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Further evidence of trans-Atlantic colonization of Western Europe by American Atlantic sturgeons

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ABSTRACT: Ancient DNA analyses were used for species identification of archaeological samples from the East Baltic region (Poland) and two archived sturgeon specimens from Great Britain. DNA of seven samples (out of 36) were successfully amplified. Only mitochondrial haplotypes of Atlantic sturgeon, *A. oxyrinchus*, were observed. Six samples shared haplotype A (Accession number AF162716); the seventh specimen (caught in the River Don at Barnby Dun 1860) had a new haplotype (EU684143) which differed in one substitution from haplotype A. European sturgeon, *A. sturio*, was not found. The outcome of this study confirms the existence of Atlantic sturgeons in Baltic rivers since the early Middle Ages.

KEYWORDS: STURGEON, *Acipenser oxyrinchus*, ANCIENT DNA, EUROPE

RESUMEN: Se han realizado una serie de análisis de ADN antiguo para determinar la asignación específica de una serie de muestras arqueológicas procedentes del Báltico oriental (Polonia) y dos especímenes almacenados de esturión procedentes de Gran Bretaña. El ADN de siete de los 36 esturiones pudo ser amplificado y sólo haplotipos del esturión atlántico *Acipenser oxyrinchus* han sido detectados. Seis muestras compartían el haplotipo A de esta especie (número de acceso AF162716), en tanto que el séptimo, capturado en 1860 en Barnby Dun, en el río Don, presentaba un nuevo haplotipo (EU684143) que difería en una substitución del haplotipo A. No se han encontrado haplotipos del esturión europeo *A. sturio*. El resultado de este estudio confirma la existencia del esturión atlántico en los ríos bálticos desde la alta Edad Media.

PALABRAS CLAVE: ESTURIÓN, *Acipenser oxyrinchus*, ADN ANTIGUO, EUROPA

INTRODUCTION

One decade ago it was commonly accepted that both species of sea sturgeon, *Acipenser sturio* and *A. oxyrinchus*, were separated by geographical distance. The European sturgeon, *A. sturio*, inhabited all major tributaries of the European coast of the Atlantic Ocean, Black, Mediterranean, Adriatic, North and Baltic seas before it became extinct during the 18th and 19th centuries. Today, there is only one relict population in the Gironde River, France. The American Atlantic sturgeon, *A. oxyrinchus*, was discussed as restricted to rivers and coastal waters ranging from the Gulf of Mexico to the Gulf of St. Lawrence. In 2002, this view was changed by a study of archived specimens and archaeological samples indicating a trans-Atlantic colonization of the Baltic Sea by this species during the Middle Ages (Ludwig *et al*., 2002; Ludwig *et al*., 2008a). The oldest evidence of sturgeons in the Baltic region dates to the 4th millennium BC (Makowiecki, 2008). There exists archaeological evidence (Table 1) that sturgeon colonized several European river systems during this time (Benecke, 2009, unpublished data). Following this first evidence for their presence in Baltic waters, sturgeon remains were subsequently found there during the Early Iron Age and are frequently observed in samples, particularly at coastal sites, from the 10th to the 14th centuries AD (Makowiecki, 2008).

Although one specimen from the North Sea (Elbe River) population was identified as American Atlantic sturgeon (Ludwig *et al*., 2002), their presence in the Western Baltic region has been under discussion. Additionally, no evidence was observed for Iberian or Mediterranean rivers recently (Ludwig *et al*., 2008b; Pagès *et al*., 2008). Knowledge about the genetic structure of extinct populations is an important prerequisite for understanding their historic colonization routes. The samples used in this study include two historic specimens from British rivers that considerably extend the range of the species and shed light on the recent history of the American Atlantic sturgeon in Europe.

