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DESCRIPTION OF THE SUBFOSSIL HEAD SHIELD OF *Alona protzi* HARTWIG 1900 (ANOMOPODA, CHYDORIDAE) AND THE ENVIRONMENTAL CHARACTERISTICS OF ITS FINDING SITES[1]

Rikke Bjerring[1], Mirva Nykänen[2], Kaarina Sarmaja-Korjonen[3], Artem Sinev[4], Karina Jensen[1], Liisa Nevalainen[3], Krystyna Szeroczyńska[5], Edyta Zawisza[5]

[1] *National Environmental Research Institute, Department of Freshwater Ecology, University of Aarhus, Vejlsøvej 25, DK-8600 Silkeborg, Denmark, e-mail: rbh@dmu.dk, kje@dmu.dk*
[2] *Department of Ecological and Environmental Sciences, University of Helsinki, Niemenkatu 73, FI-15140 Lahti, Finland, e-mail: mirva.nykanen@helsinki.fi*
[3] *Department of Geology, P.O. Box 64, FI-00014 University of Helsinki, Finland, e-mail: kaarina.sarmaja-korjonen@helsinki.fi, liisa.nevalainen@helsinki.fi*
[4] *Department of Invertebrate Zoology, Biological Faculty, Moscow State University, Moscow 119992, Russia, e-mail: artem.sinev@mail.ru*
[5] *Institute of Geological Sciences, PAS, Twarda 51/55, 00-818 Warsaw, Poland, e-mail: kszerocz@twarda.pan.pl, ezawisza@twarda.pan.pl*

Abstract
This paper gives a description of the head shield of *Alona protzi*, a rare species of Cladocera (water fleas) whose separated head shield has not yet been described in detail. Subfossil head shields of *A. protzi* were found in sediment cores taken from lakes in Denmark, Sweden, Finland, Estonia and Poland. Despite the rarity of the species this suggests a wide distribution of *A. protzi* in northern Europe. The ecology of *A. protzi* is poorly known. The environmental spectrum of the finding sites was wide and ranged from relatively nutrient poor clear water lakes to eutrophic turbid water lakes, indicating that *A. protzi* is not narrowly restricted. Most of the lakes were, however, meso-eutrophic with neutral to high pH, and with a relatively low abundance of submerged macrophytes. However, we cannot exclude the possibility that *A. protzi* mainly lives in groundwater and is only occasionally transported into lakes.

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Key words: Subfossil Cladocera, *Alona protzi*, head shield, description, paleolimnology

INTRODUCTION

Chydoridae, a diverse family of Cladocera (water fleas), appear commonly in freshwater habitats. Most of the European chydorid fauna was already described in the early 20th century. In identification literature, the intact animals are depicted from the side and the shape of the head shield is thus not clearly shown. The head shield and carapace of living animals are seamlessly attached, implying that the shape of the posterior margin of the head shield is invisible. When the animal dies or molts, the head shield is detached from the carapace by a special ecdysial suture (molting seam).

The chitinous remains of chydorids (e.g. head shields, carapaces and postabdomens) are usually well-preserved in lake sediments and can be used to reconstruct past limnological conditions (Frey 1986, Korhola, Rautio 2001). This particular field of paleolimnology developed in the latter half of the 20th century when David Frey (1958, 1959) described 'flat', detached head shields. Their characteristic pore configurations and shapes of the posterior margin enabled their identification in lake sediment studies. Separate description of subfossil remains is necessary, because some of the characteristics of living animals, for instance the outer membranes forming part of the surface sculpturing, are not always preserved.

Since Frey's pioneer work (1958, 1959), the subfossil remains of most European chydorids have been described. However, some of the rarest species, including *Alona karelica* Stenroos 1897 and *Alona protzi* Hartwig 1900, still puzzle palaeolimnologists. The carapace of *A. protzi* can be identified from its characteristic denticles on the posterior-ventral corner of the shell (e.g. Smirnov 1974, Dumont 1983, Røen 1995, Flössner 2000), but the shape of its head shield has not yet been described in detail. In addition, the biology of the species is poorly known.

