On the history of *Brasenia* Schreb. in the European Pleistocene

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Abstract *Brasenia* Schreb. is a monotypic genus in the Cabombaceae, present nowadays on all continents except Europe and Antarctica. This thermophilous aquatic plant, which originated in the Tertiary, was a frequent element of aquatic plant life during the interglacial stages of the European Pleistocene. A systematic review of the palaeobotanical records of *Brasenia* pollen and seeds reveals its history in Europe from the Plio-Pleistocene until the Eemian interglacial. Remains of *Brasenia* were typical for the climatic optima during each of these stages of the Pleistocene. In this paper the diversity of fossil *Brasenia* species is also shown. The most abundant and morphologically diverse seeds were found in sediments from eastern European sites. *Brasenia* species became extinct in Europe at the end of the last interglacial or at the beginning of the Weichselian glaciation. Different scenarios for their disappearance are proposed, including the specificity of the floral cycle, probable poor dispersal of seeds, or the scarcity of suitable water bodies for it to survive.

Keywords *Brasenia* · Europe · Pleistocene · Interglacial · Extinction of species

Introduction

Brasenia and *Cabomba* are rhizomatous aquatic perennials with floating leaf blades in the Cabombaceae family. These

two genera are similar to members of the Nymphaeaceae, where they were placed previously. There are many difficulties in defining families within the Nymphaeales. Therefore, their taxonomic affiliation has changed, as they were an object of interest for numerous authors (Goleniewska-Furmanowa 1970; Takhtajan 1980; Cronquist 1981). Nowadays, however, the position of the Cabombaceae as an independent family, which includes the genera *Cabomba* and *Brasenia*, is not questioned among taxonomists (Podoplelova and Ryzhakov 2005).

Both the Cabombaceae and Nymphaeaceae families (Nymphaeales; water lilies) are among the oldest angiosperms. Phylogenetic analyses have identified them, together with four other small groups of flowering plants (Amborellaceae, Illiciales, Trimeniaceae, Austrobaileyaceae, the ANITA grade), as the first diverging lineages from the main branch of the angiosperm phylogenetic tree. According to Friis et al. (2001), the earliest evidence of water lilies, based on fossil floral structures and associated pollen, extends their history back to the early Cretaceous (125–115 Ma). However, it is more likely that these records have not been clearly distinguished from Illiciales, in which case the oldest unequivocal record of the order is that of the water lily flower from the earliest Upper Cretaceous (approximately 90 Ma) (Gandolfo et al. 2004). Regarding the splitting of the Cabombaceae and Nymphaeaceae, there is substantial fossil evidence that the two families were distinct by the early Tertiary (Dorofeev 1973, 1974; Collinson 1980). According to Löhne et al. (2008), such diversification of the Nymphaeales into three major lineages, Cabombaceae, *Nuphar* and the other Nymphaeaceae, took place during the Palaeocene. The existence of Cabombaceae species was confirmed by well-documented data from the late Palaeocene-earliest Eocene, like fossils of *Brasenia*, *Sabrenia* (Collinson 1980), *Braseniella* and *Dusembaya* (Dorofeev 1973). Interestingly,

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according to the molecular data, the two extant genera of Cabombaceae, *Cabomba* and *Brasenia*, are thought to have diversified during the Oligocene (26.5 ± 13.1 Ma), with limits of confidence spanning from the Upper Eocene into the Middle Miocene (Löhne et al. 2008). However, the indisputable fossil evidence indicates that these genera must be older.

The genus *Brasenia* (water-shield) is today represented only by *B. schreberi* J. F. Gmel. [*B. purpurea* (Michx.) Casp.], an aquatic perennial growing in acidic (Muenscher 1944) or slightly acidic waters (Lakela 1965). It occurs in shallow lakes and ponds, as well as slow streams in eastern Asia (Taiwan, Japan, Korea, Sumatra, the Amur region in the Far East, at the foot of the Himalaya), Australia, islands of Oceania, Africa (Angola, Zambia), the West Indies, and South, Central and North America (Osborn and Schneider 1988). In this latter locality, *Brasenia* is widely represented, with a range from Alaska to California and from Nova Scotia to Florida (Środoń 1987).

