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Céline Maicher, Matthieu Le Bailly. First contribution of paleoparasitology to the study of the Neolithic lakeside settlement of Zürich-Opéra. Niels Bleicher; Christian Harb. Zürich-Parkhaus Opéra. Eine neolithische Feuchtbodenstelle. Band 3: Naturwissenschaftliche Analysen und Synthese, 50, pp.170-178, 2017, Monographien der Kantonsarchäologie Zürich, 978-3-906299-12-9. hal-01494842

HAL Id: hal-01494842

<https://hal.science/hal-01494842>

Submitted on 2 Aug 2023

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1 **FIRST CONTRIBUTION OF PALEOPARASITOLOGY TO THE STUDY OF**
2 **COPROLITES FROM THE NEOLITHIC SITE SERTEYA II (NW RUSSIA)**

3

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18

19 **Highlights:**

20

- 21 • Paleoparasitological analyses were performed on Neolithic coprolites from Russia.
- 22 • Four taxa of gastrointestinal parasites were detected in coprolites.
- 23 • The parasitic assemblage allows to define a canine origin of the material.
- 24 • This is the second record of parasites from coprolites in this region.
- 25 • The results allow discussing the human/animal relationship during the Neolithic.

26

27 **Abstract:**

28

29 Paleoparasitological analysis was performed on a set of ten coprolites recovered during
30 excavations of the Neolithic site Serteya II (NW Russia). Eggs of four gastrointestinal parasite
31 taxa were identified, namely the fish tapeworm genus *Diphyllobothrium*, the giant kidney
32 worm *Diocotophyma renale*, and two trematode taxa, including the liver lancet fluke genus
33 *Dicrocoelium*. The diversity of parasites enables us to discuss the biological origin of the
34 studied material, which can be attributed to carnivores, probably to canids. This is only the
35 second record of ancient parasites in this part of the world for the Neolithic period and our
36 results are consistent with those from the first study. They contribute to highlighting
37 relationships between humans and animals, and show how environments and human activities
38 can induce parasite transmission.

39 **Key Words:** Parasite; Dog; *Diphyllobothrium*; *Diocotophyma renale*; *Dicrocoelium*; *Alaria*.

40

41 1. Introduction

42

43 Paleoparasitology aims to detect the remains of ancient parasites, especially eggs produced by
44 adult gastrointestinal worms. The study of parasites in archaeological contexts can answer
45 various questions related to the health and living habits of past individuals and populations,
46 notably regarding paleodiet, hygiene, or the management of organic matter (Dittmar et al.,
47 2012; Le Bailly and Araujo, 2016). Among the material propitious to paleoparasitological
48 analysis, coprolites, i.e., mineralized or desiccated faecal matter, of human or animal origin
49 are regularly tested (Appelt et al., 2014). This is not the first time that such material is studied,
50 as several coprolites excavated from various Neolithic sites in Eurasia have already

51 undergone paleoparasitological analysis. This was the case for the Swiss site of Arbon-
52 Bleiche 3 (Le Bailly et al., 2003), the French sites of Chalain 3, 4 and 19 (Dommelier-Espejo
53 and Pétrequin, 2016), or for the Central European part of Russia (Savinetsky and Khrustalev,
54 2013).

55 During excavations of the Neolithic site Serteya II (NW Russia), large amounts of coprolites
56 were discovered, accompanied by cultural remains that date to the 3rd millennium BC. An
57 exploratory analysis was conducted to assess parasite diversity in these samples in order to
58 define the biological origin of the material, and, more generally, to enhance our knowledge of
59 human/animal relationships, and the distribution and importance of parasitism in prehistoric
60 Eastern Europe.