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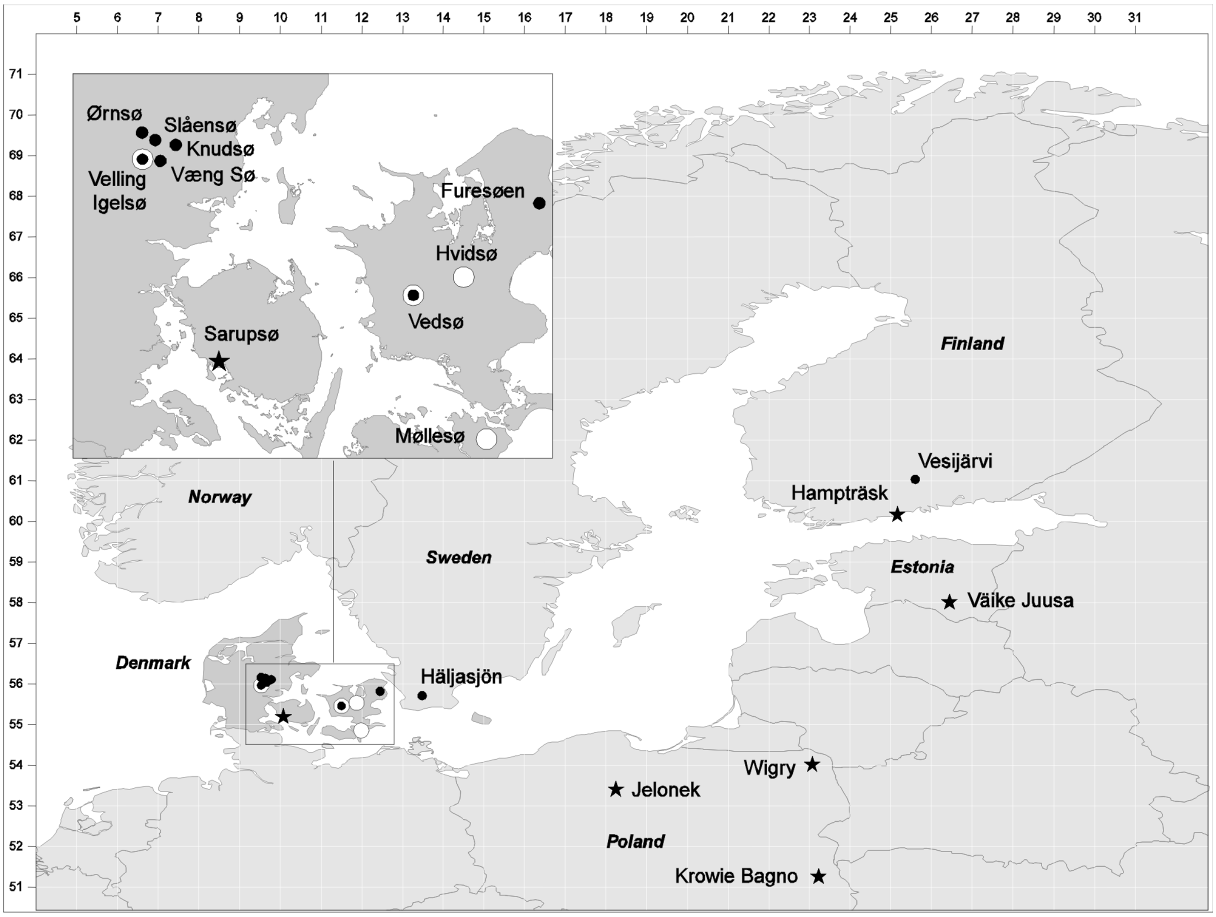

Fig. 1. The 17 finding sites of *A. protzi* subfossil head shields in Northern Europe. ● – findings in recent sediment (AD 1986–2002), ○ – findings in sediment dated AD 1850–1950, ★ – findings in old sediments (7000 BC – AD 1300).

In recent studies, the present authors have found unknown chydorid head shields in lake sediments from Denmark, Sweden, Finland, Estonia and Poland. Not until subfossil specimens with head shield and carapace still attached were found, the previously undetermined head shields could be identified as belonging to *A. protzi*. Flössner (2000) presented a somewhat sketchy drawing of the head shield of *A. protzi*, lacking several features characteristic to the subfossil specimens. In the present paper, we give a detailed description of the subfossil head shield and an overview of the environmental characteristics of the lakes in which they were found. We aimed to examine whether *A. protzi* might have an indicator value in paleolimnological research, assuming that no evolutionary adaptation of demands has occurred.