Despite being a flexible taxon with a native range extending from tropical to nearly boreal habitats, this genus does not occur in Europe nowadays. It was different in the past, which is evidenced by fossil remains, which have been found in European Tertiary sediments. Well-documented *Brasenia* fossils are known from the Eocene (> 33 Ma) (Collinson 1980). In fact, *Brasenia* was a common element of European freshwater vegetation from the Eocene to the Pleistocene (Dorofeev 1984; Mai 1995). However, probably at the end of the Eemian stage, about 115 ka, it became extinct in Europe. As before, there is a lack of a wider data set of past sites where *Brasenia* has been found in Europe. Some data were included by Dorofeev (1984) and Löhne et al. (2008). Therefore, this paper is intended to be a comprehensive review of *Brasenia* records in the European Pleistocene, with an indication of the sites where *B. schreberi* has been found, as well as other extinct species of this genus. This paper is also an attempt to gather information about the reasons for the extinction of *Brasenia* in Europe, which happened at the end of the last interglacial or at the beginning of the last glaciation.

Pleistocene fossils of *Brasenia* in Europe

The fossil record of *Brasenia* in the European Pleistocene has been compiled from published sources specifying the sites from where the remains were recovered, species (if possible), types of remains, and the stage of Pleistocene used in the quoted paper (Table 1). In some cases, to make orientation easier, synonyms of the stage names are given (in parentheses). Figure 1 shows the location of the *Brasenia* fossil finds, with records of different ages indicated with different symbols. The names of the Pleistocene stages

were used by West (1968), Zagwijn (1996), Kondratienė (1996), Ber (2006), Lindner and Marks (2008), Molodkov and Bolikhovskaya (2010), Lindner et al. (2013), as well as Yakubovskaya et al. (2014). Correlation of these stages in different countries of Europe is given in Table 2.

Generally, fossil remains of *Brasenia* are known most of all from central and eastern parts of the European continent, and these are mostly Eemian sites (Fig. 1). The presence of this taxon in Pleistocene sediments is only sporadically recognised based on pollen grains (Table 1). In sediments of the Holsteinian interglacial pollen was identified from the Gort site in Ireland, as pollen of *Brasenia* cf. *schreberi* (Jessen et al. 1959) and from Krzyżewo, Poland (Ber et al. 1998). At the Valakampiai site in Lithuania, pollen of *B.* cf. *borysthena* was detected in sediments correlated with the Snaigupele (Kärlich, Lubavian) interglacial (Molodkov et al. 2002), whereas Eemian sites with pollen of *Brasenia* are known from Belgium (*B. schreberi* species) (Verbruggen 1999), Imbramowice in Poland (*B. schreberi* species) (Mamakowa 1989), Satiki in Latvia (Kalnina et al. 2007), and the Stora Gäddevik site in Sweden (Lemdahl et al. 2013). In these two latter sites pollen was assigned only to the genus. Even such identification seems to be a rarity. Both the not very characteristic exine and its poor resistance to acetolysis could be responsible for this (Walker 1976). Leaves and leaf-traces similar to those of *Brasenia* are even rarer finds, and their identification is usually based on the fact that in the same sediment samples seeds of *Brasenia* were also found (Środoń 1935). The seeds are very characteristic. They are ovoid, and their apex has a pyramidal structure with a central micropyle (pore). Thanks to these features they are definitely the most often identified remains of this genus. Therefore, the distinction of fossil species was almost exclusively based on the characteristics of seeds. Analysis of seeds concerns their size, morphology and anatomical details of seed coat sections. A detailed overview of the Pleistocene flora, including *Brasenia*, was presented by Velichkevich (1977, 1979, 1982) and Velichkevich and Zastawniak (2008). These studies covered central and eastern Europe, mainly Belarus and western Russia, but also Lithuania and Poland (Fig. 1). According to these papers, during the Pleistocene the following species occurred in this area: *Brasenia belorussica* T. V. Jakub., *B. holsatica* (Web.) Weberb. and *B. borysthena* Wielicz. Additionally, the latter species was described in a few varieties: *B. borysthena* Wielicz. var. *borysthena* Wielicz., *B. borysthena* Wielicz. var. *dvinensis* Wielicz., *B. borysthena* Wielicz., var. *heterosperma* Wielicz. and *B. borysthena* Wielicz. var. *nemensis* Wielicz.