61

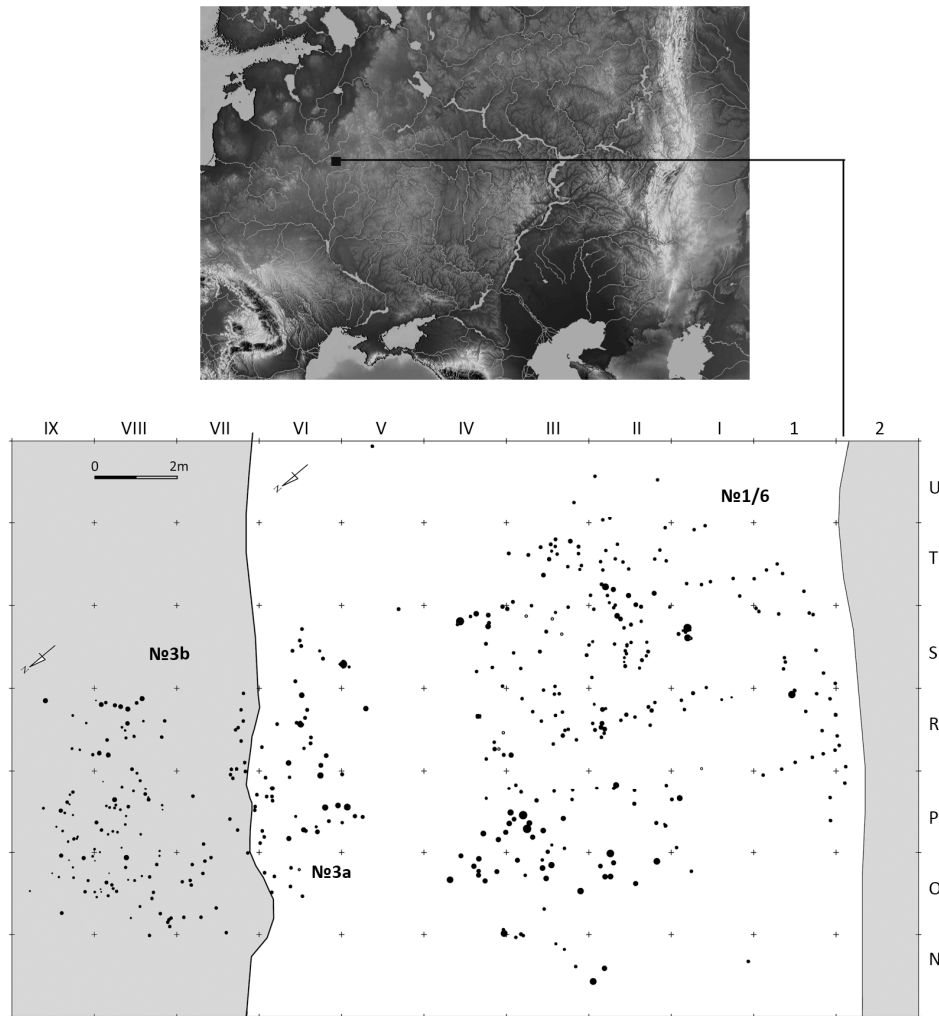
62 2. Material and methods

63

64 *2.1. The site of Serteya II and sampled material*

65

66 The site of Serteya II (55°38'22-21''N / 31°31'24-51''E) is located in the Serteya valley,
67 tributary of the Western Dvina in North Western Russia (Figure 1).



68

69 Figure 1: Above: Location of the site of Serteya II (Russia); below: Map of the excavation
 70 area of Serteya II , with location of the post holes of dwellings N°3a, 3b et 1/6. The white area
 71 corresponds to the underwater excavated zone (Photo A. Mazurkevich/E. Dolbunova).

72

73 The strong archaeological potential of the valley has been known since the 1960s, and the
 74 region was occupied by past populations periodically between the Palaeolithic and the Middle
 75 Ages (Kulkova et al., 2001; Mazurkevich et al., 2018). Studied firstly in 1970s and later from
 76 2008, the Serteya II site is an archaeological multi-layered complex with several
 77 settlements and relicts of the area occupation since the Mesolithic up to the Middle Ages. The
 78 core zone of the site located within drainage channel and its shores revealed several late

79 Neolithic pile-dwelling constructions from the 3rd millennium BC. The layer with pile-
80 dwelling constructions within coarse detritus gyttja was excavated using underwater and
81 wetland archaeological methods (Dolukhanov and Miklyayev, 1986; Mazurkevich et al.,
82 2017; Mazurkevich and Dolbunova, 2011). Until now, at least six pile-dwellings were
83 recognised, attributed to the Zhizhistskaya Culture, between ca. 2900 cal. BC and ca. 2000
84 cal. BC (Mazurkevich and Dolbunova, 2011). The constructions were established most
85 probably on a marshy shore or on the post-lake plains of an exposed lake bottom (Kittel et al.,
86 2018). Archaeological remains (lithic, ceramic, faunal, various organic artefacts and ecofacts)
87 are exceptionally preserved at Serteya II, allowing for a comprehensive approach to the study
88 of cultural influences and the complex settlement dynamics in the valley. In fact, valley
89 populations maintained a livelihood based on gathering, fishing and hunting despite contacts
90 with agro-pastoral populations (Mazurkevich et al., 2018). The inhabitants' diet was
91 dominated by hunting and fishing (Sablin and Syromyatnikova, 2009), elk (43.5% of large
92 mammal bones) and pike (52% of fish remains) (Kulkova et al., 2015; Maigrot, 2014) were
93 within the main species. During excavations, a large amount of coprolites were found,
94 especially in archaeological structure Nb. 3b with 243 pieces (Figure 1), which can be
95 attributed to middle-second half of the 3rd millennium BC. At first sight, these faeces were
96 attributed to boars and it was presumed that boars were kept on the settlement, and fed with
97 fish before being slaughtered (Mazurkevich et al., 2010).