SITES AND LABORATORY METHODS

Subfossil head shields of *A. protzi* were discovered in sediments from 17 lakes located in Denmark, Finland, Sweden, Estonia and Poland (Fig. 1). The findings were divided into three groups according to sediment type: surface sediment (AD 1986–2002) with contemporary water chemistry data, sediment accumulated in recent time (AD 1850–1950) and older sediments (7000 BC – AD 1300).

All samples were heated in 10% KOH and washed on a sieve (Korhola, Rautio 2001). Two different methods were applied. In the first method, 42–50-µm mesh size was used and the samples were counted on slides under light microscope (samples from Finland, Estonia and Poland) (Korhola, Rautio 2001). In the other method, fragments >80 µm were counted in water under a magnifying glass and an inverted light microscope (samples from Denmark and Sweden). The total number of cladoceran remains counted varied between samples and analysts: 700–2800 (Danish lakes), 200–250 (Lake Väike Juusa, Estonia), 450 (Hampträsk, Finland), and 300–1000 (Polish lakes). One head shield was found in Krowie Bagno (Poland) during a screening of more than 20 slides containing hundreds of cladoceran remains. In Lake Vesijärvi (Finland) minimum 400 individuals (converted from remains) were counted per sample.

RESULTS AND DISCUSSION

Subfossil remains of *A. protzi*

Findings of subfossil remains

We found 84 head shields distributed in 53 sediment samples from 17 lakes (the first finding was made in October 2002) (Table 1). All head shields had a peculiar shape with a notched posterior margin and a short, broadly rounded rostrum (Fig. 2). The shape resembled that of *A. phreatica* in Alonso (1996), a closely related and rare species with a relatively narrow distribution within Europe (Dumont 1987, 1995, Alonso 1996, Dumont, Negrea 1996, Brancelj, Du-

Table 1

Characteristics of the finding sites and the abundance data on *A. protzi*

Lake	Country	Sediment age	Fragment found	Area ha	Max depth m	Mean depth m	Secchi depth m	Total N μg L^{-1}	Total P μg L^{-1}	Chl a μg L^{-1}	Alkalinity mmol L^{-1}	Conductivity μS cm^{-1}	pH	Percentage plant filled volume (%)	Abundance (%)	Number of head shields per sample	Number of samples
Velling Igelsø	DK	S, R	H	8.8	14		2.5	605	15	9.7	0.22		7.5		1.6	2.3	3
Knudsø	DK	S	H	1.4	29	17	3.7	2246	27	11.8	1.94		8.5	2.4	0.1	1	1
Ørnsø	DK	S	H	0.4	10	4	1.2	1344	101	62.8	0.81		7.9	0	1.2	1	1
Ved Sø	DK	S, R	H	5	3.5	2.8	0.8		125						0.4	1.5	2
Vængsø	DK	S	H	16		1.2	0.4	1300	161	80.5	1.29	281	8.1	0	0.4	1	1
Furesø	DK	S	H	7.3	37.7	16.5	2.5	1028	245	66.2	2.1		8.7	1.9	0.1	1	1
Slåensø	DK	S	H	0.2	11.5	7.3	3.8							4.3	0.9	1	1
Häljasjön	SE	S	H	19.6		5.6	2.5	1346	39	23.7	2.18	300	7.8	0	0.6	2	1
Vesijärvi, the	FIN	S	H, C	2600	33	6.8	2.1	548	31	11.9	0.55	123	7.8		0.7	1.1	7
Enonselkä basin							(1.5 -2.4)	(505 -703)	(25 -50)	(7.5 -23.2)	(0.52 -0.57)	(120 -130)	(7.7 -7.9)		(0.4 -1.1)	(1 -2)	
Hvidsø	DK	R	H												0.7	2	1
Mølle Sø	DK	R	H												0.2	1	2
Sarup Sø	DK	O	H, C												1.8	1.8	21
															(0.7 -4.2)	(1 -4)	
Hampträsk	FIN	O	H													1	1
Väike Juusa	EST	O	H												1.6	1.4	5
															(0.9 -2.6)	(1 -2)	
Krowie Bagno	PL	O	H												# 0.2	5	3
Jelonek	PL	O	H												# 0.1	1	1
Wigry	PL	O	H												# 0.1	3	1
R. Valkjärvi *	FIN	S	C	8	9	4.5	2.3	340	15	5.8	0.05	25	6.2				
Valvatus *	FIN	S	C	303	7.5		1.1	830	42	31	0.66	150	7.4				
Lovonjärvi *	FIN	S, W	C, I	5	17.5	7.7	1	872	49	28	0.51	129	7.2				
Sylvöjärvi *	FIN	W	I	235	5.5	1.9	1.1	700	38	7	0.45	93	7				
Mean				**247**	**16.2**	**6.8**	**1.9**	**1014**	**74**	**30.8**	**0.98**	**157**	**7.6**	**1.4**	**0.7**	**1.3**	
Median				**8**	**11.5**	**5.6**	**2.1**	**872**	**40.5**	**23.7**	**0.66**	**129**	**7.8**	**0.95**	**0.6**	**1**	
Min				**0.2**	**3.5**	**1.2**	**0.4**	**340**	**15**	**5.8**	**0.05**	**25**	**6.2**	**0**	**0.1**	**1**	
Max				**2600**	**37.7**	**17**	**3.8**	**2246**	**245**	**80.5**	**2.18**	**300**	**8.7**	**4.3**	**1.6**	**2.3**	