Interestingly, the diagnostic features of seeds of the above-mentioned species are similar to those noted for Tertiary taxa. Velichkevich and Zastawniak (2008) stated the similarity of *B. belorussica* T. V. Jakub. and *B. borysthena* Wielicz. var. *borysthena* Wielicz. to Pliocene

Table 1 Records of Pleistocene remains of *Brasenia* in Europe

Locality/site	Site no	Remain type/taxon	Stage of Pleistocene	References
England, East Midlands/Wing	1	Seeds/ <i>B. schreberi</i>	Ipswichian (Eemian)	Hall (1978)
Netherlands, south-west region/Zuurland	2	Seeds/ <i>B. schreberi</i>	Eemian	Kuijper (1988)
Netherlands, centre/Raalte	3	Seeds/ <i>B. schreberi</i>	Eemian	van der Ham et al. (2008)
Netherlands, north/Vollenhove	4	Seeds/ <i>B. schreberi</i>	Eemian	van der Vlerk and Florschütz (1953)
Belgium, north	5	Pollen?/ <i>B. schreberi</i>	Eemian?	Verbruggen (1999)
Germany, east/Grabschütz	6	Seeds/ <i>B. schreberi</i>	Eemian	Mai (1990a)
Germany, east/Neumark-Nord	7	Seeds/ <i>B. schreberi</i>	Eemian	Mai (1990b, 2010)
Germany, east/Klinge	8	Seeds/ <i>Brasenia</i>	Eemian	Weber (1893)
Germany, north-west	9	Seeds/ <i>B. schreberi</i>	Eemian	Jessen and Milthers (1928)
Denmark, Jylland/Herning, Nørboelling, Solso	10–12	Seeds/ <i>B. schreberi</i>	Eemian	Jessen and Milthers (1928)
Sweden, south/Småland	13	Pollen, seeds/ <i>B. schreberi</i>	Eemian	Lemdahl et al. (2013)
Poland, west/Rusinów (formerly Rinnendorf)	14	Seeds/ <i>B. schreberi</i>	Eemian	Stark et al. (1932)
Poland, centre/Dzbanki Kościuszkowskie, Szczerców, Bedlno	15–17	Seeds/ <i>B. holsatica</i>	Eemian	Velichkevich et al. (2005)
Poland, north-east/Bohoniki	18	Seeds/ <i>B. schreberi</i>	Eemian	Kupryjanowicz et al. (2015)
Poland, north-east/Smolniki	19	Seeds/ <i>B. schreberi</i>	Eemian	Borówko-Dłużakowa (1971)
Poland, south/Jaworzyna Śląska	20	Seeds/ <i>B. schreberi</i>	Eemian	Kuszel (1980)
Poland, south/Imbramowice	21	Pollen, seeds/ <i>B. schreberi</i>	Eemian	Mamakowa (1989)
Poland, centre/Władysławów	22	Seeds/ <i>B. schreberi</i>	Eemian	Tobolski (1988)
Belarus, south-east/Loev, west/Bogatyrevichi	23, 24	Seeds/ <i>B. holsatica</i>	Eemian	Velichkevich and Zastawniak (2008)
Russia, west/Valdai Upland	25	Seeds/ <i>B. holsatica</i>	Mikulino (Eemian)	Zyuganova (2009)
Russia, East European Plain/Cheremoshnik	26	Seeds, fr./ <i>Brasenia</i>	Eemian	Novenko et al. (2005)
Lithuania, east/Medininkai	27	Seeds/ <i>B. holsatica</i>	Eemian	Šeirienė et al. (2014)
Lithuania, south/by Nemunas river	28	Seeds/ <i>B. holsatica</i>	Merkinė (Eemian)	Baltrūnas et al. (2013)