98

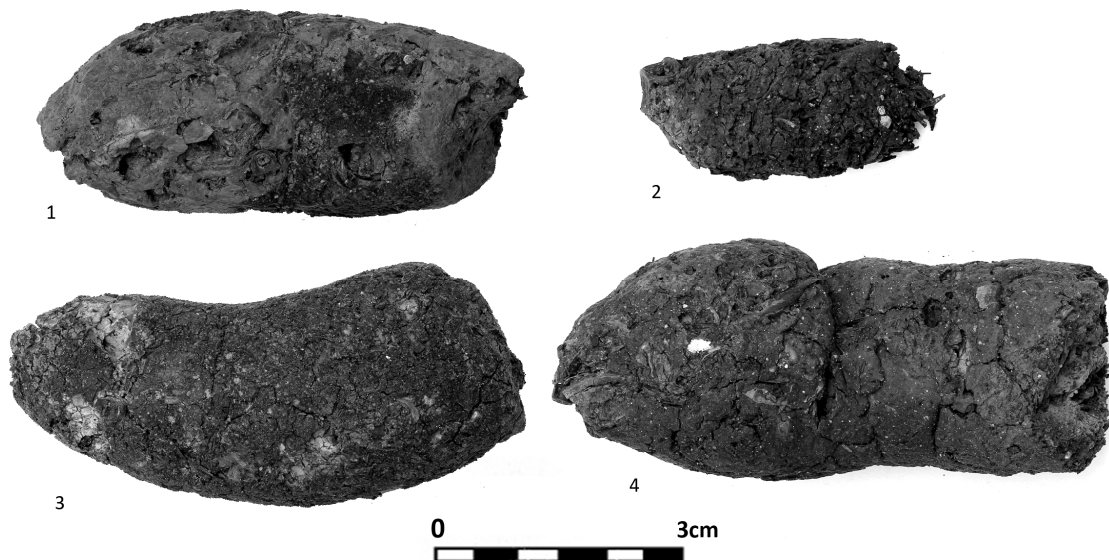
99 *2.2. Egg extraction method*

100

101 A first set of twelve samples, corresponding to ten coprolites, were proceed for
102 paleoparasitological analysis. Coprolites were first measured and weighed. They measure

103 between 3.6 to 7.2 cm in length (average 5.8 ± 1.47 cm) for 1.6 to 2.8 cm in width (average
104 2.5 ± 0.46 cm), with masses varying between 1.5 to 6 g (Figure 2).

105



106

107

108 Figure 2: Photos of four coprolites founded on the site of Serteya II: 1 – SII15 1459, 2 - SII15
109 276, 3 - SII15 1367, 4 - SII15 1495 (numbers recorded during excavations, photos: Yolaine
110 Maigrot).

111

112 In two cases (#C1 and #C5), samples were pulverulent and provided sediment associated to
113 the initial coprolite. Sediment samples were treated as single samples and labelled #C1bis and
114 #C5bis (Table I). The sizes, as well as the shapes of the coprolites, are consistent with an
115 omnivorous or carnivorous origin, and could correspond to humans, suids or canids (Chame,
116 2003). They were then prepared following the standard RHM protocol (Rehydration-
117 Homogenization-Microsieveing) used in Besancon (France) to extract and concentrate
118 gastrointestinal parasite markers (Dufour and Le Bailly, 2013). This protocol has been shown
119 as reliable and appropriate for coprolite analysis, and was used as part of a qualitative

120 approach of the parasite remains (Camacho et al., 2018). Depending on the initial weight of
121 the material, between 1 and 5 grams of each coprolite were placed for one week in a solution
122 of 0.5% tri-sodium phosphate (TSP) and 5% glycerinated water (Table 1). Samples were then
123 crushed in a mortar and placed in an ultrasound bath for one minute (50-60 Hz). Finally, the
124 sediments were filtered in a column of sieves with 315, 160, 50 and 25 μm meshes. The last 2
125 screenings were placed in 4 ml tubes with water, and drops of 10% formalin solution were
126 added to each tube to avoid fungi or algae proliferation. Ten slides from the 25 μm and 50 μm
127 fractions were observed under a light microscope (Leica DM2000 LED), and all parasite
128 markers were counted. Photos and measurements of the parasite eggs were also taken using a
129 digital camera (Leica ICC50 HD) coupled to the microscope. After analysis, all samples are
130 stored in a refrigerate room (2-4°C), and are available in the Chrono-environment laboratory
131 (Besancon, France).

132 During RHM extraction, the macroscopic content of the coprolites was screened, and a
133 number of fragments of fish scales, fish bones, vertebrae and bone splinters were observed.

134 The size of the coprolites and the contents observed during the sieving and microscopic
135 reading phase tend to attribute them to a carnivorous/piscivorous mammal.

136 In addition, the rarity of pollen grains observed during microscopic analyses is characteristic
137 of a carnivorous origin (E. Gauthier, palynologist, pers. comm.).

138

139 3. Results

140

141 Nine coprolites (90%) tested positive to the presence of gastrointestinal parasites, and only
142 one gave negative results (i.e., sample #C8). Eggs from four taxa were retrieved in the
143 samples. The number of counted eggs of each taxon is reported in Table 1.