* Nykänen & Sarmaja-Korjonen 2007; # Percentage of head shields of all counted chydorid remains in the sample (not included in mean and median abundance)

For Lake Vesijärvi contemporary data were available for each of the 7 samples. The mean value was used in order not to skew the results (ranges shown in brackets). For the remaining lakes, contemporary data was available only for one sample (surface sediment). 'Abundance %' refers to the percentage of *A. protzi* head shields from all chydorid head shields in the sample, whereas 'Number of head shields per sample' is the number *A. protzi* head shields encountered during counting per sample. Where more samples per lake are present percentage abundance and encountered head shields are given as a mean value per lake (with ranges in brackets, if found in more than three samples). DK = Denmark, EST = Estonia, FIN = Finland, PL = Poland, SE = Sweden; S = surface sediment (AD 1986-2002), R= recent sediment (AD 1850-1950), O = old sediment (7000 BC AD 1300), W = water sample; H = head shield, C = carapace, I = intact animal.

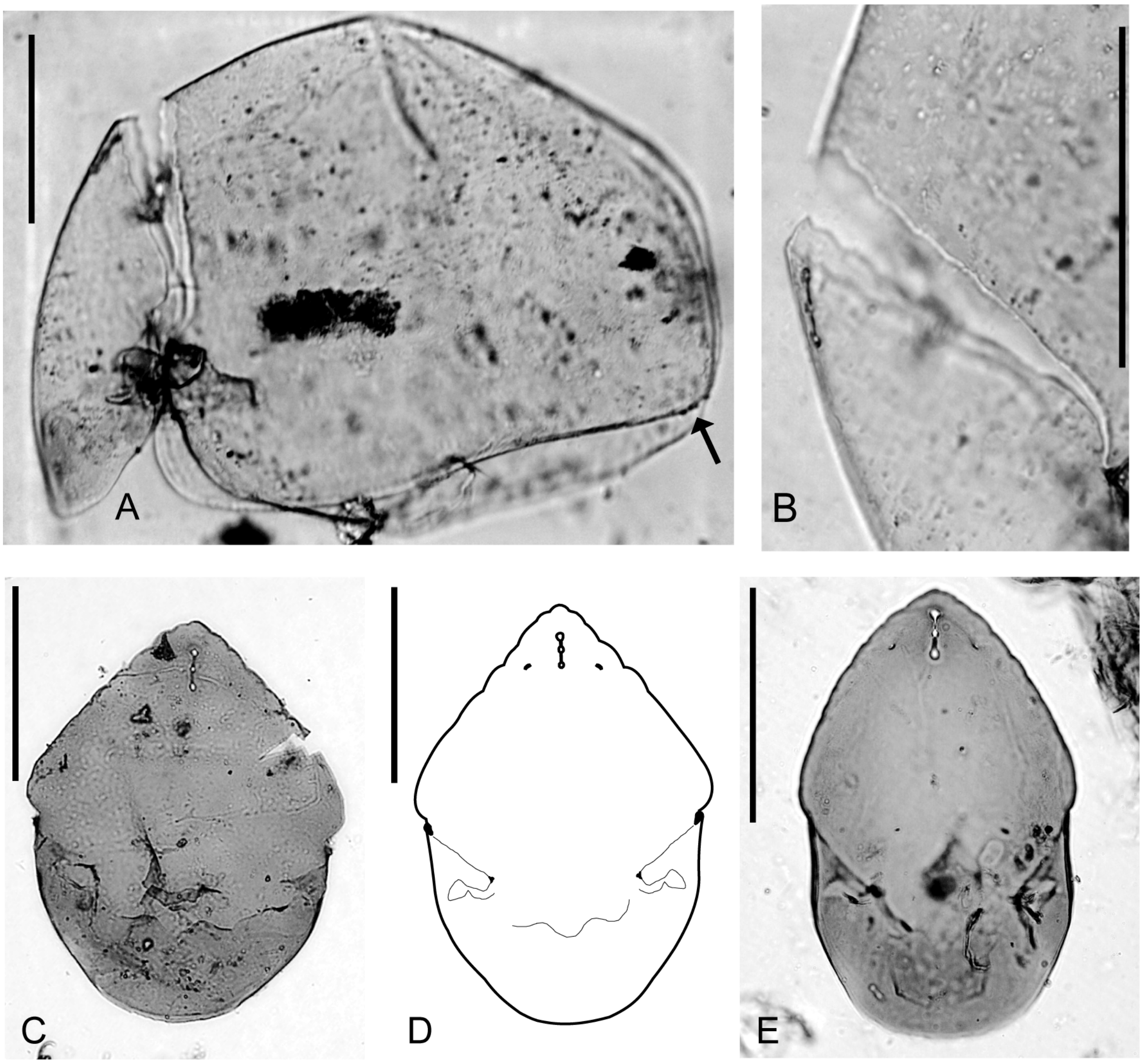

Fig. 2. A) The subfossil head shield and carapace of *Alona protzi* from Lake Sarup (ca. 6470 BC), Denmark. An arrow indicates the denticles on the posterior-ventral corner of the carapace. **B**) A detail of the opened molting seam between the head shield and carapace of *A. protzi* showing the head pores and the notched posterior margin of the head shield and the corresponding notched margin of the carapace. **C**) *A. protzi* head shield, Lake Jelonek (ca. 1000 AD), Poland. **D**) Drawing of *A. protzi* head shield, original from Lake Väike Juusa (post 0 AD; Koff *et al.* 2005), Estonia. E) *A. protzi* head shield, Lake Krowie Bagno (ca. 7000–6300 BC), Poland, the curvature of the head shield makes it look exceptionally narrow. Scale bar = 100 µm.

