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Macrofossil evidence of Late Holocene presence of *Aldrovanda vesiculosa* L. in Central-Eastern Europe (Poland) and East Africa (Tanzania)

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ABSTRACT

To date, the seeds of waterwheel plant (*Aldrovanda vesiculosa*) were only found in Europe, in sediments of the Eemian and Mazovian Interglacials. The absence of *A. vesiculosa* seeds in European Holocene deposits is probably due to unfavorable climatic conditions, i.e. lower temperature, during this period: in temperate zones, *A. vesiculosa* reproduces mainly in a vegetative way; it rarely blooms and only occasionally produces seeds. In this paper, subfossil seeds of *A. vesiculosa* were identified in two peat bogs: one (Sucha Kobyła) in SE Poland and another one (Kyambangunguru) in SW Tanzania. Single seeds of this plant were found in a peat layer from the Polish site formed after 1600 AD as well as in sediments accumulated around 440 AD in the Tanzanian one. To our knowledge, this is the first time that seeds of *A. vesiculosa* are found in Holocene deposits in the world. Our findings provide new data on the distribution of *A. vesiculosa* over the Late Holocene.

1. Introduction

The waterwheel plant – *Aldrovanda vesiculosa* L. (Droseraceae) – is an aquatic carnivorous plant, floating freely in water. It prefers well-insolated, mesotrophic and eutrophic water with a pH comprised between 6.0 and 6.6 (Adamec and Tichy, 1997; Kamiński, 2006). The plant has also been recorded from other water conditions ranging, from oligotrophic, through mesotrophic and eutrophic to dystrophic (Żukowski, 1963; Sokołowski, 1972; Radwan, 1976; Gramsz and Jasińska, 1986; Kamiński, 1987, 2006; Adamec, 1995). Noteworthy, the contemporary distribution range of *A. vesiculosa* in the world is dramatically decreasing (Adamec and Lev, 1999; Kamiński, 2006). Nowadays, *A. vesiculosa* occurs in Europe, Asia, Africa and Australia. Records indicate that *A. vesiculosa* is present in 295 sites in the world, among which about 220 are regarded as either historical sites or need to be checked (Kamiński, 2006). In Europe, its presence has been reported from 160 sites, among which 29 and 7 are natural and restored sites, respectively (Kamiński, 2006).

In Poland, the waterwheel plant was identified in 7 and 13 natural and restored sites respectively, whereas in Tanzania, the plant was found in 5 sites (Kamiński, 1995). Given the rapid disappearance of the plant, there have been efforts geared towards its reintroduction in various parts of the world, including Czech Republic (Adamec and Lev, 1999), Poland (Kamiński, 1995) and Japan (Nitta et al., 2003).

The oldest seeds of *Aldrovanda* date back to the Mesozoic (Yakubovskaya, 1991). In Central-Eastern (CE) Europe, the first seeds of *A. vesiculosa* were found in sediments of the Mazovian Interglacial (Velichkevich and Zastawniak, 2009). Nevertheless, the largest accumulations of these seeds were found in sediments of

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the Eemian Interglacial (e.g. Tobolski, 1991; Nita, 1998; Velichkevich and Zastawniak, 2009). So far the species have been distinguished based on their differences in shapes and dimensions of the seeds, including *A. borysthenica* Wieliczk., *A. dokturovskyi* Dorof., *A. zussii* T. V. Jakub. (Velichkevich, 1982; Yakubovskaya, 1991; Velichkevich and Zastawniak, 2009).