MATERIALS AND METHODS

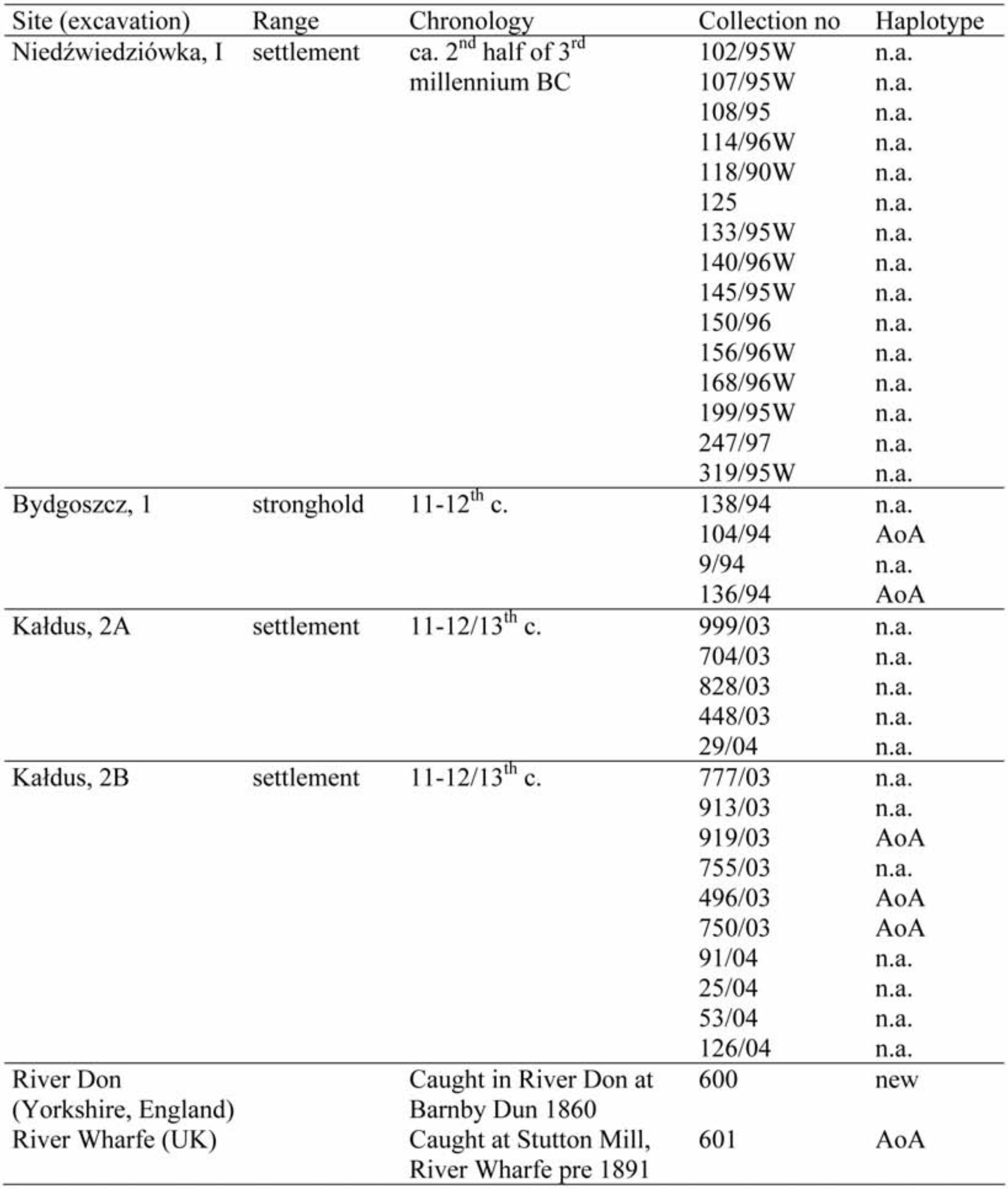
Thirty-four samples were included in these analyses originating from three Polish archaeological excavations. Additionally, two archived British specimens were analyzed (Table 2).

Extraction and PCR was carried out in the trace-lab in Mainz following the guidelines for ancient DNA (Hofreiter, 2001; Ludwig *et al*., 2009a); sequencing took place at the Leibniz Institute for Zoo and Wildlife Research in Berlin. To detect contamination and to assure the reliability of the obtained sequences blank controls and two PCRs were obtained per sample. In addition, samples were reproduced in a second extraction with at least one additional PCR. No sturgeon had been analyzed in the trace lab before. No contamination was detected during the entire study. DNA was extracted as described in Burger *et al*. (2004) [see also Ludwig *et al*. (2008a)]. Blank controls were carried out with every extraction. Concentrated DNA was diluted in 160-200µl UV-irridated HPLC H_2O and stored at –20°C for further analysis. PCR (30µl) contained 1x buffer, 0,19mM dNTP-Mix, 1,9mM $MgCL_2$, 1,5U AmpliTaq Gold, 1µl BSA, and 0,19pmol/µl primer. For this study, the primer Hetero I+II (Ludwig & Jenneckens, 2000) and RevA (Ludwig *et al*., 2000) as a possible substitute for Hetero II were used as previously described (annealing temperature 50° C). Cloning and cycle sequencing were done by standard procedures. Sequence PCR was purified in an ethanol precipitation preceded by a SDS step. Sequences were analyzed using a ABI 3100 (Applied Biosystems). Basic phylogenetic trees (distances, Neighbor-Joining, 1,000 bootstrap replicates) were calculated using MEGA 3.1. Intraspecific relationships were analyzed using NETWORK 4.5.0.0.