mont 2007). However, when compared to the drawing of *A. phreatica* in Alonso (1996), the notched structure of the head shield appeared more pronounced and symmetric. Intact *A. phreatica* was first described by Dumont (1983) and Sabater (1987) (male) and was reported to be similar to *A. protzi* but lacking the denticles on the posterior-ventral corner of the carapace. *A. phreatica* is entirely limited to a groundwater mode of life (stygobiont) (Dumont 1983, 1987, 1995, Dumont, Negrea 1996, Brancelj, Dumont 2007).

Identification of the head shield remained uncertain until the finding of five specimens with head shield and carapace still attached (Fig. 2A,B). The valves of *Alona protzi* differ from most of the European *Alona* by the presence of denticles on the postero-ventral corner of the carapace (Smirnov 1974, Røen 1995, Flössner 2000). The only other *Alona* species with denticles, *A. affinis* (Leydig, 1860) *var. dentata*, is clearly larger than *A. protzi*, the length of adult specimen exceeding 0.7 mm (see Smirnov 1974, Sinev 1997). Denticles are also found on the valves of *Karualona iberica* (Alonso, Pretus 1989), a former member of the *Alona* genus (Dumont, Silva-Briano 2000). *K. iberica* has 4–5 small, sharp, equally-sized denticles, which are located at significant length from each other on the valves that are covered by prominent lines with fine striae in between (Alonso, Pretus 1989). *A. protzi* normally has only 2–3 closely clustered denticles, which are blunt and have a relatively wide base. In addition, these species clearly differ in the number of head pores. *A. protzi* has 3 head pores, while *A. affinis var. dentata* and *Karualona iberica* have 2 head pores (Smirnov 1974, Alonso, Pretus 1989).