The post-glacial history of *Aldrovanda vesiculosa* is completely unknown, because its macrofossils (both generative and vegetative) have not been found in sediments accumulated over the last thousands of years so far. Therefore, its current origin is unknown (Berta, 1961; Adamec and Tichý, 1997). Some existing information indicates that during postglacial *A. vesiculosa* was brought into Europe from Africa (Berta, 1961; Sculthorpe, 1971), while others (e.g. Degreef, 1997) think the opposite, based on the absence of *Aldrovanda* fossil in Africa and Australia. The genus *Aldrovanda* was shown to be a Cenozoic relict (Yakubovskaya, 1991). Unfortunately, even genetic studies (Maldonado San Martin et al., 2003) could not clearly explain the origin of the European population and the post-glacial migration routes of the plant. However, some researchers linked distribution of *A. vesiculosa* with bird migration routes (Elansary et al., 2010). An example of bird is Bewick's swan which can cover a long distance from southern Japan to northern Russia (Kamiya and Ozaki, 2002) or from Siberia to Denmark, Poland and England (Klaassen et al., 2004).

This article reports the first identification of *Aldrovanda vesiculosa* seeds in Late Holocene deposits, in SE Poland and SW Tanzania. The seeds were discovered (i) in a Polish peat bog, during palaeoecological studies aiming to reconstruct the post-glacial history of *Cladium mariscus* in CE Europe and (ii) in a Tanzanian peat bog, where a core was collected to reconstruct environmental changes over the last 4000 years based on molecular proxies (Coffinet et al., unpublished data).

2. Sites of study

The peat bog "Sucha Kobyła" is located in SE Poland, between the towns of Chełm and Dorohusk (Fig. 1) and has an area of approximately 100 ha (175 m a.s.l.). Currently the peat bog, which has been drained in the past, is dominated by the vegetation build by *Carex* spp., *Cladium mariscus* and *Phragmites australis*, sometimes growing in shallow depressions with stagnant water (10–20 cm depth). The peat bog lies within moderately continental climate, with strong contrasts between the warm summer (98 days) and usually harsh winter (97 days). The growing season lasts for 210 days. Annual precipitation is 688 mm (Michalczyk and Smalisz, 1992). The average annual air temperature measured over the period 1991–1997 was 7.6 °C. The average temperature of the warmest (July) and coldest (January) months measured over the same period were 18.5 °C and −1.7 °C, respectively. *Aldrovanda* is currently present in several lakes in SE Poland.

The ombrotrophic peat bog of "Kyambangunguru" is located in the East African Rift in SW Tanzania (Fig. 1), in the center of a Quaternary maar crater at proximity of Mbambo village (660 m a.s.l.). It has no hydrological outlet and an area of approximately 4 ha. Currently, rushes, waterlilies, ferns and some scare small trees, surrounding by papyrus and reeds, dominate the peat bog vegetation. In contrast, the steep catchments crater flanks, of around 16 ha (Delalande et al., 2008a), are partially cultivated or occupied by Zambazian Miombo-type woodland. The region belongs to the humid equatorial zone of Africa and experiences alternation of a hot humid season (from November to May) and a relatively cold dry season (from June to October; Delalande et al., 2008b). Regional precipitations reach over 2000 mm/yr on average and local mean air temperature is around 24–26 °C, with low seasonal variability compared to day/night cycle. Macroscopically, ombrophic peat bog and palaeo maar-lake samples appear as no consolidated organic matter where phytoclasts such as wood, stems, and plants are visible. There are minor quantities of clay, quartz and tephra deposits.

3. Material and methods

The Polish core was collected in 2009 in the central part of the peat bog Łąka Sucha Kobyła (51°10′ N 23°38′E), densely covered by patches of *Cladium mariscus*. An Instorf peat corer (Russian corer) with a length of 50 cm and width of 5 cm was used. The water table was approximately 10 cm below the ground level. Samples of the Polish core were analysed at a resolution of 2 cm. A 4 m peat core was collected with a Wright corer in Kyambangunguru peat bog (9°22′ S 33°48′ E) in 2012. At that time, the water level reached 92 cm above the peat surface. Samples of Tanzanian core were analysed at changeable resolution, mainly 3–5 cm. The total volume of the samples was 25 cm^3. The samples were rinsed with warm water on 0.2 mm mesh sieves. Macrofossils were quantified with a stereoscopic microscope Nikon SMA 800 and a biological light microscope Olympus CX41. Species determination of individual plant macrofossils was performed using the available literature (Velichkevich and Zastawniak, 2006, 2009).

