in 12 fossil genera: *Comicilabium*, *Croomiocarpum*, *Faboidea*, *Hosiea*, *Icacinicarya*, *Icacinicaryites*, *Iodicarpa*, *Palaeohosiea*, *Palaeophytocrene*, *Perforatocarpum*, *Sphaeriodes* and *Stizocarya* and four modern genera: *Iodes*, *Natsiatum*, *Phytocrene* and *Pyrenacantha*. Only one flower has been described for this family, the extinct genus *Icacinanthium*. We also compiled 13 leaf occurrences (10 species), five of them being from two extinct genera: *Goweria* and *Huziokaeae* and four of them from two extant genera: *Merrilliodendron* and *Phytocrene*. The pollen record includes 26 occurrences (seven species) in two fossil genera, *Compositoipollenites* and *Echiperiporites,* and only an extant ones *Iodes*. Finally, we recorded 38 occurrences (14 species) of fossil wood records, with two fossil genera, *Icacinoxylon* and *Apodytoxylon*. The dominance in the fossil record of climbing genera, well represented close to rivers, could be a taphonomic bias (Burnham, 1989; Burnham et al., 1992). However, because the climbing genera are well distributed in the family, we consider our sample as representative of the entire family.

We decided to accept or reject occurrences based on the initial description and the associated figures in the literature. We checked all occurrences in accordance with new taxonomic and phylogenetic data (Stull et al. 2015). The Icacinaceae s.l. now belongs to four order in Asterids (Fig. 1), and thus some Icacinaceae characters used as criteria of fossil recognition (e.g., wood anatomy, leaves characters) cannot be longer used. We resumed the genera taxonomic changes and the associated fossil record in the Appendix 1.

We propose a reconstruction of the paleogeography of the Icacinaceae s.s. (Fig. 2) using paleomap made by Boucot et al. (2013). In this reconstruction (Fig. 2), the rejected occurrences are excluded (considered as definitively not Icacinaceae or without certainty in age of the outcrops) whereas the dubious occurrences are presented in grey (considered as potential Icacinaceae, but without certainty). Accepted occurrences are in red (Fig. 2).

We used paleoclimatic reconstruction based on lithologic indicators in order to give a brief and global idea of the link between past climate and Icacinaceae distribution (Boucot et al., 2013). This climatic ancestral reconstruction was based on the presence of lithological remains: Coal, Bauxite and Laterite indicate a warm and wet climate (assumed as tropical), the Coal and Tillites together indicate a cold and wet climate (cool temperate), the presence of Evaporite and Calcrete indicates a warm and dry climate (arid), The tillite associated with Dropstone and Glendonite indicate a dry and cool climate (cold) and the presence of Kaolinite, Crocodiles remains, palms and mangroves indicate a warm temperate climate. For more clarity, the position of the different rocks samples was removed and we only kept the climatic area reconstructions. The complete lithological data can be found in the following website: scotese.com/climate.htm. Despite more recent alternative data on reconstruction of biomes for parts of the world (e.g., South America, Jaramillo and Cardenas, 2013), we decided to keep this global view as a good proxy for our study.

3. Results

3.1 Species and occurrences rejected or dubious

The endocarp record is the most meaningful for the Icacinaceae family, and probably the most reliable. However, some occurrences need to be revisited.

Comicilabium atkinsii was considered as belonging to Icacinaceae by its unilocular endocarp, the vascular bundle on only one side and the cellular structure of the endocarp wall (Manchester, 1994). The endocarp apical structure is a bulge with a lip. The size of the endocarp and the wall thickness (2–4 mm) are surprising for a supposed Icacinaceae compared with modern species endocarps (Del Rio, 2018). Despite the fact that the wall anatomy, including interlocking digitate sclereids composing the endocarp and papillate locule lining, is a convincing argument for the proposed affinity, we decided to consider this species as dubious in order to consider the extreme differences in endocarp morphology.

Icacinicarya mucronata, Icacinicarya bognorensis, Icacinicarya rotundata, and *Icacinicarya sp.11* are considered as dubious in a recent revision of the London Clay fossils (Stull et al., 2016), because of the lack of some characteristic features and the bad preservation of the specimens. We also followed this opinion here. *Icacinicarya foveolata* was considered as a non-member of the Icacinaceae family in the same study because of the presence of large hexagonal secretory cells lining the outside part of the seed and the thicker endocarp wall. In the absence of alternative identification and another argument, we consider that at least the characters given by Reid and Chandler (1933); i.e. endocarp unilocular and wall composed with partial digitate cells, are sufficient to not totally reject the potential affinity with Icacinaceae family, so we consider it as dubious.

Icacinicarya amygdaloidea was considered as a member of Icacinaceae because of the shape, the position of the vascular bundle and the stylar canal (Chandler, 1961b). However, the specimens are smooth, which is uncommon within the Icacinaceae family (Del Rio, 2018). This trait is occasionally found in *Casimirella*, *Mappia* and especially in *Sarcostigma*. Additionally, the wall is composed of non-digitate cells, 10-12 µm in diameter. This kind of cells are never found in extant Icacinaceae (Del Rio 2018). Consequently, we rejected this species in our study.

Icacinicarya budvarensis from the Santonian of Germany (Knobloch & Mai, 1986) has a nodulose ornamentation, not common in the modern Icacinaceae family, and a shape also not found in extant species of Icacinaceae (Del Rio, 2018). Moreover, the description lacks the inner endocarp and the wall are partially not described. Therefore, we choose to consider this species as rejected.

Icacinicarya papillaris (Knobloch & Mai, 1986) resembles much more to an Icacinaceae especially belonging to *Iodes,* but the preservation seems to be insufficient to assign this species to a particular genus. We consider this species as dubious because of the rough ornamentation and the absence of the papillae on the inner endocarp surface.

According to its original description*, Iodes germanica*, from the Maastrichtian of Germany, have all the diagnostic characters of *Iodes* (reticulate ornamentation, papillae on the inner surface, vascular bundle in one side on the endocarp wall; Knobloch & Mai, 1986). Despite the lack of revision and a good illustration (Manchester, 2015), we decided to accept this last species as Icacinaceae member, based on the initial quite complete description.

Icacinicarya sp. (Chester, 1955) is rejected for this paleogeographical reconstruction because of the doubtful age of the Nigeria outcrops. Chester writes “Maastrichtian?” for this specimen. Considering the importance of species from Cretaceous in paleogeographical

reconstructions, we decided to not take the risk to include this specimen, not formerly described as a species by the author.

Icacinicarytes corruga (Pigg et al., 2008) lacks anatomical details and is based on a single unusually large specimen (38 mm x 28 mm). In addition, the morphology of this specimen seems to be difficult to interpret, in particular the ornamentation different from extant Icacinaceae. We consider it as dubious.

Icacinicaryites israelii from the Early Maastrichtian of Israel was a controversial species. Some authors disputed the attribution of this specimen to *Iodes* (Stull et al., 2016; Del Rio et al., 2019a). In fact, this specimen lacks the anatomical detail needed to assign it. The potential inner cotyledon discussed in the original article (Soudry & Gregor, 1997; figures 4, 8, 9) seems to be an artefact. The specimen on which this species is based is bilateral, slightly compressed laterally, asymmetrical at the apex and reticulate on the surface. All these characters could support an Icacinaceae assignment. However, the reticulation pattern seems to be very orderly compared to Icacinaceae that have a more randomly arranged reticulation (Del Rio, 2018). The lack of anatomical detail on the wall and locules (Unilocular? Anatropous?) led us to consider this species as very questionable.

Phytocrene microcarpa of Scott & Barghoorn 1957 is rejected by some authors (Stull et al., 2012; Manchester et al., 2015). This species shows an anatomy that cannot match with the Icacinaceae family (Manchester et al., 2015). Also, the shape and the size of the endocarp do not match with this assignment. For this reason, we consider it as rejected.

cf. Natsiatum wilkoxiana from the Eocene of the Tallahatta Formation (Blanchard et al., 2016) shows very few morphological clues and no anatomical characters. We cannot exclude that this specimen corresponds to Icacinaceae, because of the ridge structures described by the author. However, without enough diagnostic characters, we consider it as dubious.

Some occurrences have been excluded from this study: an *Iodes* from the Miocene of Yunnan (China) was mentioned by Stull et al. (2014) but not formerly published; one of us (DDF) could observe another *Iodes* species from the Miocene of Turkey, but could not study it in detail and the specimen is no longer accessible for study.

The leaves of modern Icacinaceae s.s. are in general simple, entire, mainly pinnatifid with brochidodromous secondary venation and percurrent tertiary venation (Sleumer, 1971; Villiers, 1973; Utteridge et al., 2007; Allen et al., 2015; and personal observation). There are some notable exceptions: leaves from *Hosiea* and *Natsiatum* are toothed with craspedodromous secondary veins; some *Phytocrene* and *Pyrenacantha* species have palmate primary veins (*Phytocrene borneensis*, *P. bracteata*, *P. palmata*, *P. hirsuta*, *Pyrenacantha malvifolia*). Tertiary veins are occasionally more reticulate as some species in *Casimirella*, *Desmostachys*, *Miquelia*, *Pyrenacantha*, and *Stachyanthus* in general. These examples show the great variation in leaf architecture in the family Icacinaceae but also the limited variation in the majority of species. Nevertheless, the classical type of leaves for Icacinaceae family is common in tropical flowering plants, at least for the entire leaves' trait (Bailey & Sinnott, 1916; Wolfe, 1985). Thus, the leaves of this family lack diagnostic characters. While fossil leaves might appear identical in venation to modern leaves in the Icacinaceae, the fact that overlapping venation occurs in other families means that we cannot be fully confident in the identification of fossil leaves in this family. This probably explains the poor record of fossil leaves attributed to this family (only 13 occurrences). We choose to consider the leaves as dubious if no clear diagnostic characters are given.