Two of the five specimens found with head shield and carapace attached clearly exhibited an *A. protzi* carapace with three characteristic denticles in the posterior-ventral corner (Smirnov 1974, Røen 1995, Flössner 2000) and a surface sculpture of horizontal lines typical to *A. protzi* (Kay van Damme, pers. communication). The carapace closely resembled the picture and description of the subfossil *A. protzi* carapace in Nykänen, Sarmaja-Korjonen (2007). Two other specimens exhibited at least one and two denticles, respectively, but without visible horizontal lines. The exact number of denticles was impossible to determine because of debris covering them on the permanent (mounted in glycerol gelatine) slide. The fifth specimen had neither lines nor denticles, but the shape of the carapace closely resembled those in Nykänen, Sarmaja-Korjonen (2007). According to Flössner (2000), denticles may be missing on rare occasions.

Description of A. protzi head shield

The head shield of *A. protzi* (Fig. 2B–E) is small, only ca. 200 μm long (the measured head shields ranged from 194 to 230 μm; n = 15). Its width is difficult to estimate due to the frequently occurring curvature of the head shield on sample slides, which creates a false impression of it being narrower than in reality (Fig. 2E). Three specimens appeared entirely 'flat' (Fig. 2C, D), two of which were 167 μm and one 170 μm wide.

The posterior margin is notched and more tapered than for other small European *Alona* species. The notches begin slightly anterior to the first median pores and the lateral pores. The depth of the notches varies between specimens. Three median pores are narrowly connected and situated close to the posterior margin. The postpore distance (the distance between the posterior pore and the posterior margin) is smaller than the interpore distance (the distance between the anterior and posterior pores). Two minor pores are situated laterally at approximately the level of the anterior pore. In subfossil head shields the minor pores appear as narrow oblong depressions at the same angle as the posterior margin. The head shield is widest just behind the fornices. The rostrum is short and very broadly rounded, sometimes almost flat. Chitin appears thickened in the anterior region and in many specimens the posterior edge of the thickening is undulating.

Abundance of A. protzi head shields in sediments

Generally, *A. protzi* is referred to as a rare species (Dumont 1983, Røen 1995, Flössner 2000). Most zooplankton investigations and monitoring programs focus on pelagic samples and do not encompass the littoral zone, which may partly explain the rarity of the species in contemporary samples. However, in paleolimnological studies, as well as in investigations where living individuals have been sampled directly in the littoral zone, *A. protzi* has also been rare, even in studies including numerous lakes (Smyly 1958, Whiteside 1970, Jones 1989, Cotten 1985, de Eyto *et al.* 2003, Bjerring *et al.* unpublished, Nykänen *et al.* unpublished). Admittedly, in our samples the abundance of subfossil *A. protzi* head shields was low, constituting a median of only 1% and 0.6% of the total subfossil Chydoridae head shields per sample (n = 47 samples) and per lake (n = 13 lakes, Table 1), respectively. Generally, the percentage was lower than 0.5% of all counted cladoceran remains in the samples (n = 45). To our knowledge, with one exception (Nykänen, Sarmaja-Korjonen 2007), comparable abundance data have not been reported in the literature. The low abundance has prevented the inclusion of this species in studies of the relationship between cladocerans and their environment, even in multi-lake studies (>70 lakes) (e.g. Whiteside 1970, Jones 1989).

Environmental characteristics of the lakes

Characteristics of the sites with contemporary findings

Contemporary (1986–2002) morphological and limnological data were available for 6–13 lakes depending on the variable in question (Table 1). Additionally, we had contemporary data for 4 lakes in which *A. protzi* has previously been found in the form of subfossil carapaces in the sediment or as intact animals in the littoral zone (Nykänen, Sarmaja-Korjonen 2007). The lakes varied widely in area and depth, exhibiting no clear pattern. This is in contrast to Røen (1995) who claimed that *A. protzi* prefers small clear water lakes. Most of the discovery sites were meso- to eutrophic (Table 1), although two findings were made in lakes (Lake Velling Igelsø and Lake Riikoisten Valkjärvi) with relatively low phosphorus (15 μg total P L^{-1}) and low chlorophyll *a* concentrations (≤10 μg chl *a* L^{-1}). These two lakes also had low alkalinity (≤ 0.2 mmol L^{-1}), while alkalinity was moderate (median: 0.7 mmol L^{-1}) and pH values predominantly neutral to high (6.2–8.7; median 7.8) in the other lakes. Thus, for most contemporary variables one or two measurements were in the low or high end of the spectrum (Table 1), indicating that *A. protzi* may be rather widely distributed seen from an ecological perspective.