144 Both sediment samples (#C1bis and #C5bis) gave lower parasite diversity and egg number
 145 than the coprolites from which they were obtained. In case of this preliminary qualitative
 146 study, egg number will be not considered and the results from the sediment samples will be
 147 then integrated to the results of the coprolites with which they are associated.
 148

Coprolites	Laboratory n°	Weight (g)	<i>Diphyllbothrium</i> sp.	<i>Diocotophyma renale</i>	<i>Alaria alata</i>	<i>Dicrocoelium</i> sp.
SII14 – TII	C1	1.5	16113	0	0	2
SII14 – TII	C1bis	5	122	0	0	0
SII14 – P2	C2	5	0	0	1	0
SII14 – YII 1	C3	6	15	0	0	0
SII14 – YII 2	C4	2.8	10	1	2	0
SII14 – YII 3	C5	5	4	1	1	0
SII14 – YII 3	C5bis	5	1	1	0	0
SII15 – Y18	C6	3.6	193	0	0	0
SII15 276	C7	3.9	0	1	0	0
SII15 1367	C8	16.4	0	0	0	0
SII15 1459	C9	12.7	4956	1	25	0
SII15 1495	C10	15	0	0	19	0

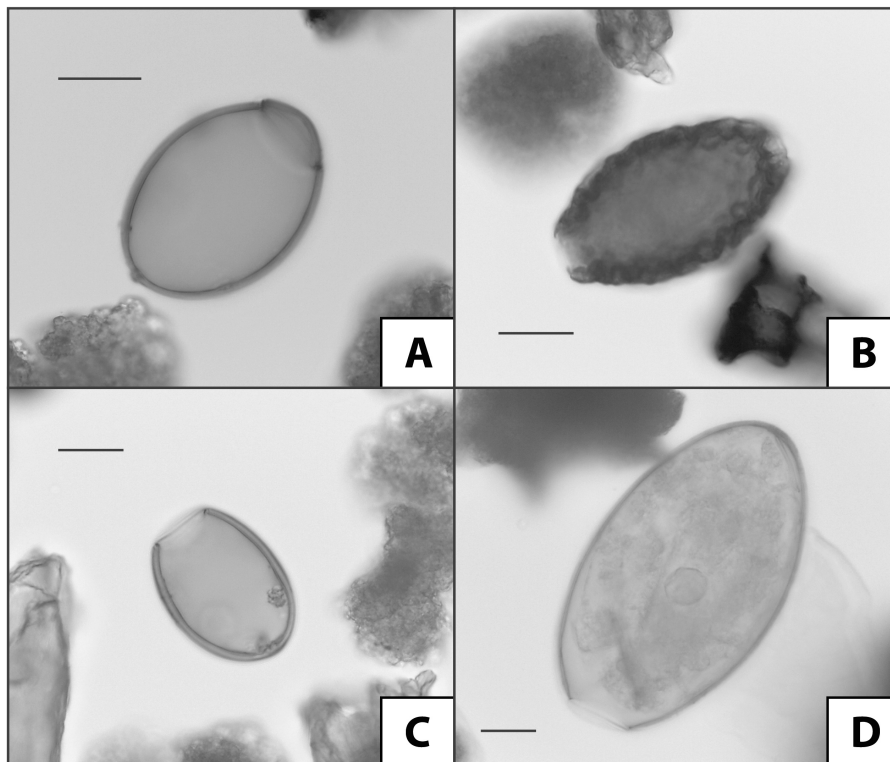
149
 150 Table 1: Results of the paleoparasitological analyses on the Neolithic site of Serteya II, with
 151 the total number of counted eggs. Greyed out samples correspond to pulverulent coprolites,
 152 which left sediment. The associated coprolites and sediment were both analysed.

153
 154 *3.1. Cestoda*

155
 156 One taxon belongs to the Cestoda class, and corresponds to the fish tapeworm genus
 157 *Diphyllbothrium*. Eggs are ovoid, operculated with a smooth thin eggshell, and present a
 158 small knob at the opposite side of the operculum. The average size is about $61 \pm 3.1 \mu\text{m}$ in

159 length and $44 \pm 3.6 \mu\text{m}$ in width (Figure 3A). The heteroxenous life cycle includes two
160 successive intermediate hosts, first a fresh water copepod, then a fish. Infection occurs when
161 fish-eating mammals ingest raw, undercooked, or insufficiently smoked or salty fish (Ash and
162 Orihel, 2007; Soulsby, 1982; Taylor et al., 2007). The parasite can cause nausea, abdominal
163 pain, diarrhoea and appetite disorder for the definitive host, sometimes accompanied by
164 anaemia. The adult worm can be up to 12 meters in length, and the possible cohabitation of
165 several worms within the same host intestine can explain the important egg concentrations in
166 some samples (Table 1). Fish tapeworm is very common in dogs and human, and its presence
167 in pigs is exceptional (Euzéby, 2008; Taylor et al., 2007).