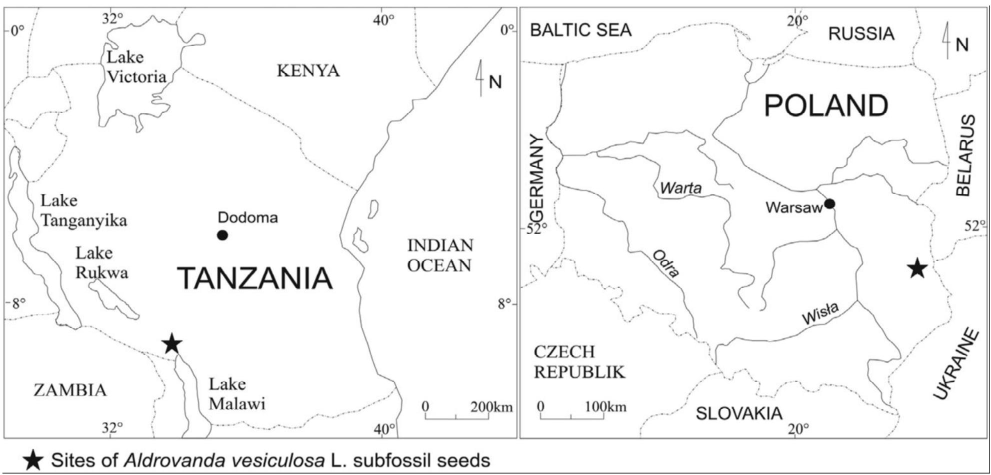

Fig. 1. Sites with subfossil seeds of *Aldrovandra vesiculosa* L.

AMS radiocarbon dating of two samples was performed at the Poznań Radiocarbon Laboratory and at the Saclay LMC14 ARTEMIS Laboratory (Table 1). The resulting conventional radiocarbon dates were calibrated with OxCal 4.1 software (Bronk-Ramsey, 2009). The IntCal13 (Reimer et al., 2013) atmospheric curve was used for date calibration.

Table 1
Radiocarbon dates.

Site/depth (cm)	Material	Nr. Lab.	C14 date	Age AD
SE Poland 14–16	*Carex* fruits	Poz-35951	145 ± 30 BP	1668–1948
SW Tanzania 116–117	Bulk Organic Fraction	SacA36761	1590 ± 45 BP	315–405

4. Results

4.1. Site in SE Poland

The peat bog in which the seed of *Aldrovanda vesiculosa* was found developed in a shallow depression, functioning in the past as a lake. The presence of a shallow lake is confirmed by lake sediments (calcareous gyttja) and the plant macroremains found in them, including *Potamogeton natans*, *Potamogeton filiformis*, *Chara* sp. and *Myriophyllum verticillatum*. The thickness of organic deposits was 158 cm. One seed of *Aldrovanda vesiculosa* was found at a depth of 14–16 cm (Fig. 2). The age of the peat layer, where seed of *A. vesiculosa* was found, was determined by radiocarbon dating to AD 1668–1948 (Table 1). The following fruits and seeds were found at 14–16 cm depth in addition to *Aldrovanda* seed: one seed of *Cladium mariscus*, two fruits of *Carex flava* s.lat. and two fruits of *Carex* sp. At 16–18 cm depth, two seeds of *Menyanthes trifoliata*, six fruits of *Carex flava* and one fruit of *Chenopodium* sp. were identified, whereas six fruits of *Carex flava* and one seed of *Mentha aquatica* were observed at 12–14 cm depth.