Due to the use of different sampling protocols there were no consistent and comparative data on macrophytes between sites. However, six lakes investigated for submerged macrophytes all showed very low or zero percente plant-filled volume of the lake (Table 1). Area-based may though be larger in some lakes owing to small macrophyte inhabitants, such as isoetids.

Characteristics of the sites with findings in older sediments

In 4 Danish lakes *A. protzi* head shields were found in 6 sediment samples (1850–1950 AD). Recently, *i.e.* in year 2000, these lakes differed as to nutrient state, alkalinity and land cover of catchments. The diatom-inferred epilimnetic total phosphorous (DI-TP) level in concurrent, old samples varied widely, from 14 to 164 μg TP L^{-1} (Bradshaw *et al.* 2006, Amsinck *et al.* 2003). The dominance of *Chydorus sphaericus* in Lake Mølle Sø and Lake Ved Sø, as well as the dominance of *Alona quadrangularis* in Lake Hvidsø, indicated relatively eutrophic conditions in these lakes. Instead, Lake Velling Igelsø (DI-TP 14–18 μg L^{-1}) was dominated by *Alonella excisa* and *Acroperus* spp. In this lake, as well as in the *C. sphaericus* dominated Lake Mølle Sø, *A. protzi* head shields occurred also in the surface sediment. These two lakes differed greatly in DI-TP values (18 and 152 μg L^{-1}, respectively), but shared the feature of a relatively constant DI-TP through 1850–2000 AD (Amsinck *et al.* 2003).

In six lakes, *A. protzi* remains were found in sediments older than 1400 AD. One head shield was found in Lake Hampträsk, Finland (Fig. 1, Table 1) (Nevalainen, unpublished), where the depth of the sample (44 cm) corresponded to the 14th century. The concurrent cladoceran assemblage suggested relatively low trophy. However, the dominance of *C. sphaericus* and the presence of *Disparalona rostrata* suggested that Lake Hampträsk was probably mesotrophic, the latter species being untypical for Finnish oligotrophic lakes (TP < 10 μg L^{-1}). Seven head shields were found in Lake Väike Juusa, Estonia (Fig. 1, Table 1) (Koff *et al.* 2005), with an approximate time range from 2000 BC to AD 1000. The cladoceran assemblage (*e.g. Alona rectangula*, *Leydigia* spp. and *Pleuroxus* spp.) indicated eutrophy. The disappearance of the species was likely connected to the transformation of the lake shore into a mire.

Nine head shields were found in Poland (Fig. 1, Table 1). Five of them occurred in Krowie Bagno Basin (ca. 7000–6300 BC) before it turned into a mire, and the concurrent faunal assemblages suggested eutrophic conditions (Szeroczyńska 2003). Three head shields were found in Lake Wigry (*ca.* 6300 BC) in a sample indicating mesotrophic conditions (Zawisza, Szeroczyńska 2007). The head shield from Lake Jelonek corresponded to ca. AD 1000, and the cladoceran assemblage indicated meso/eutrophic conditions (Zawisza, unpublished). In total 21 head shields were found in Danish Lake Sarup (ca. 6700–6000 BC) with 1 to 4 head shields encountered per sample. Generally, the assemblages indicated meso/eutrophic conditions with a trend towards increased productivity during the investigated period (Bjerring 2007).

Ecology and distribution of A. protzi

Our results showed that *A. protzi* occurs under various environmental conditions and has no clear preference to, for instance, lake area or depth. The species appeared mainly in meso-eutrophic lakes with neutral or high pH and was not found in lakes with TP < 14 μg L^{-1} or pH < 6.