168



169

170 Figure 3: Photos of parasite eggs retrieved on the Serteya II site. A: *Diphyllbothrium*; B:
171 *Dioctophyma renale*; C: *Dicrocoelium*; D: *Alaria alata*. Scale bar: 20 μm (Photo: Céline
172 Maicher).

173

174 3.2. Trematoda

175

176 Two of the retrieved taxa belong to the Trematoda class. The first corresponds to the lancet
177 liver fluke, genus *Dicrocoelium*. The operculated eggs present a typical asymmetric ovoid
178 shape with a thick shell, and the average size of the eggs is $46.8 \pm 0.6 \mu\text{m}$ in length and $31.5 \pm$
179 $2.6 \mu\text{m}$ in width (Figure 3C). The lancet liver fluke is a cosmopolitan parasite that can evolve
180 on wet or dry ground. Its life cycle is heteroxenous, and includes two intermediate hosts (a
181 terrestrial gastropod and an ant). The presence of parasite larvae in the ant's nervous system
182 induces a change in the ant's behaviour and leads to its ingestion and the infection of the final
183 herbivorous host. The pathology develops two forms: a chronic form (which can affect sheep,
184 goats and cattle), which is not specific, with weight loss and diarrhoea; and an acute form
185 (only present in sheep), which is more severe (Taylor et al., 2007). The lancet liver fluke
186 mainly infects herbivorous sheep, but also cattle and goats to a lesser extent. Experimental
187 analyses prove that *Dicrocoelium*, especially *D. dendriticum*, is host generalist (Beck et al.,
188 2014). In North America, where it was introduced from Europe (Le Bailly and Bouchet,
189 2010), it is commonly found in elk populations. However, in this part of the globe, *D.*
190 *dendriticum* corresponds to an invasive species and is less prevalent in elk populations in the
191 Russian central plain (Paridon et al., 2017). It has also been occasionally noted in boars, and
192 never in dogs (Euzéby, 2008; Taylor et al., 2007). Only a few cases are reported in humans,
193 and most of these correspond to a false parasitosis, resulting from the consumption of the liver
194 of an infected animal or infected ants (Euzéby, 2008). The eggs of the second trematode taxon

195 are operculated ellipsoids with an average size of about $113.5 \pm 4 \mu\text{m}$ in length and 79 ± 12.8
196 μm in width (n=10) (Figure 3D). Egg size and morphology are consistent with the species
197 *Alaria alata*. This species is common in Eastern Europe today. It can infect humans, felids,
198 mustelids and other wild carnivorous, but it is predominant in canids, especially dogs and
199 foxes (Taylor et al., 2007). Canids can be infected after the ingestion of the intermediate host
200 in the parasite lifecycle, i.e., frogs or tadpoles (Euzéby, 2008).

201 3.3. Nematoda

202

203 The last taxon belongs to the Nematoda phylum, and is identified as the giant kidney worm,
204 *Dioctophyma renale*. This uncommon parasite produces ovoid-shaped eggs with two polar
205 plugs, a thick and characteristic shell presenting polygonal depressions (Nozais et al., 1996).
206 The average size of the recovered eggs was $67.4 \pm 5.9 \mu\text{m}$ in length, and $39.3 \pm 1.2 \mu\text{m}$ in
207 width (n=5) (Figure 3B). The heteroxenous life cycle of *Dioctophyma* includes one
208 intermediate host, an oligochaete annelid, often of the genus *Lumbriculus*. A paratenic host,
209 corresponding to freshwater fish (Cyprinidae or Siluridae), or frogs of the *Rana* genus, can
210 integrate the parasite lifecycle. The definitive host becomes infected after the ingestion of the
211 intermediate host, but more often after the consumption of the paratenic hosts. Eggs are
212 produced by adult worms located in the kidney of the definitive host and are evacuated during
213 urination. The giant kidney worm is currently commonly found in the urinary systems of
214 carnivore mammals such as canids, felids and mustelids (Measures, 2008). However, during
215 the past decade, it has been observed in the abdominal cavity of harbour seals, rats and
216 capuchin monkeys (Hoffman et al., 2004; Ishizaki et al., 2010; Tokiwa et al., 2011). Humans
217 may also be infected even though such mentions are much more sporadic (Li et al., 2010)
218 since they correspond to an accidental definitive host (Acha and Szyfres, 2005; Li et al.,
219 2010). Clinical signs of dioctophymiasis are mainly due to the presence of the worm in the

220 kidneys and can lead to haematuria, pyuria, renal colic and dysuria (Soulsby, 1982; Taylor et
221 al., 2007).

222

223 4. Discussion

224

225 Since the 1990s, several paleoparasitological investigations have contributed to our

226 knowledge of parasites in ancient Eastern Europe (Slepchenko and Reinhard, 2018).