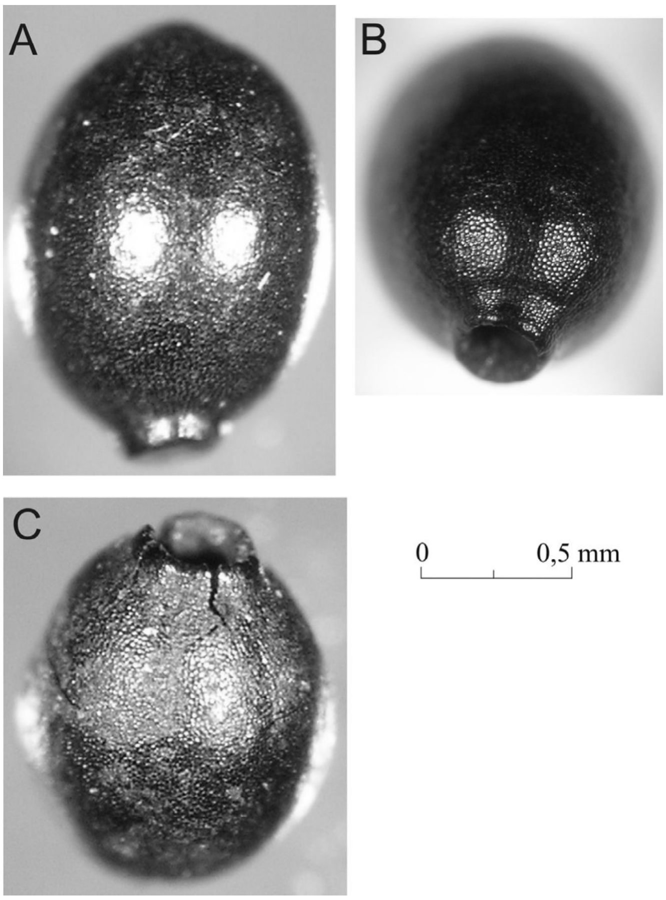

Fig. 2. *Aldrovandra vesiculosa* L. seeds. A–B) SW Tanzania (1.55 × 1.15 mm), C) SE Poland (1.25 × 0.95 mm).

4.2. Site in SW Tanzania

The Tanzanian peat bog is located in the center of Kyambangunguru Quaternary maar crater. The base of the 4 m core shows that the center of the crater was occupied by a shallow palaeo-lake, which was replaced by a peat bog. One seed of *A. vesiculosa* was found in gyttja at a depth of 110 cm (Fig. 2). The age of this 110 cm depth level is estimated, from two radiocarbon dates obtained on 7–9 and 116–117 cm levels (Table 1) and considering a constant accumulating rate, at around 440 AD. This sample also included 11 fruits of *Eleocharis* sp. and 15 oospores of *Nitella* sp. At 113 cm depth, five fruits of *Eleocharis* sp. and one oospores of *Nitella* sp. were found, whereas two fruits of *Eleocharis* sp. and two oospores of *Nitella* sp. were observed at 108 cm depth. In these three samples, small pieces of wood were also found.

5. Discussion

5.1. Palaeoecology of Aldrovanda vesiculosa

The contemporary studies of *Aldrovanda vesiculosa* in CE Europe show that it is present in widely diverse ecological environments (Kamiński, 2006). Generally, *A. vesiculosa* can be found in shallow lakes, in which it develops homogeneous populations, or can be concomitantly present with *Stratiotes aloides*, *Hydrocharis morsus-ranae*, *Nymphaea alba* and *Nuphar lutea* (Kamiński, 2006). It can also be found among the rushes of *Typha latifolia* and *Thelypteris palustris* (Urban and Wójciak, 2014). In the Polish site investigated in this paper, *Aldrovanda vesiculosa* was growing among *Cladium mariscus*. *Cladium mariscus* prefers moist places. In Poland, it grows either along lake shores (Gałka and Tobolski, 2012) or in peat bogs developed in large depressions with stagnant water (Buczek, 2005), as observed in this study. Our data show that in the past *Aldrovanda vesiculosa* grew among rushes in such peat bogs. Currently, *Chara* spp. is growing among the *Cladium* rushes in SE Poland (Gałka, personal observation).