Latvia, west/Satiki	29	Pollen, seeds <i>Brasenia</i>	Eemian	Kalnina et al. (2007)
Lithuania, east/Valakampiai	30	Pollen/ <i>B. cf. borysthena</i>	Snaigupele (Lubavian, Kärlich)	Molodkov et al. (2002)
Germany, west (Middle Rhine)/Kärlich	31	Seeds/ <i>B. holsatica</i>	Kärlich	Bittmann (1992)
Ireland, west/Gort	32	Pollen/ <i>B. cf. schreberi</i>	Mindel-Riss (Holsteinian, Mazovian)	Jessen et al. (1959)
England, south/Denham	33	Seeds/ <i>B. schreberi</i>	Hoxnian (Holsteinian)	Gibbard et al. (1986)
Netherlands, centre/Loosdrecht	34	Seeds/ <i>Brasenia</i>	Mindel-Riss (Holsteinian)	Florschütz and Jonker (1942)
Poland, north-east/Krzyżewo	35	Pollen/ <i>Brasenia</i>	Mazovian (Holsteinian)	Ber et al. (1998)
Poland, east/Dobropol	36	Seeds/ <i>B. borysthena</i>	Mazovian (Holsteinian)	Hrynowiecka et al. (2014)
Poland, east/Nowiny Żukowskie	37	Seeds/ <i>B. borysthena</i>	Mazovian (Holsteinian)	Hrynowiecka and Winter (2015)
Poland, centre/Olszewice, east/Ciechanki Krzesimowskie, south/Stanowice	38, 39, 40	Seeds/ <i>B. borysthena</i> , <i>Brasenia</i>	Mazovian (Holsteinian)	Velichkevich et al. (2004)
Belarus	41	Seeds/ <i>B. borysthena</i>	Mazovian (Holsteinian, Alexandryan)	Velichkevich and Zastawniak (2008)
Latvia, west/Pulvernieki	42	Seeds/ <i>B. borysthena</i>	Pulvernieki (Mazovian, Holsteinian)	Zelčs et al. (2011)
Poland, east/Wylezin	43	Seeds/ <i>B. cf. holsatica</i>	Mazovian (Holsteinian)	Velichkevich et al. (2004)
Poland, east/Luków	44	Seeds/ <i>B. borysthena</i>	Sanian 2 (Elsterian 2) glaciation	Stachowicz-Rybka (2015)
Poland, east/Luków	45	Seeds/ <i>B. borysthena</i> , <i>Brasenia</i>	Ferdynandovian 2 (Mogilevian, Cromerian IV)	Stachowicz-Rybka (2015)
Poland, centre/Ferdynandów	46	Seeds/ <i>B. borysthena</i>	Ferdynandovian 2	Pidek et al. (2015); Stachowicz-Rybka et al. (2017)
Belarus, west/Nikolaev	47	Seeds/ <i>B. belarussica</i>	Borkovian (Ferdynandovian 1, Cromerian III)	Velichkevich and Zastawniak (2008)
Belarus, Russia	48, 49	Seeds/ <i>B. borysthena</i>	Borkovian	Velichkevich and Zastawniak (2008)
France, Alsace/Fort-Louis	50	Seeds/ <i>B. cf. schreberi</i>	Waalien (Celestynovian)	Geissert (1979)
Greece, Peloponnese/Megalopolis	51	Seeds/ <i>B. victoria</i>	Early Pleistocene	Mädler (1971), Velitzelos et al. (2014)
Russia, east/Nikolskoe	52	Seeds/ <i>Brasenia</i>	Early Pleistocene	Dorofeev (1992)
Czech Republic, west/Cheb basin	53	Seeds/ <i>B. cf. tanaïtica</i>	Plio-Pleistocene	Teodoridis et al. (2017)