227 However, very few analyses have focused on the Neolithic period. In 1996, Engovatova and

228 Khrustalev published an article on the study of three sites from the Upper Volga basin,

229 Zamostje 1, Zamostje 2 and Vojmezhnoe. Among them, the sole study comparable to the

230 present work is the analysis performed on the site of Zamostje 2 (Engovatova and Khrustalev,

231 1996). The site is dated between the Late Mesolithic (7000-6600 cal. BC) and the Middle

232 Neolithic (4900-4300 cal. BC) and is characterized by a significant fishery industry (Lozovski

233 and Lozovskaya, 2016), marked by the presence of a very large number of archaeological and

234 faunal remains. Although the taxonomic diversity of fish declines over time, the site is still

235 characterized by an economy based on fishing (Clemente-Conte et al., 2016). During the

236 analysis of 35 coprolite samples, four gastrointestinal parasite eggs were retrieved, namely

237 *Diphyllbothrium* sp., *Opisthorchis felineus*, *Alaria alata* and eggs of the Capillaridae family.

238 In addition, in 2013, Savinetsky & Khrustalev published a synthesis of their work in

239 paleoparasitology, and evoked the presence of two *Dioctophyma renale* eggs in a sample from

240 Zamostje 2, with no details of the archaeological layer or period concerned (Savinetsky and

241 Khrustalev, 2013). *Diphyllbothrium* is often mentioned during the Neolithic period in

242 Western Europe and has been retrieved from many archaeological sites, mainly on lakeside

243 settlements in Switzerland, France, Germany and Austria (Le Bailly and Bouchet, 2013). Its

244 frequency varies depending on the cultures and the proportion of fishing in the local diet

245 (Bouchet et al., 1995; Dommelier-Espejo and Pétrequin, 2016; Le Bailly, 2011; Le Bailly et
246 al., 2005). Recent research also tends to demonstrate that fish tapeworm prevalence can vary
247 depending on the social organization in the site itself (Maicher et al., 2019). The pathoecology
248 of the fish tapeworm is clearly related to freshwater hydric systems (lakes or rivers), and
249 develops in populations where fish and fishing play a role in the diet and economy. The lancet
250 liver fluke was retrieved from ten lacustrine sites in Western Europe, around the lakes of
251 Federsee, Bodensee, Zurich, Neuchatel and Chalain (Dommelier-Espejo and Pétrequin, 2016;
252 Le Bailly and Bouchet, 2010; Maicher et al., 2019). The oldest mention of this parasite comes
253 from the Pleistocene site of Tautavel (south-western France), and is dated to around 550 000
254 BP (Jouy-Avantin et al., 1999). Finally the giant kidney worm, *Dioctophyma renale*, was
255 retrieved twice from the Neolithic period, in coprolites from the Swiss site of Arbon-Bleiche 3
256 (Le Bailly et al., 2003), and in the Russian Late Mesolithic-Middle Neolithic site of Zamostje
257 2 (Savinetsky and Khrustalev, 2013).

258 Owing to the diversity of the recovered parasites, it is possible to discuss the biological origin
259 of the studied coprolites. As all the coprolites were taken from same occupation layer and
260 present similar shapes, it is likely that they share the same biological origin. The presence of a
261 number of bone splinters and the scarcity of pollen grains in the coprolites suggest a
262 carnivorous origin. The parasitic assemblage, in particular *Alaria alata*, but also
263 *Diphyllobothrium* and *Dioctophyma*, corresponds to a probable canid origin. Among the
264 faunal remains retrieved on the site, both dog and fox bones were identified (Mazurkevich et
265 al., 2020). However, fox bones were present in small proportion, which suggests an on-site
266 butchering of foxes for furs. It is so unlikely that foxes were present on the site, but just
267 hunted for their furs. Also, location of the studied coprolites, nearby and within (under) a
268 dwelling or household construction/platform, testify to species living close to human. All
269 these statements point toward a dog origin of the coprolites. Moreover, the presence of fish-

270 eating related parasites in the coprolites (*Dioctophyma renale* and *Alaria alata*) suggests that
271 dogs were probably fed with fishes. The feeding of dogs with fish remains (heads in this case)
272 was recently proposed in the case study of dog coprolites retrieved from the Neolithic site of
273 Črnelnik in Slovenia (Tolar and Galik, 2019). The consequence on the health status of dogs
274 cannot be documented in our studies, as pathogenicity varies between individuals and may
275 have varied throughout time. However, some parasites, such as the giant kidney worm, are
276 known today to be potentially lethal (Ash and Orihel, 2007).

277 As seen above (section 3.3), *Dioctophyma* is rare in archaeological contexts, with only two
278 mentions in Switzerland. Nevertheless, this is the second time that it has been found in
279 Western Russia during the Neolithic period, also in probable dog coprolites (Savinetsky and
280 Khrustalev, 2013). *Alaria alata* is also mentioned for the second time in archaeological
281 samples, in a region which correspond today to an endemic area of this parasite (Taylor et al
282 2007). The presence of *Dicrocoelium* eggs probably indicates the accidental consumption of
283 the raw offal of an infected wild or domesticated herbivore during population movement, or
284 the intentional feeding of dogs by humans on the site. The coprological analysis demonstrates
285 that the coprolites from Serteya II are very probably of dog origin. This could suggest dog
286 breeding for consumption or other activities, as the faunistic collections include fragments of
287 domestic dogs.