The genus *Goweria*, attributed to Icacinaceae by Wolfe (1977) and primarily to Menispermaceae (Wolfe, 1968), accommodates oval to lanceolate leaves with palmate primarily venation (in fact pinnatifid, see discussion in Allen et al., 2015), five primaries, brochydodromous secondary venation and percurrent tertiary veins. This diagnosis could

correspond to Icacinaceae family but not exclusively. Indeed, we found a similar type of leaves for at least the Metteniusaceae family (Fig. 1) in some genera previously considered as Icacinaceae (*Emmotum*, *Dendrobangia*, *Platea*, *Apodytes*, *Pittosporopsis*, personal observation). We decided to consider all *Goweria* species as dubious. *Goweria linearis*, in particular, seems to be very ambiguous (Wolfe, 1968). Actually, the specimen has a strongly asymmetrical apex, which is uncommon in Icacinaceae species. In our opinion, *Goweria bluerimensis* is the most convincing assignment (Allen et al., 2015). These specimens possess expanded petioles with a narrow, resistant vascular strand that could be a diagnostic character.

Huziokaea eoutilus partially resembles Icacinaceae, but is closer to *Gomphandra* (Tanai, 1990), which is currently in Stemonuraceae (Kårehed, 2001). The assignment of this extinct genus to Icacinaceae s.s is here considered as wrong.

Merrilliodendron ezoanum identification seems to be based on traits (wide-elliptic shape, intercostal tertiary veins, diverging perpendicular from the midvein), now shared by several families including Icacinaceae and Stemonuraceae (Tanai, 1990); we consider it as dubious.

The fossil record for *Phytocrene* leaves is composed of three species. However, *Phytocrene acutissima* from Eocene of Alaska corresponds to a partial fossil leaf (Wolfe, 1977; pl. 12, 1–6). *Phytocrene sordida* from Eocene of USA seems to be more convincing (MacGinitie, 1941), but the main traits correspond to the common characters discussed above for *Goweria*. The author of this species notes the similarity between the fossil species and modern *Phytocrene blancoi* and *Hyperbaena hondurensis* (Menispermaceae), showing the ambiguity of the determination at the family level. Finally, *Phytocrene ozakii* from the Eocene of Japan is based on a partial fossil (Tanai, 1990; pl. 6) and no diagnostic characters were clearly used.

Both descriptions of *Pyrenacantha* sp. from Alaska and Japan (Wolfe, 1977; Tanai, 1990) are based on fragmentary material. They have mainly in common a pinnate venation and a weak pair of basal secondary venes that form marginal loops whose apical sides are oriented basally. This shape seems to appear many times in Asterids (e.g., Stemonuraceae, *Lasianthera*) and thus we consider these occurrences as dubious.

The genus *Icaciniphyllum* (not shown in Table 1.) was described for simple leaves, with a non-entire margin (undulate, crenulate, and irregularly dentate) and with craspedodromous venation (Kvaček & Bůžek, 1995). These characteristics are rare in Icacinaceae. In fact, only *Hosiea* and *Natsiatum* could roughly correspond to this description, but the non-entire margin is very different. Other genera (e.g., *Iodes*, *Pyrenacantha*…) have entire margins and brochidodromous venation. Indeed, the type species *Icaciniphyllum artocarpites* (Ettingshausen) Kvaček & Bůžek is now considered as a member of *Sloanea* L., (Elaeocarpaceae), which invalidates the previous assignment (Kvaček et al., 2001; Allen et al., 2015). Thus, the affinity is probably wrong for all the species attributed to the genus.

To sum up, all fossil leaves are considered as dubious or as rejected for our paleogeographical reconstruction. We are convinced that some occurrences (e.g., *Goweria bluerimensis*) are adequately documented; however, we show that the main traits of leaves correspond mostly to the Icacinaceae s.l. are now shared by some more or less closely related families.

The fossil record of potential icacinaceous pollen is poor in term of species diversity but rich in occurrences, especially in Europe. To our knowledge, only one pollen type was considered as "*Iodes* type" in the USA (Leopold & MacGinitie, 1972). This specimen was not represented nor described so we rejected this occurrence. The two other occurrences outside Europe are from the Miocene of Cameroon (Salard-Cheboldaeff, 1975). *Echiperiporites minor* is described as a periporate (5 pores) and echinulate pollen, which is apparently close to

Phytocrene pollen. However, a re-examination of the original material (KWI-1 lame B, W35/W36) led us to recognize about ten pores (J. Dejax com. Pers.), which allow the rejection of this species, because no modern Icacinaceae pollen shows more than eight pores (Lobreau-Callen, 1972). *Echiperiporites icacinoides* is described as three (4-5?) porate and echinulate pollen which could correspond to *Stachyanthus*, *Deptaulus* (*Leptaulus*?, Aquifoliaceae) and (mostly) *Iodes*. The original material is decayed. We are waiting for its potential restoration to eliminate the doubt and we decided here to reject this occurrence.

Four species of the fossil pollen genus, *Compositoipollenites*, have been considered related to the Icacinaceae family. Manchester (2015) considers that "*a comprehensive comparative investigation remains to be done with attention to other families that also share echinate pollen*", in order to confidently conclude about the affinity of these pollen specimens. We decided to follow the same caution and we used the dubious status for all *Compositoipollenites* pollen.

The wood attributed to Icacinaceae possesses a wide occurrence and stratigraphic range (100.5–5.3 Ma). Unfortunately, they do not correspond to Icacinaceae s.s. and we rejected them all. Indeed, Icacinaceae s.s. have simple perforation plates (Lens et al., 2008), whereas *Icacinoxylon* has scalariform perforation plates. The explanation of this paradoxical nomenclature consists in the initial affinity of this fossil genus was made with *Citronella*, which is now in Cardiopteridaceae (Fig.1, Appendix), (Stull et al., 2015). The other wood taxon, *Apodytoxylon hamamelidoides* has *Apodytes* affinity, which is now in Metteniusaceae family (Fig. 1, Appendix).

3.2 Paleogeographic reconstruction

We accepted 92 occurrences (mainly from endocarps), considered 45 occurrences as dubious (mainly leaves and pollen species) and rejected 46 occurrences (mainly from the wood species). According to our selection criteria, it has to be considered that all dubious species could be false identifications. We represent them in the following part in order to provide information about the potential range of the family, which could be a subject of discussion, only accepted species will be used in the biogeographic discussions.

The occurrences of Icacinaceae all belong to a warm temperate or boreotropical and tropical climate, except for the Paleocene Egyptian occurrence, which apparently belongs to an arid climate (*Icacinicarya youssefi*). The Northern Hemisphere, in particular European and North American areas, has almost all confident fossil occurrences. We have only one occurrence for the Cretaceous period and the most of the occurrences are from the early and middle-late Eocene. The Oligocene record is very poor. In term of (accepted) species richness (Table 2.), only one species belongs to the Cretaceous period, 14 are Paleocene, 59 are Eocene (38 from the early Eocene and 24 from the middle-late) and only 3 species are from the Oligocene epoch.

Records of *Iodes* extend from the Upper Cretaceous until the Oligocene. *Phytocrene* appears in the fossil record during the Paleocene or during the Eocene. Endocarp fossils of *Pyrenacantha* and *Natsiatum* were found during the Eocene, but only *Pyrenacantha* is known from the Oligocene. We did not identify other extant genera represented in the fossil record. No extinct genus is present during the Upper Cretaceous: almost all extinct records are found in the Paleogene, mainly during the Eocene epoch. Removing the unnatural genera (based on characters that allow us to assign specimens to Icacinaceae family, but not to a genus, e.g., *Icacinicarya*, *Icacinicarytes*), we can consider only one extinct genus during the Paleocene, six genera from the Eocene and one genus from the Oligocene.

4. Discussion

4.1 Age of the family

The age of Icacinaceae was estimated at 96.7 Ma with the help of molecular phylogeny (Magallón et al., 2009). In another recent study, the estimated age was 104 Ma (Wikström et al., 2015). This analysis used 17 fossil calibration points, but these are from various asterids, no Icacinaceae fossil records were included. In another molecular study, the estimated age is between 103 and 110 Ma, with the maximum likelihood method and between 65.5 and 100.3 Ma with a Bayesian analysis (Magallón et al., 2015). This last publication used numerous fossils as calibration points and in particular three fossils attributed to Icacinaceae family: *Icacinoxylon alternipuncata*, *Icacinicarya papillaris*, and *Iodes germanica*. The icacinaeous affinity of *Icacinoxylon* is rejected in this review, and *Icacinicarya papillaris* was considered as dubious. Only *Iodes germanica* seems to be an unambiguous Icacinaceae fossil. The authors used 65.5 Ma as the age of calibration base on this record. Two reviews of the fossil record of asteridae were made (Martínez-Millán, 2010; Manchester, 2015), highlighting a Maastrichtian minimum age for the Icacinaceae family. In our review of the fossil record, 13 species belong to the Cretaceous epoch but only *Iodes germanica* is accepted. The minimum appearance age selected for *Iodes* is 66 Ma (Upper Maastrichtian, following the International chronostratigraphic chart v2017/02).

According to the previous studies, we consider the Upper Maastrichtian as the minimum age given by the fossil record for the Icacinaceae family. However, the calibration point for future molecular studies could be more precise including this minimum age at the internal node *Iodes-Mappianthus* (Stull et al., 2015) rather than at the Icacinaceae divergence.

4.2 Major changes in the family Icacinaceae

In our review, only *Iodes germanica* species already occurs during the Upper Cretaceous of Europe, showing that the Icacinaceae family is present in Europe (Fig. 2A). This species is also found during the Upper Paleocene, at least this species crosses the Cretaceous-Palaeogene boundary and persists during the Paleocene in the same area. This could be a clue to the resilience of some families, and could explained by the previous results based on the family level showing that the land plants did not suffer from global extinction (but local turnover) during the Cretaceous-Palaeogene boundary (Cascales-Miñana & Cleal, 2014). In addition, we show an increase of occurrences, genera, and species for the Icacinaceae family during the Paleocene and new occurrences outside of Europe, mainly in North America (Fig. 2B, Fig. 3), following the expansion of the boreotropical forest area (Mai, 1989; Wolfe, 1975). The genus *Iodes* seems to be limited to Europe during the Upper Cretaceous. With seven new *Iodes* species described for the Paleocene epoch, we show an increase of species richness. All species of *Iodes* from the Paleocene are very similar in term of shape and only differ for some precise traits (size of the endocarp, reticular pattern, shape of the ridges, Del Rio et al. 2019a).