B. tuberculata C. & E. M. Reid. This species was widely distributed in Pliocene sediments of western Europe, Russia and Belarus, whereas the smaller seeds of *B. borysthena* Wielicz. var. *heterosperma* Wielicz. are reminiscent of the seeds of Pliocene *B. obovata* Dorof. and *B. pripiatensis* Dorof. Importantly, these authors did not mention *B. schreberi* among Pleistocene species. The revision of the Pleistocene flora from several sites in Poland made by Velichkevich et al. (2004, 2005) showed a wrong identification of *B. borysthena* seeds as those of *B. schreberi*. Therefore, there is a question whether other data from European sites are also incorrect, but because they have not been revised, this question cannot be answered. Concerning *Brasenia* species found in Pleistocene sediments, the occurrence of *Brasenia* cf. *tanaitica* Dorof. and *B. victoria* (Caspary) Weberbauer in lower Pleistocene layers, both Tertiary relics, must also be stressed (Table 1).

Generally, seeds of *Brasenia* have been found in Eemian interglacial sediments (Ipswichian, Mikulino, Merkiné), and less often in sediments of older interglacials, Waalian (Celestynovian), Ferdynandovian 1 (Borkovian, Cromerian III), Ferdynandovian 2 (Mogilevian, Cromerian IV), Holsteinian (Hoxnian, Mindel-Riss, Mazovian, Alexandryan, Pulverniki), Kärlich (Snaigupele, Lubavian) (Table 1). At one site (Łuków, eastern Poland; Table 1; Fig. 1) seeds of *Brasenia borysthena* were found in deposits correlated with a glacial sequence related to the early Sanian 2 (Elsterian 2) glaciation (Stachowicz-Rybka 2015). However, this seems to be only due to the re-bedding of older sediments, probably connected with the Ferdynandovian 2 interglacial, into the basin. There is a clear trend in the occurrence of certain *Brasenia* species in particular stages of the Pleistocene. For the Holsteinian interglacial *B. borysthena* was a characteristic species; for the Eemian—*B. schreberi* and *B. holsatica*. However, seeds and pollen of *Brasenia* from western and northern Europe (the British Isles, The Netherlands, Belgium and Sweden) represent almost entirely *B. schreberi*, and are connected exclusively with Eemian sediments (Table 1). The second typical Eemian species, the now extinct *B. holsatica*, is known from sites in Belarus, Russia, Poland and Lithuania (Velichkevich and Zastawniak 2008). In Lithuania the occurrence of this species is scanty, whereas in Belarus tens of thousands of individuals representing these species have been found. Possibly, the northern boundary of *B. holsatica* distribution during the Eemian interglacial ran through Lithuania (Velichkevich 1982). Interestingly, seeds very similar to those of *B. holsatica* were also found in sediments of the Holsteinian (Mazovian) interglacial, in Wylezin (eastern Poland; Table 1; Fig. 1) (Velichkevich et al. 2004) and in the sediments of the Kärlich interglacial, in the German middle Rhine region (Table 1; Fig. 1) (Bittmann 1992).

On the palaeoecology of *Brasenia*

Brasenia species known from the European Pleistocene belonged to the thermophilous elements of the flora during several interglacials. In the Ferdynandovian 2 (Cromerian IV, Mogilevian) interglacial *B. borysthena* occurred in shallow, warm waters as a component of the so-called *Brasenia* complex (Velichkevich 1977, 1979). The term means the association of thermophilous aquatic plants, like *Nuphar lutea* (L.) Sibth. & Sm., *Ceratophyllum demersum* L., *Myriophyllum spicatum* L., *M. verticillatum* L., with the predominance of *Brasenia*, which were characteristic of the optimal climatic phases of this interglacial. In the Ferdynandów 2011 stratotype site, *Brasenia* is connected with another thermophilous taxon, *Euryale ferox* Salisb. (as well as in Kärlich, Bittmann 1992). Modern *E. ferox* can be found in tropical and subtropical zones of south-east Asia, where mean July temperatures attain 21 °C. According to Stachowicz-Rybka et al. (2017), today this species has similar ecological tolerances as in the past.