288

289 5. Conclusion

290

291 The analysis on several coprolites provides new paleoparasitological evidence in prehistoric
292 Russia, and also raises questions concerning the human/dog relationship during the Neolithic.
293 More coprolites need to be analysed to confirm these hypotheses. A new set of samples,
294 coprolites and samples from the occupation layers, were recently collected from several

295 occupation areas — central part of the pile-dwelling 3 and residential area of the shore zone in
296 order to address further questions about human-animal relationships in the 4th-3rd millennium
297 BC. These samples are stored at The State Hermitage Museum in St. Petersburg and will be
298 analysed shortly.

299

300 Acknowledgments

301 Celine Maicher PhD was funded by ministerial grant. The archaeological research was
302 supported by grant of Russian Science Foundation (project 'Lacustrine sites of the 4th-3rd
303 mill BC - the origins and development of pile-dwelling settlements phenomenon in NW
304 Russia' N°19-78-00009) and the archaeological mission 2NOR support by the French
305 Ministry for Europe and Foreign Affairs. The authors would like to thank the reviewers of
306 this publication.

307

308 Litterature cited:

309 Acha, P.N., Szyfres, B., 2005. Zoonoses et maladies transmissibles communes à l'homme et
310 aux animaux, third ed. OMS, Paris.

311 Appelt, S., Armougom, F., Le Bailly, M., Robert, C., Drancourt, M., 2014. Polyphasic
312 Analysis of a Middle Ages Coprolite Microbiota, Belgium. PLOS ONE 9, 1–8.
313 <https://doi.org/10.1371/journal.pone.0088376>.

314 Ash, L.R., Orihel, T.C., 2007. Ash & Orihel's atlas of human parasitology. ASCP Press,
315 Chicago.

316 Beck, M.A., Goater, C.P., Colwell, D.D., van Paridon, B.J., 2014. Fluke abundance versus
317 host age for an invasive trematode (*Dicrocoelium dendriticum*) of sympatric elk and
318 beef cattle in southeastern Alberta, Canada. *Int. J. Parasitol. Parasites Wildl.* 3, 263–
319 268. <https://doi.org/10.1016/j.ijppaw.2014.08.003>.

320 Bouchet, F., Pétrequin, P., Paicheler, J.-C., Dommelier, S., 1995. Première approche
321 paléoparasitologique du site Néolithique de Chalain (Jura, France). *Bull Soc Path Ex*
322 88, 265–268.

323 Camacho, M., Araujo, A., Morrow, J., Buikstra J., Reinhard K. 2018. Recovering parasites
324 from mummies and corpolites: an epidemiological approach. *Parasites & Vectors*
325 11:248, 1-17. <https://doi.org/10.1186/s13071-018-2729-4>.

326 Chame, M., 2003. Terrestrial mammal feces: a morphometric summary and description. *Mem.*
327 *Inst. Oswaldo Cruz* 98, 71–94. <https://doi.org/10.1590/S0074-02762003000900014>.

328 Clemente-Conte, I., Lozovski, V.M., Gassiot Ballbe, rmengol, Mazurkevich, A., Lozovskaya,
329 O., 2016. Prehistoric fish traps and fishing structures from Zamostje 2, Russian Euro-
330 pean Plain: Archaeological and ethnographic contexts, in: *Wild Harvest: Plants in the*
331 *Hominin and Pre-Agrarian Human Worlds*. Oxbow Books, Oxford, pp. 253–272.

332 Dittmar, K., Araújo, A., Reinhard, K., 2012. The Study of Parasites Through Time:
333 Archaeoparasitology and Paleoparasitology, in: Gauer, A. (Ed), *A Companion to*
334 *Paleopathology*. Blackwell Publishing, Oxford UK, pp. 170–190.

335 Dolukhanov, P.M., Miklyayev, A.M., 1986. Prehistoric lacustrine pile dwelling in the North-
336 Western part of the USSR. *Fennosc. Archaeol.* III 3, 81–89.

337 Dommelier-Espejo, S., Pétrequin, P., 2016. Analyses paléoparasitologiques à Clairvaux et à
338 Chalain, in: *Clairvaux et Le “Néolithique Moyen Bourguignon,” Les Cahiers de La*
339 *MSHE Ledoux*. Presses Universitaires de Franche-Comté, pp. 1175–1192.

340 Dufour, B., Le Bailly, M., 2013. Testing new parasite egg extraction methods in
341 paleoparasitology and an attempt at quantification. *Int. J. Paleopathol.* 3, 199–203.
342 <https://doi.org/10.1016/j.ijpp.2013.03.008>.