Generally, *A. protzi* is described as a pelophilic and phytophilic species living in silt, on algae-covered stones or among macrophytes (Røen 1995, Dumont, Negrea 1996, Flössner 2000). In correspondence with this, two intact individuals of the species were found on a sampling site with rocky bottom and only sparse vegetation in Lake Sylvöjärvi, Finland (Nykänen, Sarmaja-Korjonen 2007). In Lake Lovonjärvi, Finland, *A. protzi* inhabited artificial substratum placed among submerged littoral macrophytes (Uimonen 1985). However, the 6 lakes investigated for submerged macrophytes in this study all showed very low or no plant-filled volume of coverage (Table 1). At our finding sites, the overall submerged plant-filled volume seemed insignificant for *A. protzi.* Furthermore, *A. protzi* abundance correlated significantly ($p < 0.05$, n = 21 samples) with the abundance of the sediment-associated species *Leydigia leydigi* and *Pleuroxus uncinatus*, as well as with the sum of all sediment-associated Cladocera species found in the old sediment of Lake Sarup (Bjerring *et al.*, unpublished).

The obvious rarity of *A. protzi* and the relatively wide environmental spectrum of finding sites (Table 1) may have two explanations: (i) unknown species specific requirements or (ii) the proposed connection of *A. protzi* to groundwater, which implies that *A. protzi* only occasionally appears in open fresh water or streams (Dumont 1983, 1987, 1995, Dumont, Negrea 1996). Formerly, Dumont and Negrea (1996) classified *A. protzi* as a stygophile, because the species had been found both in and outside of groundwater. Recently, however, Brancelj and Dumont (2007) reviewed the expanding studies of caves and gravel-beds and reclassified *A. protzi* as a stygobiont, implying more strict connection to subterranean waters. With a new sampling method the species had been found regularly in the interstitial zone in Europe. However, strict stygobionts may lack eyes and ocelli, and *A. protzi* has both. Therefore, the species may still occur both in ground- and surface (epigean) waters (Brancelj, Dumont 2007). Six of our Danish finding sites and at least 2 of the Finnish sites containing *A. protzi* head shields or carapaces are to some extent groundwater fed (Bradshaw *et al.* 2006, Nykänen, Sarmaja-Korjonen, Bjerring, unpublished data). Therefore, we cannot exclude the possibility that the species mainly lives in groundwater and is only occasionally transported into lakes.

All the lakes of the present study, except Krowie Bagno (presently a bog), are situated inside the area of the Scandinavian Ice Sheet and were created after the retreat of the glacier in the late Pleistocene or the early Holocene. Therefore, *A. protzi* must have spread northwards from unglaciated refugia, together with other cladoceran species, colonizing new water bodies. Our results indicate that in spite of its rarity the species has a relatively wide geographical distribution in northern Europe. According to the recent data, *Alona protzi* is distributed mostly in Europe. It has been found in the European part of Russia from Karelia to Caucasus, North and Central Europe, including Scandinavia and Finland, Ireland, England, Belgium, Germany, Poland, the Czech Republic, Slovakia, Hungary and Romania (see Smirnov 1974, Negrea 1988, Flössner 2000, Brancelj, Dumont 2007). It has also been observed in Turkey (Ustaoglu 2004), but not in Italy or Spain (Alonso 1996, Margaritora 1985).

CONCLUSIONS

In this study, we described the subfossil head shield of *Alona protzi*, which can be distinguished by its characteristic shape with a short rounded rostrum and a tapering, notched posterior margin. The head shield of *A. protzi* closely resembles that of *Alona phreatica* in Alonso (1996), although the notches of *A. protzi* seem more pronounced and symmetric.

We found *A. protzi* head shields and carapaces in lake sediments from Denmark, Sweden, Finland, Estonia and Poland, and *A. protzi* is thus relatively widely distributed in the northern part of Europe. Despite its wide distribution, the abundance numbers were low. The environmental spectrum of the finding sites was wide, ranging from relatively nutrient poor clear water lakes to highly eutrophic, turbid lakes. Most lakes, however, were meso-eutrophic with neutral to high pH and relatively low abundance of submerged macrophytes. Therefore, provided that the occurrence of *A. protzi* in lakes is not merely occasional due to a groundwater mode of life (c.f. Brancelj, Dumont 2007), its remains in lake sediments could tentatively be used as indicators of higher trophy and pH.

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