We show a clear increase in Icacinaceae diversity during the early Eocene, in term of species, new genera with new shapes, (Fig. 3). Among the 14 species present from the Paleocene, only three species were found among the 38 early Eocene species. This shows a turnover and an increase of diversity in the Icacinaceae family. Two genera were more diverse, *Palaeophytocrene* and *Iodes*, which are probably climber species. This increase could be due to the new evergreen thermophilic flora, highly diversified and favourable to climbers, flora that occurs during the PETM (Upchurch Jr & Wolfe, 1987; Collinson & Hooker, 2003) and rapid turnover but not catastrophic changes for plants (Cavagnetto, 2000; Wing et al., 2005; Collinson et al., 2009; Pigg & DeVore, 2009). In terrestrial diversity, studies show less

perturbation but migrations of the fauna probably following the flora change (Godinot & de Broin, 2003; Gingerich, 2006).

The genus *Palaeophytocrene* only has one species from Bogota (South America) during the Paleocene and eight species during the Eocene from North America and Europe. This could indicate a diversification and an expansion of the area of *Paleophytocrene* during the PETM, following the expansion of the megathermal vegetation. Indeed, a geological connection between North and South America for the *Paleophytocrene* was proposed during the Paleocene (Stull et al., 2012). This connection became possible by the renewal of the magmatic arc of the Northern Andes during the Paleocene-Eocene (Bayona et al., 2011; Cardona et al., 2011). Therefore, this genus shows a strong evidence of potential exchanges between tropical South America and boreotropical flora during this period. Changes during the PETM in North America could be partially due to the flora spreading from South America, followed by an expansion of these floras to Europe during the late Ypresian. New endocarp shapes appeared at the end of early Eocene in Europe, as *Faboidea*, *Perforatocarpum*, *Sphaeriodes, Stizocarya*, all of these genera are now extinct. Among the eight *Iodes* species from the Paleogene, three were found from the early Eocene showing a partial but important change in Icacinaceae floristic composition (Del Rio & De Franceschi, in press). In particular, among the 14 species that occur during the early Eocene, four have no horn-like protrusions at the apex (associated to the vascularisation of the fruit), whereas in the Paleocene, all *Iodes* species have it (Del Rio et al. 2019a). Thus, we found new shapes and new endocarp types during the early Eocene. These new shapes could be due to local diversifications or migrations of new floras from other areas. All species from the Paleocene are in Europe, whereas at least three species of *Iodes* (one with horn-like protrusions, two without) are in North America during the early Eocene. The connection between North America and Europe during the Paleocene and early Eocene was well-documented (Wolfe,

1975; Manchester, 1994, 1999). This connexion remains possible via the North Atlantic land bridge (McKenna, 1975; Tiffney, 1985) and following the extension of the boreotropical forest during the global warming. The migrating direction of exchanges (Asia-North America-Europe or Asia-Europe-North America) was intensively discussed in mammal palaeontology (Godinot & de Broin, 2003; Smith et al., 2006; Beard, 2008). Here, we have clues for an exchange from Europe during the early Eocene. In fact, all species with or without horn-like protrusions are older in Europe than in North America. However, an *Iodes multireticulata* specimen, dated from 55.5 Ma was found in the USA, the occurrence of this species in Europe was dated to about 51 Ma (Reid & Chandler, 1933; Tiffney, 1999). Nevertheless, we suspected that the specimen from the Fisher/Sullivan site can be a new species instead of a specimen of I. *multireticulata*. In fact, the size of the specimens from Fisher and London Clay site seems distinctive. We show that the size of the endocarps could be used to differentiate modern species when it exists a clear gap between the sizes within species (Del Rio, 2018). This is here the case. With *Iodes* and *Paleophytocrene*, we have in consequence two examples of interchanges between North America and Europe, showing that the dispersion of floras was bilateral.

Due to particularly warm climate, the widest fossil extension of the Icacinaceae (in term of species richness and probable area) was reached during the early Eocene. However, this is from the middle-late Eocene that were found the fossil records attributed to modern genera as *Natsiatum* (Stull et al., 2011), *Phytocrene*, at first in Europe and then in the USA (Stull et al., 2011; Collinson et al., 2012) and *Pyrenacantha* (Manchester, 1994). Therefore, it is probably during the Eocene that the main modern genera appeared and diversified (Fig. 2D, Table 2). In *Iodes*, we show less species richness during the middle-late Eocene. These "species richness regression" could be attributed to the cooling climate (Collinson et al., 1981; Keller, 1983; Zachos et al., 2008), what Tiffney (1985) called a "*climatic*

426 *deterioration*". This climate induced a change in floral structure, less favourable to the
427 climber species (Collinson & Hooker, 2003).
428 Only three occurrences of Icacinaceae were found during the Oligocene (Fig. 2E, Fig.
429 3B). This result shows an important decrease of diversity in the fossil record and is consistent
430 with a regression of the boreotropical forest. At the Oligocene-Eocene boundary, the climate
431 was probably the coolest of the Paleogene and remained cold throughout the Oligocene
432 (Zachos et al., 2001, 2008). The boreotropical flora regressed and the deciduous vegetation,
433 with less diversity, expanded (Tiffney, 1985). There are only two extant genera represented,
434 *Pyrenacantha* and *Iodes* and one extinct genus, *Palaeophytocrene*. The species *Pyrenacantha*
435 *austroamericana* is from the Oligocene of Peru (Stull et al., 2012). The oldest fossil remains
436 of this genus is *Pyrenacantha occidentalis* of Lutetian age from Oregon, USA (Manchester,
437 1994). Thus, these two species show a connection between North and South America during
438 the Eocene. On the other side, the Oligocene *Iodes* species is from Europe. This presence of
439 this species allows for the consideration of *Iodes* as being present in Europe throughout the
440 Palaeogene. This genus was probably part of a remnant of the boreotropical forest, also which
441 is almost completely replaced in Europe by cold-tolerant species during the Neogene. (Wolfe,
442 1975, 1985, Tiffney, 1985). In this way, the *Iodes* fossil from Miocene of Turkey (DDF obs.)
443 could also correspond to a late remain of this thermophilic European flora. Finally,
444 *Palaeophytocrene* sp. from Oregon, USA also shows a symmetrical pattern in North
445 American than *Iodes* in Europe (Meyer & Manchester, 1997).

446 **4.3. Comparison with the history of other angiosperm families**

447 Our results are in accordance with the boreotropical regression hypothesis (Lavin & Luckow,
448 1993). In particular, Wen (1999) establishes a disjunction of 65 genera between North

American and Asian floras, which occurred during the Miocene. This pattern could be explained by an expansion of a boreotropical flora during the Paleocene and Eocene followed by a high regression during the Neogene.

Some families, including Icacinaceae and Menispermaceae, were considered as closely associated with the boreotropical flora (Wolfe, 1975). These two families have in common a majority of species with a climber habit and a similar present-day distribution. Thus, we can hypothesize that both families could have a similar history linked with the boreotropical expansion and regressions. A fossil history of the Menispermaceae was documented (Jacques, 2009). The Menispermaceae appeared during the Paleocene in the fossil record (recorded from Cretaceous but dubiously), diversified during the Eocene and then regressed during the Oligocene in Europe and North America. In particular, the maximum of diversity was found during the PETM event. A new species of Menispermaceae, *Sinomenium macrocarpum* Liu et Jacques, was found after this review from the Miocene of North America (Liu & Jacques, 2010). However, this is probably a late refuge of the boreotropical flora. New studies show Menispermaceae in South America during the Paleocene (Herrera et al., 2011; Jud et al., 2018). These discoveries reveal a complex relationship between North and South America during the Paleocene. The same pattern is observed for the Icacinaceae family during the Paleocene (Stull et al., 2011).

In the Vitaceae, also a climber family, the oldest known fossil found is from India before the continental collision (Manchester et al., 2013), followed by a rapid widespread radiation during the Paleocene and Eocene in Northern Hemisphere. Other routes of dispersion have been highlighted from South America (Manchester et al., 2012). In addition, a study on the genus *Parthenocissus* (climber) shows a disjunction between Asia and North America in the Early Miocene, which is congruent with the boreotropical regression (Nie et al., 2010, 2012).

Some other evidence of expansion during the Paleogene and regression/extinction of tropical floras in some areas (mainly North America and Europe) during the Neogene are found for *Paliurus* (Rhamnaceae), Sabiaceae family, *Canarium* (Burseraceae), *Deviacer* (? Polygalaceae), Ulmaceae, *Carya* (Juglandaceae), Sapindaceae and *Anacardium* (Anacardiaceae), (McClain & Manchester, 2001; Manchester et al., 2007; Burge & Manchester, 2008; Wang et al., 2013; Zhang et al., 2013; Chen & Manchester, 2015; Jia et al., 2015; Han et al., 2018). Therefore, the results in the dynamic of flora on the Menispermaceae and other families are very congruent with what we found in the Icacinaceae family.

Conclusion

Among the 183 occurrences previously described as Icacinaceae, only 92 were accepted as belonging to this family in this study and are mainly from endocarp remains. The minimum age of the Icacinaceae family is probably the Upper Maastrichtian given by the fossil record for the Icacinaceae family. With the accepted samplings, we show an increase of the species richness during the Paleocene, probably due to the increase of temperature during the Thanetian. A great increase of diversity in term of genera, species, and morphology is shown through the Paleocene-Eocene boundary and during the Ypresian. Exchanges were shown between North America and Europe during the PETM in both ways. This is during the middle and late Eocene that most of the modern genera appear in the fossil record as *Natsiatum*, *Phytocrene*, and *Pyrenacantha*. Finally, the cooling period during the Oligocene, less favourable to climbers, could explain the decrease in the diversity of the Icacinaceae in the fossil record. We show the same pattern of diversification and regression in other megathermal families (Menispermaceae, Vitaceae…) showing a global dynamic of the North Hemisphere forest (boreotropical sensu. Wolfe, 1975) during the Paleogene.