RESULTS AND DISCUSSION

The outcome of our study indicates that *A. oxyrinchus* was the common species in the entire Baltic region as early as at the 8th century AD. Taking previous studies (Ludwig *et al*., 2002) into account, we further conclude that *A. sturio* was very rare during the Middle Ages in Baltic waters. Archaeological evidence (Table 1; Makowiecki, 2008) suggested an earlier colonization of Baltic waters probably by European sturgeons. However, without genetic proof, it is not possible to decide which species originally occupied this region. Early remains are very rare and often of poor quality. Taking into account the state of the art of ancient DNA techniques, it makes little sense to use these for genetic profiling at the moment.

Although sturgeon hybrids have been described (Ludwig *et al*., 2009b), we observed no evidence



Site (excavation)	Range	Chronology	Collection no	Haplotype
Niedźwiedziówka, I	settlement	ca. 2nd half of 3rd millennium BC	102/95W	n.a.
			107/95W	n.a.
			108/95	n.a.
			114/96W	n.a.
			118/90W	n.a.
			125	n.a.
			133/95W	n.a.
			140/96W	n.a.
			145/95W	n.a.
			150/96	n.a.
			156/96W	n.a.
			168/96W	n.a.
			199/95W	n.a.
			247/97	n.a.
			319/95W	n.a.
Bydgoszcz, 1	stronghold	11-12th c.	138/94	n.a.
			104/94	AoA
			9/94	n.a.
			136/94	AoA
Kałdus, 2A	settlement	11-12/13th c.	999/03	n.a.
			704/03	n.a.
			828/03	n.a.
			448/03	n.a.
			29/04	n.a.
Kałdus, 2B	settlement	11-12/13th c.	777/03	n.a.
			913/03	n.a.
			919/03	AoA
			755/03	n.a.
			496/03	AoA
			750/03	AoA
			91/04	n.a.
			25/04	n.a.
			53/04	n.a.
			126/04	n.a.
River Don (Yorkshire, England)		Caught in River Don at Barnby Dun 1860	600	new
River Wharfe (UK)		Caught at Stutton Mill, River Wharfe pre 1891	601	AoA

TABLE 1

Origin of samples.

for a Baltic hybrid population between the European and Atlantic sturgeon as has been recently suggested (Tiedemann *et al*., 2007). More likely, if *A. sturio* was present during the Early Middle Ages, it was completely replaced by *A. oxyrinchus* in the western, eastern and southern part of the Baltic Sea. Absence of genetic data from today extinct Lake Ladoga population, connected to the Baltic Sea by the Neva River, are not available thus far. Drawings of archaeological scutes of the Ladoga sturgeon are

Location	I	II	III	IV	V	VI	VII	VIII	IX
Sweden				2	3		1	6	
Denmark					1		1	1	1
Great Britain								10	
The Netherlands				1	10	8	5	5	
Belgium								8	5
Germany				2		2	7	19	2
Poland				2	1	4		50	3
France				1		1	1	2	
Spain	5		1	1	2	4	1	1	
Portugal			2	1				1	

TABLE 2

Evidence of sturgeon on archaeological sites of Western and Central Europe according to periods: I 15000-9000 BC, II 9000-7000 BC, III 7000-5500 BC, IV 5500-3000 BC, V 3000-1000 BC, VI 1000 BC – 0, VII 0-600 AD, VIII 600-1500, IX 1500-1900 (Source: N. Benecke, unpublished database).