During the Holsteinian interglacial *B. borysthena* was still present in aquatic vegetation of shallow water. Regarding the trophic preferences of *Brasenia* there are different data. Its occurrence in acid water was stressed by Muenscher (1944) and Lakela (1965), while Mai (1985) described this genus as an indicator of eutrophic conditions. According to Hrynowiecka and Winter (2015), in Nowiny Żukowskie *Brasenia* occurred only with *Aldrovanda dokturovskyi* Dorof. (now an extinct carnivorous thermophilous plant) and *Potamogeton natans* L. Both *B. borysthena* and (*A. dokturovskyi*) were typical of the climatic optimum flora of the Holsteinian interglacial, whereas at the Dobropol site, besides (*B. borysthena*), *Najas flexilis* (Willd.) Rostk. & W.L.E. Schmidt, *Stratiotes aloides* L. and *Myriophyllum spicatum* were also present in the water body (Hrynowiecka et al. 2014).

The thermophilous character of *Brasenia* was also confirmed during the Eemian interglacial. In the optimal phase of the last interglacial, this plant was a regular component of the vegetation of shallow water bodies. According to Zyuganova (2009), besides *B. holsatica*, this *Brasenia* assemblage could have been formed by *Salvinia natans* (L.) All., *Nuphar lutea*, *Trapa natans* L., *Aldrovanda vesiculosa* L., *Dulichium arundinaceum* (L.) Britt., or *Caulinia flexilis* Willd. The assemblage reflects the vegetation of shallow organic-rich water bodies, so-called lake-swamps, which existed in warm and mild climate conditions. The past plant communities with *Brasenia*, like *Brasenia-Aldrovanda*, *Brasenia-Nuphar-Aldrovanda* or *Brasenia-Nymphaea*, were also described (Mai 1985). In contrast, at the site of Wing, United Kingdom, *B. schreberi* represented a mire community encroaching on a lake with increasingly acid waters, perhaps with birch woodland in the drier parts and *Taxus*

Fig. 1 Map of sites with Pleistocene *Brasenia* remains in Europe. Numbers as in Table 1

(yew) on the base-rich soils skirting the basin. *Menyanthes*, *Carex* spp., *Eriophorum vaginatum* L., and a number of mosses, notably *Cratoneuron commutatum* var. *falcatum* (Brid.) Mönk., *Meesia longiseta* Hedw. and species of *Sphagnum* accompanied it (Hall 1978). *Brasenia schreberi* is connected with such mildly acidic quiet and shallow (less than 1 m) waters with floating mats of vegetation in North America nowadays. *Nuphar*, *Nymphaea*, *Potamogeton*, *Utricularia vulgaris* L. and Charophyta are associated with it (Birks 1973). This plant is seen to grow equally well in sub-arctic and tropical regions. Why then is it absent from Europe at present? Why were European populations, which were so numerous in the Pleistocene, not able to survive the last glaciation?

It is hard to disagree with Marie-Victorin and Léon (1944) that the disappearance of *B. schreberi*, which equally favours the cold lakes of Canada and the warm lagoons of Cuba and in America, and is seen to grow equally well in sub-arctic and tropical regions, cannot be attributed to climatic changes. Therefore, the reason for its extinction seems to lie in plant specificity. Wood (1959) points out that there is a difference in the mode of seasonal growth to accommodate this: in the northern parts of its range *Brasenia* overwinters as winter buds or turions, which are produced in autumn and fall to the lake bottom, and further south the plant is ever-green and reproduces more readily by seed. This ability to adapt to changing climate is clearly an advantage in a plant exposed to the climatic fluctuations of the Pleistocene. Raymond and Dansereau (1953) suggest that the overwintering

Table 2 Correlation of the selected Pleistocene stages in European countries and regions