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Author Contributions

DDF designed the project, CDR did the references work, CDR & DDF wrote the manuscript and the discussion part.

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866

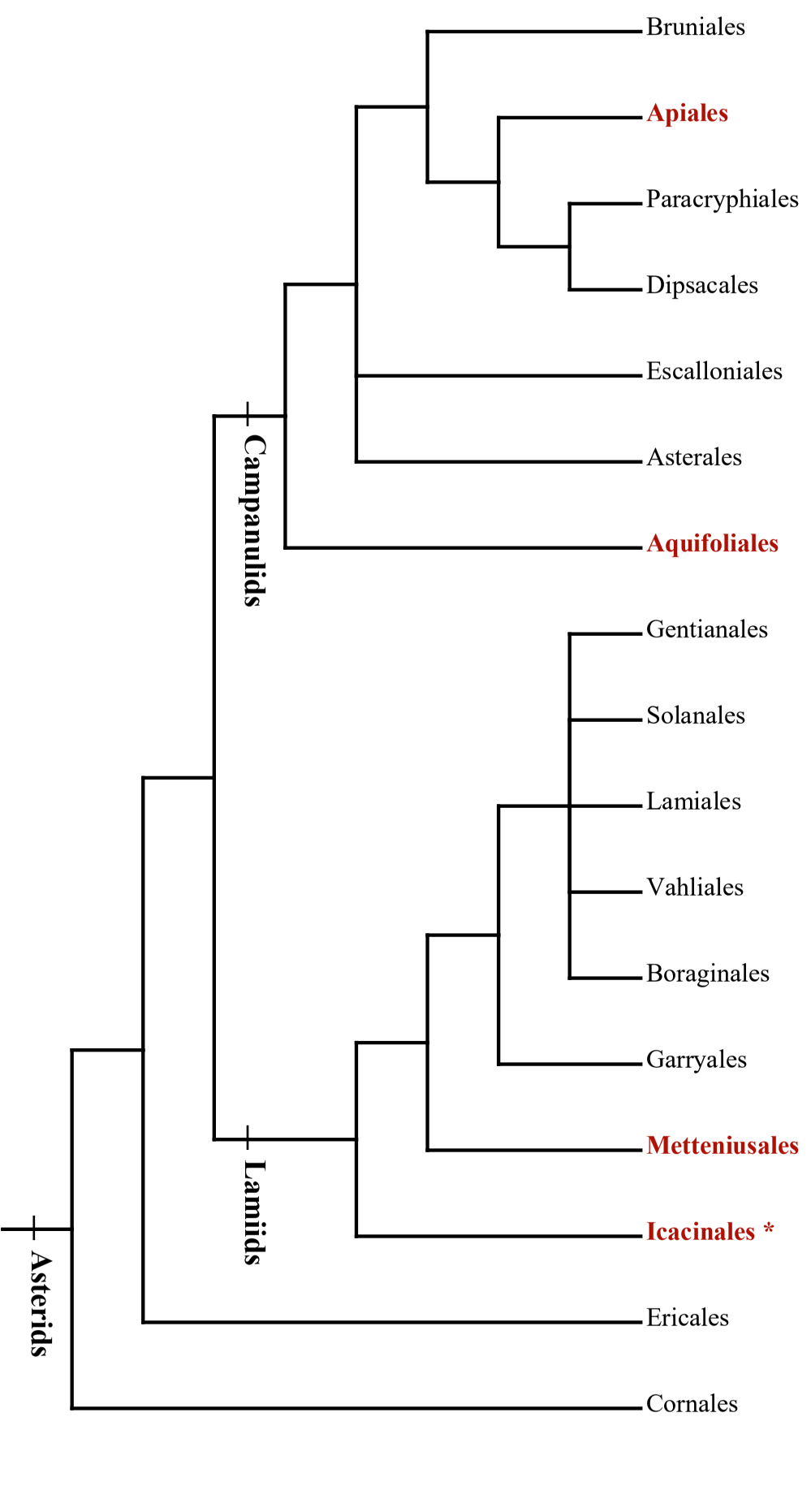
867 **Figure caption**

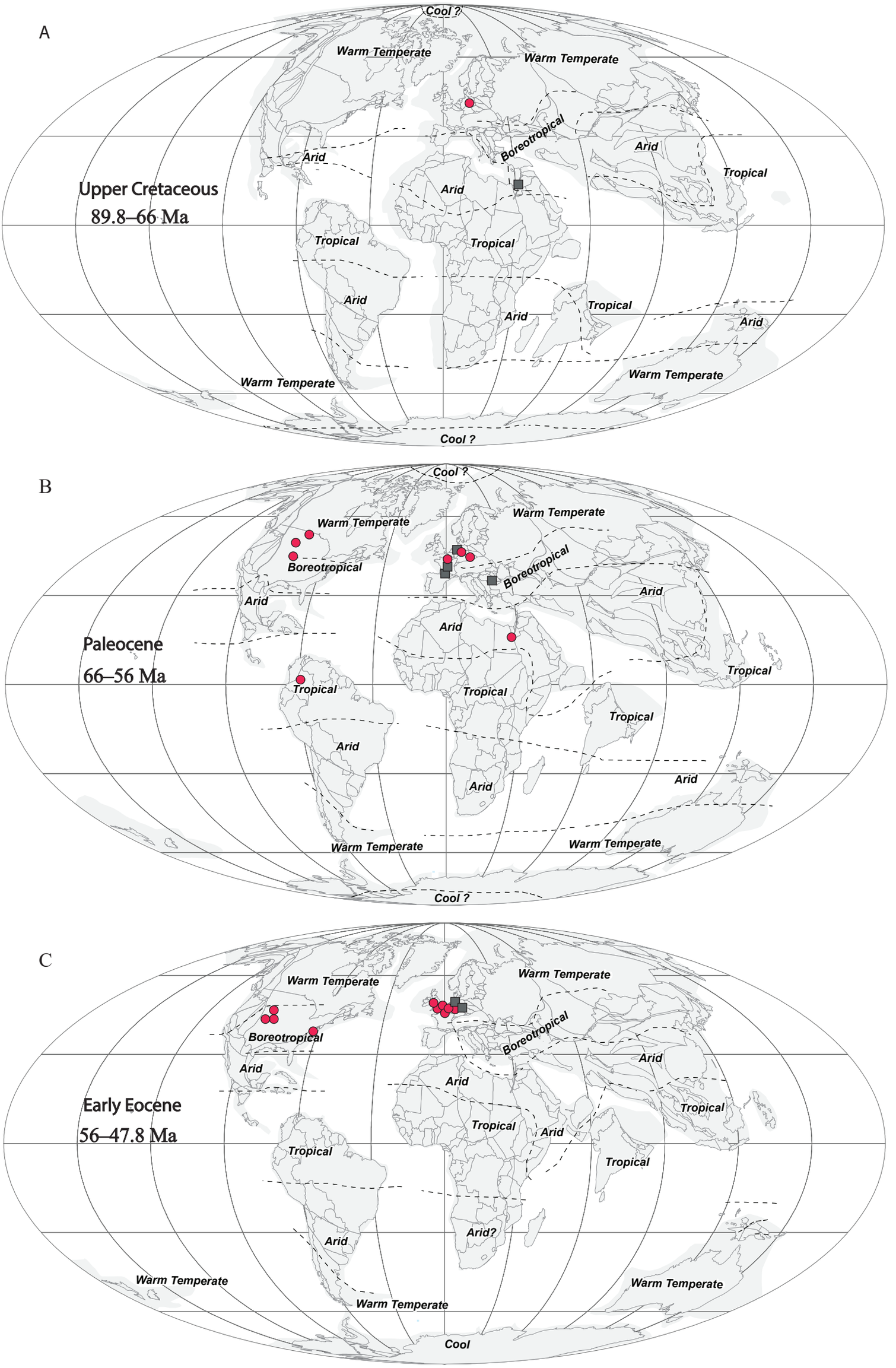
868

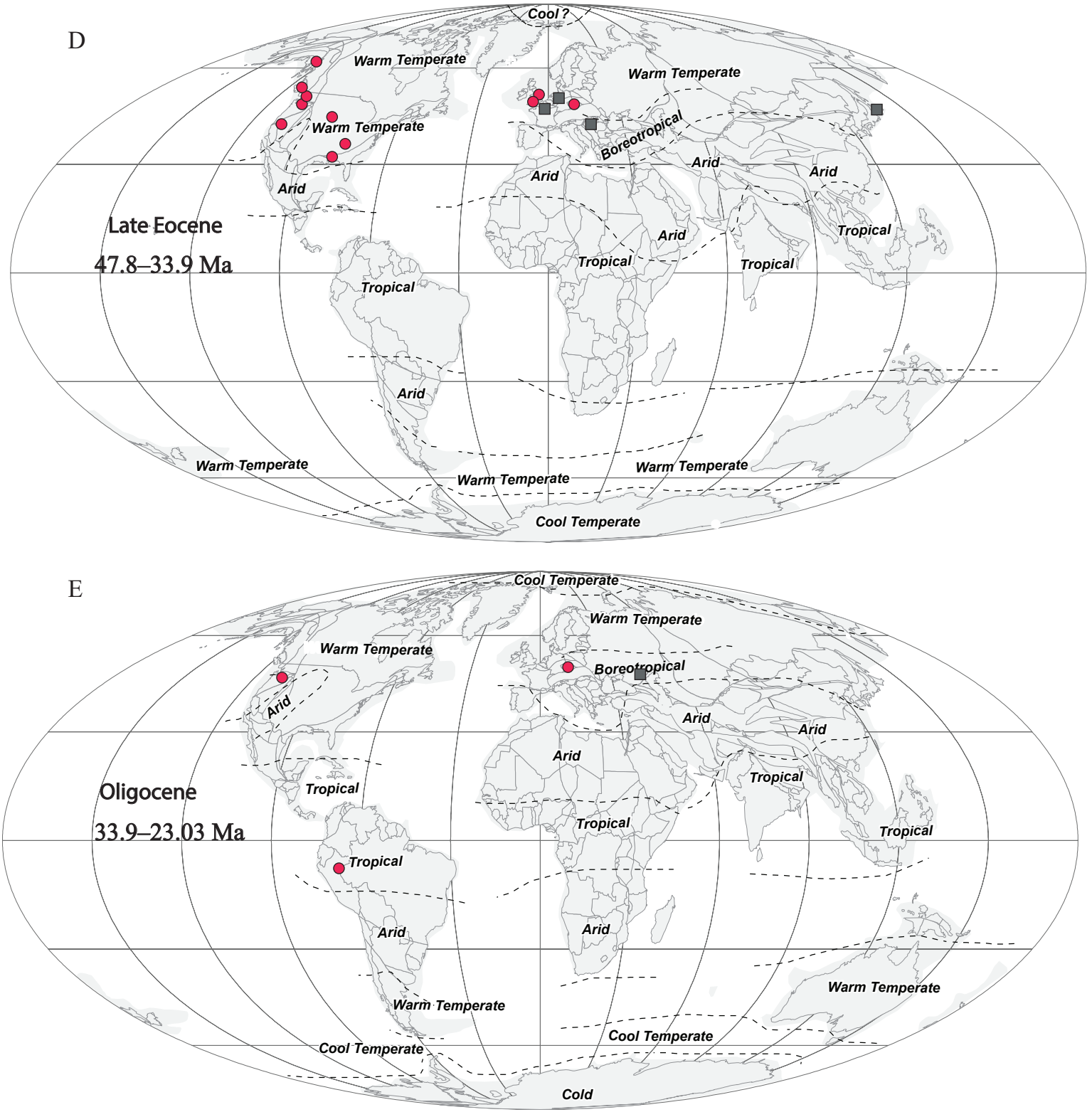
869 **Figure 1.** Phylogeny of Asterids following APG IV. In red: Position of the genera of
870 Icacinaceae s.l. (Sleumer, 1942). The asterix indicates the emplacement of the Icacinaceae s.s.
871 as circumscribed by Stull et al. (2015).

872 **Figure 2.** Paleomaps showing the distribution of the Icacinaceae family in the fossil record.
873 (A) Upper Cretaceous, (B) Paleocene, (C) early Eocene, (D) middle-late Eocene and (E)
874 Oligocene. Red dots: accepted occurrence; grey squares: dubious occurrence. Paleomaps
875 modified from Boucot et al., 2013.

876 **Figure 3.** Diversity of Icacinaceae (A) Number of genera by ages, (B) Number of species by
877 ages, (C) Number of *Iodes* species by ages. C: Cretaceous, P: Paleocene, E: Eocene, O:
878 Oligocene.


Bruniales
Apiales
Paracryphiales
Dipsacales
Escalloniales
Asterales
Aquifoliales
Gentianales
Solanales
Lamiales
Vahliales
Boraginales
Garryales
Metteniusales
Icacinales *
Ericales
Cornales
Campanulids
Lamiids
Asterids


A
Upper Cretaceous
89.8–66 Ma
Cool ?
Warm Temperate
Warm Temperate
Boreotropical
Arid
Arid
Arid
Tropical
Tropical
Tropical
Arid
Arid
Tropical
Arid
Warm Temperate
Warm Temperate
Cool ?
B
Paleocene
66–56 Ma
Cool ?
Warm Temperate
Warm Temperate
Boreotropical
Boreotropical
Arid
Arid
Arid
Tropical
Tropical
Tropical
Tropical
Arid
Arid
Arid
Warm Temperate
Warm Temperate
Cool ?
C
Early Eocene
56–47.8 Ma
Warm Temperate
Warm Temperate
Boreotropical
Boreotropical
Arid
Arid
Arid
Tropical
Tropical
Arid
Tropical
Tropical
Arid?
Arid
Warm Temperate
Warm Temperate
Warm Temperate
Cool


D
Cool ?
Warm Temperate
Warm Temperate
Warm Temperate
Boreotropical
Arid
Arid
Arid
Arid
Arid
Tropical
Tropical
Tropical
Tropical
Late Eocene
47.8–33.9 Ma
Arid
Warm Temperate
Warm Temperate
Warm Temperate
Cool Temperate
E
Cool Temperate
Warm Temperate
Warm Temperate
Boreotropical
Arid
Arid
Arid
Tropical
Tropical
Tropical
Tropical
Tropical
Oligocene
33.9–23.03 Ma
Arid
Arid
Warm Temperate
Warm Temperate
Cool Temperate
Cool Temperate
Cold

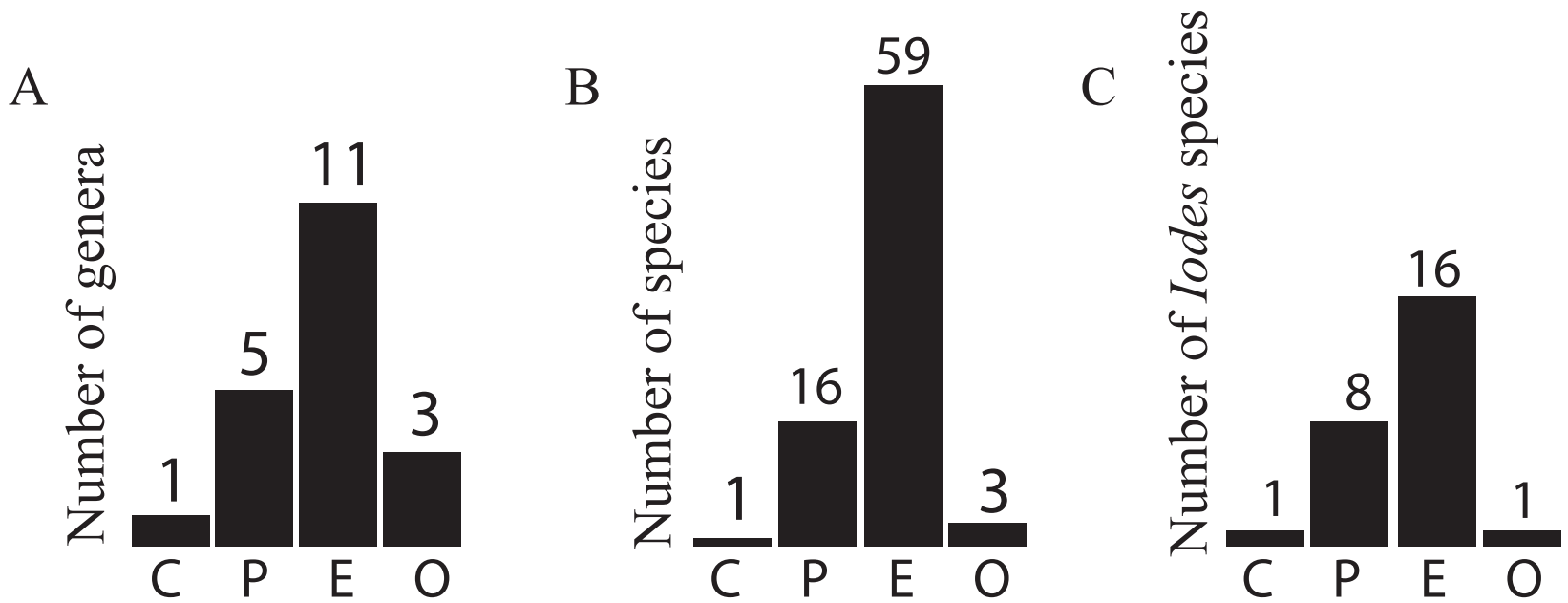

A
Number of genera
1
5
11
3
C
P
E
O
B
Number of species
1
16
59
3
C
P
E
O
C
Number of *Iodes* species
1
8
16
1
C
P
E
O

TABLE 1. Occurrencces of Icacinaceae fossils in the fossil record.