In Tanzania, *Aldrovanda vesiculosa* grew in an environment where the water depth was unlikely to exceed 1 m. This is confirmed by the concomitant presence of *Eleocharis* sp. fruit and *A. vesiculosa* seed. In the deeper sediments (below 278 cm depth), endocarps of *Caldesia parnansifolia*, *Potamogeton* sp., and *Nitella* sp. were also found, inter alia, suggesting that also in the past the depth of the paleolake fluctuated around 1 m. Indeed, the optimal conditions for the growth of *C. parnansifolia* correspond to shallow waters (less than 1 m depth; Piękoś-Mirkowa and Mirek, 2003).

5.2. Lack of seeds of Aldrovanda vesiculosa in the Holocene sediments

The lack of seeds of *A. vesiculosa* in European Holocene deposits, especially in CE Europe, may be due to unfavorable climatic conditions for the growth of this plant. This hypothesis is confirmed by recent observations. In subtropical and tropical climates *A. vesiculosa* produces seeds, while in temperate climates it blooms only sometimes and does not produce seeds (Kamiński, 2006; Kłosowski and Kłosowski, 2007). In CE Europe the waterwheel plant reproduces mainly vegetatively, producing turions (Adamec, 2003; Kamiński, 2006). However, recent observations (2010–2012) proved that *A. vesiculosa* produces seeds in SE Poland (Urban and Wójciak, 2014). Producing of seeds by *A. versiculosa* in Lakes Płotycze and Perespa was closely associated with very warm summer seasons (air temperature exceeding 30 °C during the day and water temperature ranging between 26 and 31 °C; Urban and Wójciak, 2014). Similarly, air temperature was estimated to be ~31–32 °C (Coffinet et al., unpublished data) at the time when *A. vesiculosa* seed was found in the Kyambangunguru peat bog. This shows that the temperature is very important in the development of this plant. Indeed, according to Kamiński (2006), in Poland, the growing season temperature – optimal for the development of *A. vesiculosa* – oscillates between 20 and 28 °C. In autumn, the temperature drops below 16 °C, thus causing the stop of plant growth. Additionally, a drop or a rise in temperature below 10 °C or above 40 °C, respectively, leads to the loss of the grip property of *A. vesiculosa* traps (Czaja, 1924). Another argument for the relationship between the presence of *Aldrovanda* seeds in CE European deposits and climatic conditions is their prevalence in sediments of the Eemian Interglacial (e.g. Tobolski, 1991; Nita, 1998; Velichkevich and Zastawniak, 2009). Paleoclimatic data show that maximal temperatures were higher during the Eemian Interglacial (average temperature of ~20–21 °C in June) than during the Holocene (Tobolski, 1991). The warmer climate during the Eemian Interglacial is indicated by the presence of (i) *Aldrovanda* seeds and (ii) macrofossils of plants requiring high temperature for growth and development, such as *Brasenia schreberi*, which currently does not exist in Europe. According to Szafer (1972), modern occurrences of *A. vesiculosa* in Poland are considered to be relicts from the Holocene climatic optimum.

Similarly, climate was observed to impact the reproduction of *Stratiotes aloides* (Gałka, 2010) and *Lemna* spp. (Gałka, 2006; Landolt, 1986), which changed from a generative to a vegetative state between the Eemian Interglacial and the Holocene. This can explain why the seeds of these plants are very rare in Holocene deposits (Cook and Urmi-König, 1983; Landolt, 1986; Bennike and Hoek, 1999; Gałka, 2010). *Aldrovanda* seeds will likely be found in additional Holocene sediments from tropical areas such as Africa due to the increasing development of plant macroremain analysis.

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