Poland	Other European countries/regions
Eemian interglacial	Eemian/Eem (W/NW Europe) Ipswichian (England) Merkinė (Lithuania) Mikulino (Russia)
Lubavian interglacial	Snajgupele (Lithuania) Kärlich (Germany)
Mazovian interglacial	Holsteinian (W/NW Europe) Mindel-Riss (W Europe) Hoxnian (England) Pulvernieki (Latvia) Alexandryan (Belarus)
Sanian 2 glaciation	Elsterian/Elster (W/NW Europe)
Ferdynandovian 1 interglacial	Cromerian III (W Europe) Borkovian (Belarus)
Ferdynandovian 2 interglacial	Cromerian IV (W Europe) Mogilevian (Belarus)
Celestynovian interglacial	Waalian/Waal (W/NW Europe)

habit was, to some extent, responsible for the survival of this taxon as a relic of an “early Tertiary megaphyllous flora” in North America. European populations were probably unable to alter their growth mode. Therefore, the increasingly cold winters could have exterminated *Brasenia*, which was unable to produce overwintering turions instead of seeds. The lack of adaptations by European *Brasenia*, which are possessed by North American populations, could be the key to its extinction in Europe. According to Hall (1978), a further factor in explaining the extinction of *Brasenia* may be the possible lack of suitable glacial refugia for Eemian *Brasenia* in the southern part of the continent. Actually, the area of lakes in the interglacials was greater than nowadays. Such an abundance and extent of lakes resulting from the wet climate would have provided excellent conditions for *Brasenia*, while after the last glaciation, lake areas were much smaller. However, the same author did not entirely exclude the possibility that *Brasenia* occurred in Europe during the Weichselian glaciation. It could just have been isolated in the south and unable to migrate to the north at the beginning of the Holocene. The lack of any particular adaptation for the dispersal of the seeds of *Brasenia* by birds, such as hairs or spikes, did not help. However, according to Yoo et al. (2005), before its extinction in Europe this genus probably migrated with success southward, to Africa. Water lily seeds are an important food source for ducks and other diving waterfowl, so during bird migrations, which generally follow a north–south directional pattern (Berthold 1993), *Brasenia* seeds could have been transported to the south

for a great distance. Such transport to the north was probably more questionable because of the mountain ranges in Europe.

The floral cycle of modern *B. schreberi* also provides information about some possible reasons for its extinction. Its flowers appear with one sex functioning at a time (dichogamous) (Osborn and Schneider 1988), first the functionally female flower (protogynous) (Thien et al. 2009) followed by its re-appearance as a functionally male one, and this is a mechanism for eliminating self-pollination. Maybe this feature was also present in Pleistocene *Brasenia*. However, at that time self-fertilisation (autogamy) could have been desirable as a way to survive in the conditions of a cooling climate at the beginning of the Weichselian glaciation. Unfortunately, it was not possible, and cross fertilisation (alogamy) or even cross pollination between different flowers on the same plant (geitonogamy) may have been impeded as a result of the weakness of the specimens (maybe the number of flowers was reduced) and the decrease in their numbers. Therefore, this is another possible contribution to the extinction of *Brasenia*.

Conclusions

In light of the palaeobotanical records of *Brasenia* from the Pleistocene sediments of Europe it was then an important component of aquatic plant life in Europe. As a thermophilous taxon which originated in the Tertiary, *Brasenia* managed to survive numerous glacial stages during the Pleistocene. However, the last one of them seemed to bring its history in Europe to an end. This curious fact of *Brasenia* extinction was undoubtedly caused by a combination of several factors. Its fate was shared by another Tertiary relic of the Pleistocene flora, *Dulichium arundinaceum*, which occurs only in North America nowadays, where it is a frequent constituent of vegetation around small lakes. Interestingly, as a component of floating mats (together with *Lycopus uniflorus* Michx., *Menyanthes*, *Potentilla palustris* (L.) Scop., *Eupatorium maculatum* L. and *Sagittaria latifolia*) it is found close by aquatic vegetation including *Brasenia* (Hall 1978). However, these two plants seem to be associated not only today, but were also in the past. This is confirmed by numerous macrofossil finds of *Brasenia* and *Dulichium* occurring together in sediments across Europe (Jessen and Milthers 1928; Hall 1978; Velichkevich 1982; Gibbard et al. 1986). Therefore, *Brasenia* is not the only known case of a puzzling extinction on the European continent.

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