Species name	Organ	Occurrence (locality)	Country	Minimum Age	Series	Stage	Status	References
Comicilabium atkinsii Manchester	Endocarp	Clarno Nut Beds (OR)	USA	43	Eocene	Lutetian	Dubious	Manchester, 1994
Croomiocarpon missippiensis Stull, Manchester et Moore	Endocarp	Tallahatta Fm., Claiborne Group (MI)	USA	37	Eocene	Early-Middle	Accepted	Stull et al., 2011
Faboidea crassicutis Bowerbank	Endocarp	Herne bay, Sheppey, London Clay	United Kingdom	≈ 51– 47,8	Eocene	Ypresian	Accepted	Bowerbank, 1840; Reid & Chandler, 1933
Hosiea pterojugata Mai	Endocarp	Gonna, Abschnitt IV, graue Tone	Germany	56	Paleocene	Upper	Accepted	Mai 1987
Icacinicarya mucronata Chandler	Endocarp	Bognor, London Clay	United Kingdom	47.8	Eocene	Ypresian	Dubious	Chandler, 1961b; Cleal et al., 2001
Icacinicarya amygdaloidea Chandler	Endocarp	Herne Bay, London Clay	United Kingdom	≈ 51	Eocene	Ypresian	Rejected	Chandler, 1961b; Collinson, 1983; Cleal et al., 2001
Icacinicarya bartonensis Chandler	Endocarp	Headon bed, London Clay	United Kingdom	41.3	Eocene	Lutetian	Accepted	Chandler, 1961a
Icacinicarya becktonensis Chandler	Endocarp	Hordle Cliffs, London Clay	United Kingdom	37.8	Eocene	Bartonian	Accepted	Chandler, 1961b
Icacinicarya bognorensis Reid and Chandler	Endocarp	Bognor, London Clay	United Kingdom	47.8	Eocene	Ypresian	Dubious	Reid & Chandler 1933; Cleal et al., 2001
Icacinicarya budvarensis Knobloch and Mai	Endocarp	České Bude`jovice Budvar	Germany	83.6	Cretaceous	Santonian	Rejected	Knobloch & Mai, 1986
Icacinicarya collinsonae Pigg, Manchester et Devore	Endocarp	Almont (ND)	USA	56.8	Paleocene	Tiffanian Ti3	Accepted	Pigg et al., 2008
Icacinicarya davisii (Chandler) Stull, Adams, Manchester et Collinson	Endocarp	Suffolk, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Chandler, 1961b; Collinson, 1983
Icacinicarya densipunctata Collinson, Manchester et Wilde	Endocarp	Messel biota	Germany	≈ 47	Eocene	Lutetian	Accepted	Collinson et al., 2012
Icacinicarya dictyota Pigg, Manchester et Devore	Endocarp	Beicegel (ND)	USA	56.8	Paleocene	Tiffanian Ti3	Accepted	Pigg et al., 2008
Icacinicarya elegans (Bowerbank) Reid and Chandler	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933; Cleal et al., 2001
Icacinicarya emarginata Chandler	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Chandler, 1961b; Cleal et al., 2001
Icacinicarya forbesii Chandler	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Chandler, 1961b; Collinson, 1983; Cleal et al., 2001
Icacinicarya foveolata Reid and Chandler	Endocarp	Herne Bay, Sheppey, London Clay	United Kingdom	≈ 51–47,8	Eocene	Ypresian	Dubious	Reid & Chandler, 1933; Collinson, 1983; Cleal et al., 2001
Icacinicarya glabra Chandler	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Chandler 1961,Cleal et al. 2001
Icacinicarya inornata Chandler	Endocarp	Lake, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Chandler, 1962; Cleal et al., 2001
Icacinicarya jenkinsi Reid and Chandler	Endocarp	Herne Bay, London Clay	United Kingdom	≈ 51	Eocene	Ypresian	Accepted	Reid & Chandler, 1933; Cleal et al., 2001
Icacinicarya minima Reid and Chandler	Endocarp	Bognor, Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933; Collinson, 1983; Cleal et al., 2001
Icacinicarya nodulifera Reid and Chandler	Endocarp	Herne Bay, Sheppey, London Clay	United Kingdom	≈ 51–47,8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933; Collinson, 1983; Cleal et al., 2001
Icacinicarya ovalis Ried and Chandler	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933
Icacinicarya ovoidea Reid and Chandler	Endocarp	Herne Bay, Sheppey, London Clay	United Kingdom	≈ 51–47,8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933; Cleal et al., 2001
Icacinicarya papillaris Knobloch and Mai	Endocarp	Eisleben	Germany	66	Cretaceous	Maastrichian	Dubious	Knobloch & Mai, 1986
Icacinicarya platycarpa Reid and Chandler	Endocarp	Herne Bay, Bognor, Sheppey, London Clay	United Kingdom	≈ 51–47,8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933; Chandler 1978; Collinson, 1983;
Icacinicarya pygmaea Chandler	Endocarp	Headon beds, London Clay	United Kingdom	41.3	Eocene	Lutetian	Accepted	Chandler, 1961a ; Cleal et al., 2001
Icacinicarya reticulata Chandler	Endocarp	Herne Bay, Bognor, London Clay	United Kingdom	≈ 51–47,8	Eocene	Ypresian	Accepted	Chandler, 1961b; Collinson, 1983; Cleal et al., 2001
Icacinicarya rotundata (Bowerbank) Reid and Chandler	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Dubious	Reid & Chandler, 1933; Cleal et al., 2001
Icacinicarya sp.	Endocarp	Igala Division, Kabba Province	Nigeria	66?	Cretaceous?	Maastrichian?	Rejected	Chesters, 1955
Icacinicarya sp11	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Dubious	Reid & Chandler, 1933
Icacinicarya sp12	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933
Icacinicarya youssefi Chandler	Endocarp	Gebel Atshai and Kosseir Area, Red Sea	Egypt	61.6	Paleocene	Danian	Accepted	Chandler, 1954
Icacinicaryites corruga (Brown) Pigg, Manchester et Devore	Endocarp	Almy, Animas FM., Coalmont, Ferris, Fort Union (CO)	USA	56	Paleocene	?	Dubious	Brown, 1962; Pigg et al., 2008
Icacinicaryites israelii (Soudry & Gregor) Del Rio, Thomas & De Franceschi	Endocarp	Har Nishpeh area, central Negev	Israel	about 72,1	Cretaceous	Early Maastrichtian	Dubious	Soudry & Gregor, 1997
Icacinicaryites linchensis Pigg, Manchester et Devore	Endocarp	Linch, Sand Draw (WY), Animas Fm. (CO)	USA	56	Paleocene	Thanetian	Accepted	Pigg et al., 2008
Icacinicaryites lottii Stull, S.E. Allen, & Manchester	Endocarp	Kinsinger Lakes (WY)	USA	48.5	Eocene	Ypresian	Accepted	Allen et al., 2015
Icacinicarytes sp.	Endocarp	Prémontré	France	49	Eocene	Cuisian Sup.	Accepted	Del Rio & De Franceschi in prep.
Iodes acuta Del Rio & De Franceschi	Endocarp	Le Quesnoy, Oise	France	55-56	Eocene	Basal sparnatian	Accepted	Del Rio et al., 2019b
Iodes acutiformis Chandler	Endocarp	Lake, Arne, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Chandler, 1962; Cleal et al., 2001
Iodes bilinica (Ettingshausen) Stull, Adams, Manchester et Collinson	Endocarp	Messel biota	Gremany	≈ 47	Eocene	Lutetian	Accepted	Collinson, 2012
Iodes bilinica (Ettingshausen) Stull, Adams, Manchester et Collinson	Endocarp	Bohemia	Czech Republic	33.9	Eocene	Upper	Accepted	Kvacek & Buzek, 1995
Iodes bilinica (Ettingshausen) Stull, Adams, Manchester et Collinson	Endocarp	Hordle Cliffs, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Von Ettingshausen, 1866; Chandler, 1925; Takhtajan, 1966; Kvacek & Buzek, 1995
Iodes brownii (Berry) Stull, Adams, Manchester et Collinson	Endocarp	Tipperary flora (WY), Kisinger Lakes (WY), Blue Rim (WY), Bonanza (UT),	USA	49,5 – 43,0	Eocene	End Ypresian - Lutetian	Accepted	Manchester, 1994; Allen et al., 2015; Stull et al., 2016
Iodes chandlerae Manchester	Endocarp	Clarno Nut Beds (OR)	USA	43	Eocene	Lutetian	Accepted	Manchester, 1994
Iodes corniculata Reid and Chandler	Endocarp	Herne bay, Sheppey, London Clay	United Kingdom	≈ 51–47,8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933; Chandler 1978; Collinson, 1983; Cleal et al., 2001