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#AsG  TAAGATTCTACATTAAACTATTCTCTGACCACATGTCTGACCCAT---ACCAATGTCTGCATACATTAAA[70]
#Asl7 .............................................---......................[70]
#AoA  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoA1 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoA2 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoA3 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoA4 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoB  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoB1 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoC  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoC1 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoC2 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoC3 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoD  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoD1 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoD2 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoE  ...........................G...T..CA-..CT.GCCTAC........T.--.C........[70]
#AoE1 ...........................G...T..CA-..CT.GCCTAC........T.--.C........[70]
#AoE2 ...........................G...T..CA-..CT.GCCTAC........T.--.C........[70]
#AoE3 ...........................G...T..CA-..CT.GCCTAC........T.--.C........[70]
#AoN  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoN1 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoN2 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoO  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP1 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP2 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP3 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP4 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP5 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP6 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP7 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP8 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP9 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoP10...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoQ  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoR  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoS  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoS1 ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoT  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AoU  ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AodF ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AodG ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AodH ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
#AodI ...........................G...T..CA-..CT.GCCTAC........T.--..........[70]
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FIGURE 1

Alignment of partial d-loop sequences. Accession number of new sequence (Ao600) is EU684143; all others are available at Genbank. Reference sequences for *Acipenser sturio* (AsG [AJ249673] = Gironde sturgeon and As17 [AJ428274] = archived sample originating from the Adriatic Sea) as well as *A. oxyrinchus* haplotype AoA (AF162716) were taken from Genbank.

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#AodJ ...........................G...T..CA-..CT.GCCTAC........T.--...........[70]
#AodK ...........................G...T..CA-..CT.GCCTAC........T.--...........[70]
#Ao600...........................G...T..CA-..CT.GCCTAC........T.--...........[70]

#AsG  TTGTACATACATAAACATACTATGTTTAATCCCCATTAATTTCTAGCCACCAATACTAATGTTTACCTAT[140]
#Asl7 ........................................................C.............[140]
#AoA  ...CTT..G...GG.....T..........................T.....-...C........TA...[140]
#AoA1 ...CTT..G...GG.....T..........................T.....-...C........TA...[140]
#AoA2 ...CTT..G...GG.....T..........................T.....-...C........TA...[140]
#AoA3 ...CTT..G...GG.....T..........................T.....-...C........TA.G.[140]
#AoA4 ...CTT..G...GG.....T..........................T.....-...C........TAC..[140]
#AoB  ..ACTT..G...GG.....T..........................T.....-...C........TA...[140]
#AoB1 ..ACTT..G...GG.....T..........................T.....-...C........TA...[140]
#AoC  ...CTT..G...GG................................T.....-...C........TA...[140]
#AoC1 ...CTT..G...GG................................T.....-...C........TA...[140]
#AoC2 ...CTT..G...GG................................T.....-...C........TA...[140]
#AoC3 ...CTT.CG...G.................................T.....-...C........TA...[140]
#AoD  ...CTT..G...GG................................T.....-..TC........TA...[140]
#AoD1 ...CTT..G...GG................................T.....-..TC........TA...[140]
#AoD2 ...CTT..G...GG................................T.....-..TC........TA...[140]
#AoE  ...CTT..G...GG.....T..........................T.....-...C........TA...[140]
#AoE1 ...CTT..G...GG.....T..........................T.....-...C........TA...[140]
#AoE2 ...CTT..G...GG.....T..........................T.....-...C.........A...[140]
#AoE3 ...CTT..G...GG.....T..........................T.....-...C........TA...[140]
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#AoO  ...CTT..G...GG................................T.....-..TC.......GTA...[140]
#AoP  ...CTT......GG................................T.....-...C....C...TA...[140]
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#AoP3 ...CTT......GG................................T.....-...C........TA...[140]
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#AoP6 ...CTT......GG................................T.....-...C........TA...[140]
#AoP7 ...CTT......GG................................T.....-...C........TA...[140]
#AoP8 ...CTT......GG................................T.....-...C........TA...[140]
#AoP9 ...CTT..G...GG................................T.....-...C........TA...[140]
#AoP10...CTT..G...GG................................T.....-...C........TA...[140]
#AoQ  ...CTT..G...GG................................T.....-..TC........TA...[140]
#AoR  ..ACTT..G...GG................................T.....-...C........TA...[140]
#AoS  ...CTT..G...GG................................T.....-..TC........TA...[140]
#AoS1 ...CTT..G...GG................................T.....-..TC........TA...[140]
#AoT  ...CTT..G...GG................................T.....-...C........TA...[140]
#AoU  ...CTT..G...GG................................T.....-...C........TA...[140]
#AodF ...CTT......GG................................T.....-...C........TA...[140]
#AodG ...CTT......GG................................T.....-...C........TA...[140]
#AodH ...CTT......GG.....T..........................T.....-...C........TA...[140]
#AodI ...CTT......GG................................T.....-...C........TA...[140]
#AodJ ...CTT......GG................................T.....-...C........TA...[140]
#AodK ...CTT......GG................................T.....-...C........TA...[140]
#Ao600...CTT..G...GG.....T..........................T.....-...C........TA...[140]