Iodes eocenica Reid and Chandler	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933; Chandler 1964; Cleal et al., 2001
Iodes germanica Knobloch and Mai	Endocarp	Eisleben	Germany	66	Cretaceous	Maastrichtian	Accepted	Knobloch & Mai, 1986; Mai, 1987
Iodes germanica Knobloch and Mai	Endocarp	Gonna	Germany	56	Paleocene	Upper	Accepted	Mai, 1987
Iodes hordwellensis ? Chandler	Endocarp	Hordle Cliffs, London Clay	United Kingdom	37.8	Eocene	Bartonian	Accepted	Chandler, 1961b
Iodes multireticulata Reid and Chandler	Endocarp	Sheppey, Herne bay, London Clay	United Kingdom	≈ 51–47,8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933; Cleal et al., 2001
Iodes multireticulata Reid and Chandler	Endocarp	Clarno Nut Beds (OR)	USA	43	Eocene	Lutetian	Accepted	Manchester, 1994
Iodes multireticulata Reid and Chandler	Endocarp	Fisher/Sullivan Site (VI)	USA	55.5	Eocene	Early	Accepted	Tiffney, 1999
Iodes occidentalis S.E. Allen, Stull, & Manchester	Endocarp	Blue Rim (WY)	USA	49.5	Eocene	Ypresian	Accepted	Allen et al., 2015
Iodes parva Del Rio, Thomas & De Franceschi	Endocarp	Petit Pâtis, Rivecourt, Oise	France	57-56	Paleocene	Thanetian	Accepted	Del Rio et al., 2019a
Iodes parva Del Rio, Thomas & De Franceschi	Endocarp	Le Quesnoy, Oise	France	55-56	Eocene	Basal sparnatian	Accepted	Del Rio et al., 2019b
Iodes sp. nov.	Endocarp	Passy	France	about 55	Eocene	Middle sparnatian	Accepted	Del Rio & De Franceschi in prep.
Iodes reidii Del Rio, Thomas & De Franceschi	Endocarp	Petit Pâtis, Rivecourt, Oise	France	57-56	Paleocene	Thanetian	Accepted	Del Rio et al., 2019a
Iodes reidii Del Rio, Thomas & De Franceschi	Endocarp	Passy	France	about 55	Eocene	middle sparnatian	Accepted	Del Rio & De Franceschi in prep.
Iodes rigida Del Rio & De Franceschi	Endocarp	Le Quesnoy, Oise	France	55-56	Eocene	Basal sparnatian	Accepted	Del Rio et al., 2019b
Iodes rivecourtensis Del Rio, Thomas & De Franceschi	Endocarp	Petit Pâtis, Rivecourt, Oise	France	57-56	Paleocene	Thanetian	Accepted	Del Rio et al., 2019a
Iodes rivecourtensis Del Rio, Thomas & De Franceschi	Endocarp	Petit Pâtis, Rivecourt, Oise	France	57-56	Paleocene	Thanetian	Accepted	Del Rio et al., 2019a
Iodes sinuosa Del Rio, Thomas & De Franceschi	Endocarp	Petit Pâtis, Rivecourt	France	57-56	Paleocene	Thanetian	Accepted	Del Rio et al., 2019a
Iodes sp.	Endocarp	Chuckanut Formation (WA)	USA	33.9	Eocene	"Late"	Accepted	Pigg & Wehr, 2002
Iodes sp.	Endocarp	Bognor, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Chandler, 1961b
Iodes sp.	Endocarp	Grès de Belleu	France	49	Eocene	Cuisian Sup.	Accepted	Del Rio & De Franceschi in prep.
Iodes sp.	Endocarp	Dormaal	Belgium	55	Eocene	Ypresian	Accepted	Fairon-Demaret & Smith, 2002
Iodes tubulifera Del Rio, Thomas & De Franceschi	Endocarp	Petit Pâtis, Rivecourt, Oise	France	57-56	Paleocene	Thanetian	Accepted	Del Rio et al., 2019a
Iodes tubulifera Del Rio, Thomas & De Franceschi	Endocarp	Passy	France	about 55	Eocene	middle sparnatian	Accepted	Del Rio & De Franceschi in prep.
Iodicarpa ampla Manchester	Endocarp	Clarno Nut Beds (OR)	USA	43	Eocene	Lutetian	Accepted	Manchester, 1994
Iodicarpa lenticularis Manchester	Endocarp	Clarno Nut Beds (OR)	USA	43	Eocene	Lutetian	Accepted	Manchester, 1994
Natsiatum wilcoxiana (Bery) Stull, Moore & Manchester	Endocarp	Fayette County, Wilbanks II Clay Pits (TE)	USA	37.8	Eocene	Middle	Accepted	Stull et al., 2011
(cf) Natsiatum wilcoxiana (Bery) Stull, Moore & Manchester	Endocarp	Tallahatta Fm., Claiborne Group (MI)	USA	37	Eocene	Early	Dubious	Blanchard et al., 2016
Palaeohosiea marchiaca (Mai) Kvacek & Buzek	Endocarp	Bohemia	Czech Republic	59.2	Paleocene	Middle	Accepted	Mai, 1987; Kvacek & Buzek 1995
Palaeohosiea marchiaca (Mai) Kvacek & Buzek	Endocarp	Shepey, Bognor, London Clay	United Kingdom	47.8	Eocene	Lower	Accepted	Kvacek & Buzek, 1995
Palaeohosiea suleticensis (Mai) Kvacek & Buzek	Endocarp	Suletice, Bohemia	Czech Republic	28.1	Oligocene	Lower	Accepted	Kvacek & Buzek ,1995
Palaeophytocrene ambigua Reid and Chandler	Endocarp	Bognor, Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Read & Chandler, 1933
Palaeophytocrene foveolata Reid and Chandler	Endocarp	Herne Bay, Bognor, Sheppey, London Clay	United Kingdom	≈ 51–47,8	Eocene	Ypresian	Accepted	Read & Chandler, 1933
Palaeophytocrene foveolata var. minima Reid and Chandler	Endocarp	Herne Bay, Bognor, Sheppey, London Clay	United Kingdom	≈ 51–47,8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933
Palaeophytocrene hammenii Stull	Endocarp	Bogota fm. Checua clay pit	Colombia	58	Paleocene	Middle-Late	Accepted	Stull et al., 2012
Palaeophytocrene hancockii (Scott) Manchester	Endocarp	Clarno Nut Beds (OR)	USA	43	Eocene	Lutetian	Accepted	Scott, 1954; Manchester, 1994
Palaeophytocrene lacunosum (MacGinitie) Wolfe	Endocarp	Independence Hill (SN)	USA	37.8	Eocene	Middle	Accepted	MacGinitie, 1941; MacGinitie, 1969
Palaeophytocrene kressenbergensis (Schafhäutl)	Endocarp	St, Pankraz, Bavaria	Germany	33.9-56	Eocene		Accepted	Tichy, 1979
Palaeophytocrene manchesteri Rankin, Stockey et Beard	Endocarp	Vancouver island	Canada	33.9	Eocene	?	Accepted	Rankin et al., 2008
Palaeophytocrene pseudopersica Scott emend Manchester	Endocarp	Clarno Nut Beds (OR)	USA	43	Eocene	Lutetian	Accepted	Scott, 1954; Manchester, 1994
Palaeophytocrene sp.	Endocarp	Ronald, Kittitas County (WA)	USA	33.9	Eocene	Late	Accepted	Pigg & Wehr, 2002
Palaeophytocrene sp.	Endocarp	Almont (ND)	USA	56	Paleocene		Accepted	Crane et al., 1990
Palaeophytocrene sp.	Endocarp	John Day Formation (Or)	USA	32,2-33,6	Oligocene		Accepted	Meyer & Manchester, 1997
Palaeophytocrene sp.	Endocarp	St, Pankraz, Bavaria	Germany	33.9-56	Eocene		Accepted	Tichy, 1979
Paleophytocrene sp.	Endocarp	Grès de Belleu	France	49	Eocene	Cuisian Sup.	Accepted	Del Rio & De Franceschi in prep.
Palaeophytocrene vancouverensis Rankin, Stockey et Beard	Endocarp	Vancouver island	Canada	33.9	Eocene	?	Accepted	Rankin et al., 2008
Paleophytocrene elytraeformis (Holl.) Wolfe	Endocarp	Yakutat Frm.	Alaska	33.9	Eocene	Middle-Late	Accepted	Wolfe, 1977; Hollick, 1936; Heer, 1870
Perforatocarpum echinatum (Chandler) Stull, Adams, Manchester et Collinson	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Chandler, 1961b; Cleal et al., 2001; Stull et al., 2016
Phytocrene densipunctata Stull, Moore et Manchester	Endocarp	Wilbanks II Clay Pits (TE)	USA	37.8	Eocene	Bartonian	Accepted	Stull et al., 2011
Phytocrene microcarpa Scott & Barghoorn	Endocarp	Androvette Pit, Kreischerville (NY)	USA	66	Cretaceous	Early-Late	Rejected	Scott & Barghoorn, 1957
Phytocrene punctilinearis Collinson, Manchestet et Wilde	Endocarp	Messel biota	Gremany	≈ 47	Eocene	Lutetian	Accepted	Collinson, 2012
Cf. Phytocrene sp.	Endocarp	Guajira peninsula	Colombia	58	Paleocene	Thanetian	Accepted	Stull et al., 2012
Pyrenacantha austroamericana Stull	Endocarp	Belen flora	Peru	28.5	Oligocene	Late early	Accepted	Stull et al., 2012
Pyrenacantha occidentalis Manchester	Endocarp	Clarno Nut Beds (OR)	USA	43	Eocene	Lutetian	Accepted	Manchester, 1994
Pyrenacantha sp. 1	Endocarp	Messel biota	Germany	≈ 47	Eocene	Lutetian	Accepted	Collinson et al., 2012
Pyrenacantha sp. 2	Endocarp	Messel biota	Germany	≈ 47	Eocene	Lutetian	Accepted	Collinson et al., 2012
Sphaeriodes ventricosa (Bowerbank) Reid and Chandler	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933
Stizocarya communis Reid and Chandler	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933
Stizocarya oviformis Reid and Chandler	Endocarp	Sheppey, London Clay	United Kingdom	47.8	Eocene	Ypresian	Accepted	Reid & Chandler, 1933
Icacinanthium tainiaphorum Del Rio & De Franceschi	Flower	Le Quesnoy, Oise	France	55-56	Eocene	Basal sparnatian	Accepted	Del Rio et al., 2017
Goweria alaskana Wolfe	Leaf	Kushtaka Frm.	Alaska	33.9	Eocene	Middle-Late	Dubious	Wolfe, 1977
Goweria bibaiensis Tanai	Leaf	Okuno-sawa, Bibai, Hokkaido	Japan	≈ 46	Eocene	Middle	Dubious	Tanai, 1990
Goweria bluerimensis S.E. Allen, Stull, & Manchester	Leaf	Blue Rim (WY)	USA	49.5	Eocene	Ypresian	Dubious	Allen et al., 2015
Goweria dilleri (Knowlton) Wolfe	Leaf	Kushtaka Frm.	Alaska	33.9	Eocene	Middle-Late	Dubious	Wolfe, 1968; Wolfe 1977
Goweria linearis Wolfe	Leaf	Green river (WY)	USA	37.8?	Eocene	Middle?	Dubious	Wolfe, 1968
Huziokaeae eoutilus (Endo) Tanai	Leaf	Am-site,Shimizusawa,Yubari, Hokkaido	Japan	≈ 40	Eocene	Middle	Rejected	Tanai, 1990
Merrilliodendron ezoanum Tanai	Leaf	Am-site,Shimizusawa,Yubari, Hokkaido	Japan	≈ 40	Eocene	Middle	Dubious	Tanai, 1990
Phytocrene acutissima Wolfe	Leaf	Kushtaka Frm.	Alaska	33.9	Eocene	Middle-Late	Dubious	Wolfe, 1977
Phytocrene ozakii Tanai	Leaf	Reisui-zan,Yubari, Hokkaido	Japan	≈ 40	Eocene	Middle	Dubious	Tanai, 1990
Phytocrene sordida (Lesuereux.) MacGinitie	Leaf	Kulthieth Frm.	Alaska	33.9	Eocene	Middle-Late	Dubious	Wolfe, 1977
Phytocrene sordida (Lesuereux.) MacGinitie	Leaf	Chalk Bluffs, Buckeye Flat, Independence hill (SN)	USA	37.8	Eocene	Middle	Dubious	Macginitie, 1941
Pyrenacantha sp.	Leaf	Kulthieth Frm.	Alaska	33.9	Eocene	Middle-Late	Dubious	Wolfe, 1977
Pyrenacantha sp.	Leaf	Ishikari coal field Ic-9	Japan	≈ 40	Eocene	Middle	Dubious	Tanai, 1990
Compositoipollenites medius Krutzch & Vanhoorne 1977	Pollen	Houdancourt	France	56	Eocene	Ypresian	Dubious	Cavagnetto, 2000
Compositoipollenites medius Krutzch & Vanhoorne 1977	Pollen	Epinois	Belgium	56	Eocene	Ypresian	Dubious	Krutzsch & Vanhoorne, 1977
Compositoipollenites microechinatus Kruttzch & Vanhoorne 1977	Pollen	Epinois	Belgium	56	Eocene	Ypresian	Dubious	Krutzsch & Vanhoorne, 1977
Compositoipollenites minimus Krutzch & Vanhoorne 1977	Pollen	Houdancourt	France	56	Eocene	Ypresian	Dubious	Cavagnetto, 2000
Compositoipollenites minimus Krutzch & Vanhoorne 1977	Pollen	Epinois	Belgium	56	Eocene	Ypresian	Dubious	Krutzsch & Vanhoorne, 1977
Compositoipollenites minimus Krutzch & Vanhoorne 1977	Pollen	Messel	Germany	≈ 47	Eocene	Middle	Dubious	Thiele-Pfeiffer, 1988; Lenz et al., 2007
Compositoipollenites minimus Krutzch & Vanhoorne 1977	Pollen	Petite Pyrénées	France	61.6	Paleocene	Danian	Dubious	Guas-Cavagnetto et al., 1992
Compositoipollenites minimus Krutzch & Vanhoorne 1977	Pollen	Nointel	France	53	Eocene	Sparnacian sup.	Dubious	Kedves, 1970
Compositoipollenites minimus Krutzch & Vanhoorne 1977	Pollen	Menat	France	59.2	Paleocene	Selandian	Dubious	Kedves & Russel, 1982 (for the datation Mélanie Tanrattana com. pers.)
Compositoipollenites rhizophorus burghasungensis (Murriger & Pflug 1952) Thomson & Pflug 1949	Pollen	Houdancourt	France	56	Eocene	Ypresian	Dubious	Cavagnetto, 2000
Compositoipollenites rhizophorus burghasungensis (Murriger & Pflug 1952) Thomson & Pflug 1950	Pollen	Borkener	Germany	58-33,9	Paleocene-Eoc	Thanecian-Priabonian	Dubious	Thomson & Pflug, 1953
Compositoipollenites rhizophorus burghasungensis (Murriger & Pflug 1952) Thomson & Pflug 1951	Pollen	Central Anatolia	Turkey	33.9	Oligocene	inf.	Dubious	Akkiraz & Akgun, 2005
Compositoipollenites rhizophorus burghasungensis (Murriger & Pflug 1952) Thomson & Pflug 1952	Pollen	Messel biota	Germany	≈ 47	Eocene	Middle	Dubious	Lenz et al., 2007
Compositoipollenites rhizophorus burghasungensis (Murriger & Pflug 1952) Thomson & Pflug 1953	Pollen	Saint-Lege-en-Bois, Guitrancourt	France	56-53	Paleocene	Sparnacian	Dubious	Kedves, 1970; Kedves & Pardutz 1970
Compositoipollenites rhizophorus (R. Potonié 1934) R. Potonié 1960	Pollen	Houdancourt	France	56	Eocene	Ypresian	Dubious	Potonié, 1960; Cavagnetto, 2000
Compositoipollenites rhizophorus (R. Potonié 1934) R. Potonié 1960	Pollen	Salaj District, Jibou	Romania	58	Paleocene	Thanetian	Dubious	Petrescu & Codrea, 2004
Compositoipollenites rhizophorus (R. Potonié 1934) R. Potonié 1960	Pollen	Merseburg	Germany	56	Eocene	Ypresian	Dubious	Hofmann et al., 2011
Compositoipollenites rhizophorus (R. Potonié 1934) R. Potonié 1960	Pollen	Weißelster	Germany	33.9	Eocene	Upper	Dubious	Knobloch & Konzalova, 1998
Compositoipollenites rhizophorus (R. Potonié 1934) R. Potonié 1960	Pollen	Bracklesham Beds, Surrey	United Kingdom	41.2	Eocene	Ypresian-Lutetian	Dubious	Potter, 1977
Compositoipollenites rhizophorus (R. Potonié 1934) R. Potonié 1960	Pollen	Buda Marl	Hungary	33.9	Eocene	?	Dubious	Kedves & Endredi, 1968
Compositoipollenites rhizophorus (R. Potonié 1934) R. Potonié 1960	Pollen	Saint-Leger-en-Bois	France	56	Eocene	Sparnacian	Dubious	Kedves, 1970
Compositoipollenites rhizophorus (R. Potonié 1934) R. Potonié 1960	Pollen	Paris Austerlitz	France	41.2	Eocene	Lutetan sup.	Dubious	Kedves, 1970
Compositoipollenites rhizophorus (R. Potonié 1934) R. Potonié 1960	Pollen	Borken, Kassel, Lower Hesse	Germany	47.8	Eocene	Middle	Dubious	Hofmann & Gregor, 2018
Echiperiporites icacinoides Samard-Cheboldaeff 1975	Pollen	Douala	Cameroon	5.33	Miocene	inférieur	Rejected	Salard-Cheboldaeff, 1975
Echiperiporites minor Samard-Cheboldaeff 1975	Pollen	Douala	Cameroon	5.33	Miocene	inférieur	Rejected	Salard-Cheboldaeff, 1975
Iodes type	Pollen	Wagon Bed Frm. (WY)	USA	46.2	Eocene	Bridgerian	Rejected	Leopold & Macginitie, 1972
Apodytoxylon hamamelidoides Grambast-Fessard	Wood	Castellane	France	5.3	Miocene	Sup.	Rejected	Grambast-Fessard, 1969
Icacinixylon kokubunii Takahashi & Suzuki	Wood	Rumoi County	Japan	100.5	Cretaceous	Albian	Rejected	Takashi & Suzuki, 2003
Icacinoxylon ?	Wood	Petit Pâtis, Rivecourt, Oise	France	57-56	Paleocene	Thanetian	Rejected	Personnal observation
Icacinoxylon alternipunctata Wheeler	Wood	Ilinois	USA	66	Cretaceous	Upper	Rejected	Wheeler et al., 1987
Icacinoxylon crystallophorum Greguss	Wood	Dorog	Hungrary	23.03	Oligocene		Rejected	Greguss, 1969
Icacinoxylon densiporosum Petrescu	Wood	Transilvania	Romania	28.1	Oligocene	Middle	Rejected	Petrescu, 1978
Icacinoxylon grambast-fessardi Petrescu & Dragastan	Wood	Telega-Prahova	Georgia	23.03	Oligocene	Upper	Rejected	Petrescu & Dragastan, 1972
Icacinoxylon hotobagyii Greguss	Wood	Balaton	Hungary	11.6	Miocene	Helvetian	Rejected	Greguss, 1969
Icacinoxylon laticiphorum Greguss	Wood	Dorog	Hungary	23.03	Oligocene		Rejected	Greguss, 1969
Icacinoxylon nishidae Takahashi & Suzuki	Wood	Rumoi County	Japan	89,8?	Cretaceous	Turonian?	Rejected	Takahashi & Suzuki, 2003