#AsG  ATATTAAATTATCTAAGTACATAGACATACTATGTTTAATCCCCATTAATTTCTAGTCAACATATCA[207]
#Asl7 ...................................................................[207]
#AoA  .C.....GCC..T.........GA.............T...........C......C..CT...A..[207]
#AoA1 .C.....GC...T.........GA.............T...........C......C..CT...A..[207]
#AoA2 .C.....GCC..T..G......GA.............T...........C......C..CT...A..[207]
#AoA3 .C.....GCC..T.........GA.............T...........C......C..CT...A..[207]
#AoA4 .C.....GCC..T.........GA.............T...........C......C..CT...A..[207]
#AoB  .C.....GCC..T.........GA.............T...........C......C..CT...A..[207]
#AoB1 .C.....GCC..T.........GA.............T...........C.........CT...A..[207]
#AoC  .C......CC..T.........GA.............T...........C......C..CT...A..[207]
#AoC1 .C......CC..T.........GA.............T...........C..T...C..CT...A..[207]
#AoC2 .C......CC..T.........GA.............T...........C......C..GT...A..[207]
#AoC3 .C......CC..TC........GA.............T...........C......C..CT...A..[207]
#AoD  .C.....GCC..T.........GA.............T...........C.........C....A..[207]
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#AoD2 .C.....GCC..T.........GA.............T...........C..T......C....A..[207]
#AoE  .C.....GCC..T.........GA.............T...........C......C..CT...A..[207]
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#AoE3 .C.....GCC..T.........GA.............T...........C.........CT...A..[207]
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#AoN2 .C.....GCC..T.........GA.............T...........C......C..CT...A..[207]
#AoO  .C.....GCC..T.........GA.............T...........C.........C....A..[207]
#AoP  .C.....GCC..T.........GA....G........T....T......C......C..CT...A..[207]
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FIGURE 1

(cont.)

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#AoP1 .C.....GCC..T.........GA.....T.......T...........C......C..CT...A..[207]
#AoP2 .C.....GCC..T.........GA....G........T...........C......C..CT...A..[207]
#AoP3 .C.....GCC..T.........GA....G........T...........C......C..CT...A..[207]
#AoP4 .C......CC..T.........GA.............T...........C......C..CT...A..[207]
#AoP5 .C.....GCC..T.........GA....G........T...........C.........CT...A..[207]
#AoP6 .C.....GCC..T.........GA....G........TG..........C.........CT...A..[207]
#AoP7 .C.....GCC..T.........GA....G.......CTG...T......C......C..CT...A..[207]
#AoP8 .C.....GCC..T.........GA....G........TG...T......C......C..CT...A..[207]
#AoP9 .C.....GCC..T.........GA....G........T....T......C......C..CT...A..[207]
#AoP10.C.....GCC..T.........GA....G........T...........C.........CT...A..[207]
#AoQ  .C.....GCC............GA.............T....T......C......C..C....A..[207]
#AoR  .C......CC..TC........GA.............T...........C......C..CT...A..[207]
#AoS  .C.....GCC..T.........GA.............T...........C......C..C....A..[207]
#AoS1 .C.....GCC..T.........GA.............T...........C...C..C..C....A..[207]
#AoT  .C.....GCC..T.........GA.............T...........C......C..C....A..[207]
#AoU  .C.....GCC..T.........GA.............T...........C.........C....A..[207]
#AodF .C.....CCC..T.........GA....GT.......T....T......C.........CT...A..[207]
#AodG .C.....CCC..T..........A....GT.......T....T......C.........CT...A..[207]
#AodH .C.....GCC..T.........GA....GT.......T...........C.........CT...A..[207]
#AodI .C.....GCC..T.........GA....GT.......T...........C.........CT...A..[207]
#AodJ .C.....CCC..T.........GA....GT.......T....T......C.........C....A..[207]
#AodK GC.....GCC..T..........A....GT.......T....T................CT...A..[207]
#Ao600.C.....GCC..T.........GA.T...........t...........C......C..CT...A..[207]
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FIGURE 1

(cont.)