Accommodation Name	Type	Location	Rating	Price	Amenities	Contact
Accommodation 1	Hotel	City A	4.5	$100	Pool, Gym, Spa	123-456-7890
Accommodation 2	Resort	Beach Town	4.8	$200	Beach Access, Restaurant, Bar	987-654-3210
Accommodation 3	Apartment	Downtown	4.2	$150	Kitchen, Laundry, Parking	555-123-4567
Accommodation 4	Hostel	City B	3.9	$50	Shared Kitchen, Lockers, Wi-Fi	111-222-3333
Accommodation 5	Villa	Countryside	4.7	$300	Private Pool, Garden, BBQ	444-555-6666
Accommodation 6	Hotel	City C	4.3	$120	Gym, Restaurant, Bar	777-888-9999
Accommodation 7	Resort	Mountain Town	4.6	$250	Ski Access, Spa, Restaurant	222-333-4444
Accommodation 8	Apartment	Suburb	4.1	$130	Kitchen, Laundry, Parking	666-777-8888
Accommodation 9	Hostel	City D	3.8	$40	Shared Kitchen, Lockers, Wi-Fi	999-000-1111
Accommodation 10	Villa	Lakeside	4.9	$350	Private Pool, Garden, BBQ	333-444-5555
Accommodation 11	Hotel	City E	4.4	$110	Gym, Restaurant, Bar	888-999-0000
Accommodation 12	Resort	Island	4.7	$280	Beach Access, Spa, Restaurant	555-666-7777
Accommodation 13	Apartment	Uptown	4.0	$140	Kitchen, Laundry, Parking	111-222-3333
Accommodation 14	Hostel	City F	3.7	$45	Shared Kitchen, Lockers, Wi-Fi	444-555-6666
Accommodation 15	Villa	Countryside	4.8	$320	Private Pool, Garden, BBQ	777-888-9999
Accommodation 16	Hotel	City G	4.2	$105	Gym, Restaurant, Bar	222-333-4444
Accommodation 17	Resort	Mountain Town	4.5	$240	Ski Access, Spa, Restaurant	666-777-8888
Accommodation 18	Apartment	Suburb	4.3	$135	Kitchen, Laundry, Parking	999-000-1111
Accommodation 19	Hostel	City H	3.6	$35	Shared Kitchen, Lockers, Wi-Fi	333-444-5555
Accommodation 20	Villa	Lakeside	4.9	$360	Private Pool, Garden, BBQ	888-999-0000

TABLE 2. Number of species of extinct and modern Icacinaceae accepted genera in different epochs. *Palaeohosiea* , *Hosiea* and *Croomiocarpum* species are considered as part of *Iodes* .

Epoch	Number of species	Extinct genus	Modern genus
Oligocene	3	*Palaeophytocrene*	*Iodes* (*Palaeohosiea*) *Pyrenacantha*
Eocene	59	*Faboidea* *Icacinanthium* *Icacinicarya* *Iodicarpa (Iodes?)* *Palaeophytocrene* *Perforatocarpum* *Sphaeriodes* *Stizocarya*	*Iodes (Iodes, Croomiocarpum, Palaeohosiea*) *Natsiatum* *Phytocrene* *Pyrenacantha*
Paleocene	16	*Icacinicarya* *Icacinicarytes* *Palaeophytocrene*	*Iodes (Iodes, Palaeohosiea, Hosiea*) *Phytocrene* ?
Upper Cretaceous	1	Ø	*Iodes*