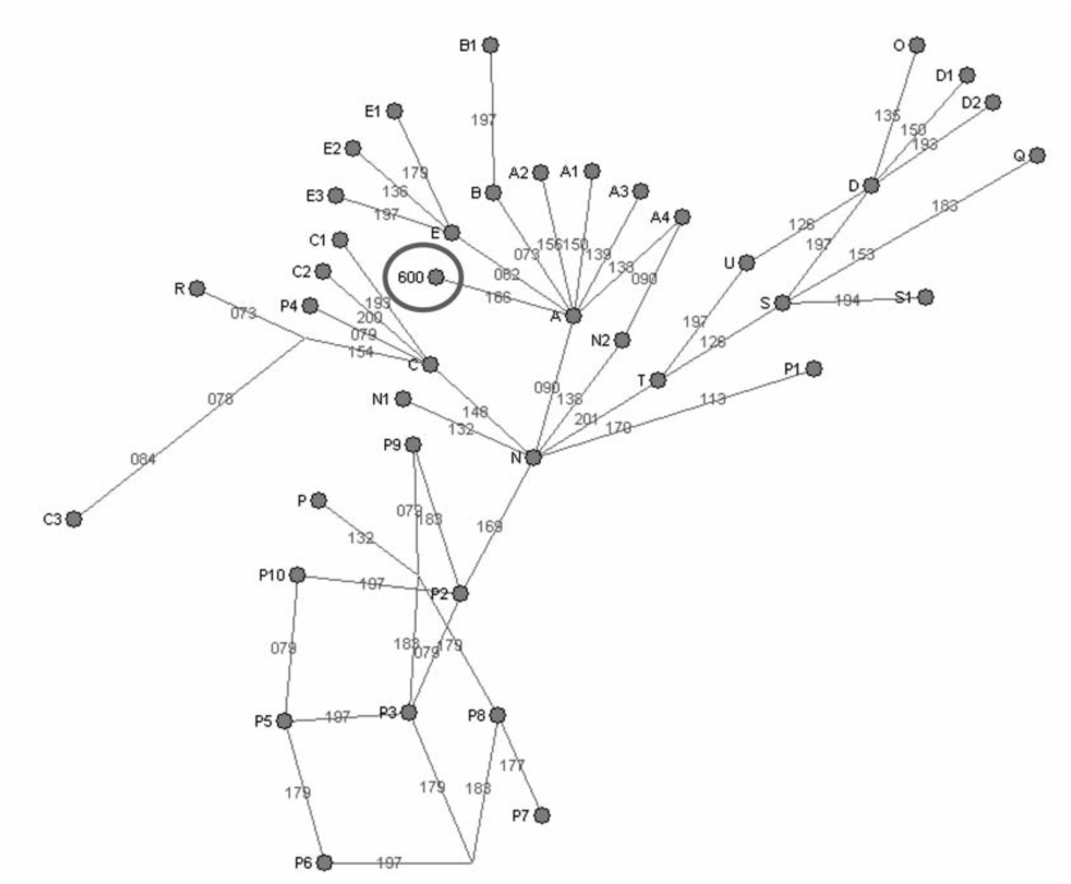

FIGURE 2

Median Joining network calculated in Network 4.5.0.0 (Fluxus Technology Ltd.) based on partial d-loop sequences. New haplotype is marked by a circle.

very similar those of *A. sturio*. Thus, a population of *A. sturio* can not be excluded for this area, but these scutes were not archived, and therefore are not available for genetic analysis.

In agreement with Ludwig *et al*. (2002) all Polish samples shared *A. oxyrinchus* haplotype A (Figure 1), which is the dominant haplotype of the Canadian (St. Lawrence, St. John) and Mid-American (Hudson, Delaware) populations today. Most likely, haplotype A was dominant within founder individuals. Our data produced no evidence for a population subdivision of the Baltic sturgeons (Figure 2).

Although the historic existence of American Atlantic sturgeon is nowadays accepted for the Baltic Sea, evidence for other European water bodies is rare until now. The two archived samples of British origin caught during the 19th century (Table 1) provide the earliest evidence for the existence of American Atlantic sturgeon in British rivers. Depending on the path of the Gulf Stream, this finding may not be all that surprising. However, a detailed study of genetic variability of sturgeons from the British Islands is still missing, especially for sturgeons from the Atlantic side. At present, there are only a few records of European sturgeons caught in the French Canal (Williot *et al*., 1997).

Our results support the conclusion that American Atlantic sturgeon was the dominating sturgeon species in the Baltic region during the Middle Ages. For the first time, we likewise find genetic evidence for the historic existence of American Atlantic sturgeon in British rivers as well as in the South-Eastern Baltic region.

ACKNOWLEDGEMENTS

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