343 Engovatova, A.V., Khrustalev, A., 1996. Coprolites from stone age sites of Podmoskovye.
344 *Tver. Sb.* 2, 148–154.

345 Euzéby, J., 2008. Grand dictionnaire illustré de parasitologie médicale et vétérinaire, Tec and
346 Doc. ed. Lavoisier, Paris.

347 Hoffman, V., Nolan, T.J., Schoelkopf, R., 2004. First Report of the Giant Kidney Worm
348 (*Diectophyme renale*) in a Harbor Seal (*Phoca vitulina*). *J. Parasitol.* 90, 659–660.
349 <https://doi.org/10.1645/GE-198R>.

350 Ishizaki, M.N., Imbeloni, A.A., Muniz, J.A.P.C., Scalercio, S.R.R. de A., Benigno, R.N.M.,
351 Pereira, W.L.A., Cunha Lacreata Junior, A.C., 2010. *Diectophyma renale* (Goeze,
352 1782) in the abdominal cavity of a capuchin monkey (*Cebus apella*), Brazil. *Vet.*
353 *Parasitol.* 173, 340–343. <https://doi.org/10.1016/j.vetpar.2010.07.003>.

354 Jouy-Avantin, F., Combes, C., (de), H.L., Miskovsky, J.-C., Moné, H., 1999. Helminth Eggs
355 in Animal Coprolites from a Middle Pleistocene Site in Europe. *J. Parasitol.* 85, 376–
356 379. <https://doi.org/10.2307/3285652>.

357 Kittel, P., Mazurkevich, A., Dolbunova, E., Kazakov, E., Mroczkowska, A., Pavlovskaja, E.,
358 Piech, W., Płóciennik, M., Sikora, J., Teltevskaia, Y., Wieckowska-Lüth, M., 2018.
359 Palaeoenvironmental reconstructions for the Neolithic pile-dwelling Serteya II site
360 case study, Western Russia. *Acta Geogr. Lodz.* 107, 191–213.

361 Kulkova, M., Mazurkevich, A., Dolbunova, E., Regert, M., Mazuy, A., Nesterov, E., Sinai,
362 M., 2015. Late Neolithic Subsistence Strategy and Reservoir Effects in ¹⁴C Dating of
363 Artifacts at the Pile-Dwelling Site Serteya II (NW Russia). *Radiocarbon* 57, 611–623.
364 https://doi.org/10.2458/azu_rc.57.18427.

365 Kulkova, M., Mazurkevich, A., Dolukhanov, Pavel., 2001. Chronology and paleoclimate of
366 prehistoric sites in western Dvina-Lovat' area of north-western Russia.
367 *Geochronometria* 20, 87–94.

368 Le Bailly, M., 2011. Les parasites dans les lacs nord alpins au Néolithique (3900-2900 BC), et
369 nouvelles données dans la détection des paléoantigènes de Protozoa. Editions
370 Universitaires Européennes, Sarrebruck.

371 Le Bailly, M., Araujo, A., 2016. Past intestinal parasites. *Microbiol Spectr.* 4, 143–152.
372 <https://doi.org/10.1128/microbiolspec.PoH-0013-2015>.

373 Le Bailly, M., Bouchet, F., 2013. Diphyllbothrium in the past: Review and new records. *Int.*
374 *J. Paleopathol.* 3, 182–187. <https://doi.org/10.1016/j.ijpp.2013.05.004>.

375 Le Bailly, M., Bouchet, F., 2010. Ancient dicrocoeliosis: Occurrence, distribution and
376 migration. *Acta Trop.* 115, 175–180.
377 <https://doi.org/10.1016/j.actatropica.2010.03.004>.

378 Le Bailly, M., Leuzinger, U., Bouchet, F., 2003. Dioctophymidae Eggs in Coprolites From
379 Neolithic Site of Arbon–Bleiche 3 (Switzerland). *J. Parasitol.* 89, 1073–1076.
380 <https://doi.org/10.1645/GE-3202RN>.

381 Le Bailly, M., Leuzinger, U., Schlichtherle, H., Bouchet, F., 2005. Diphyllbothrium:
382 Neolithic Parasite? *J. Parasitol.* 91, 957–959. <https://doi.org/10.1645/GE-3456RN.1>

383 Li, G., Liu, C., Li, F., Zhou, M., Liu, X., Niu, Y., 2010. Fatal Bilateral Dioctophymatosis. *J.*
384 *Parasitol.* 96, 1152–1154. <https://doi.org/10.1645/GE-2132.1>.

385 Lozovski V., Lozovskaya O. 2016. New Evidence of the Fishing Economy of Stone Age
386 Waterlogged Sites in Central and North- Western Russia: The Example of Zamostje 2.
387 In: Pirjo Uino, Kerkko Nordqvist (eds.), *New sites, New methods.* " Proceedings of
388 the Finnish-Russian Archaeological Symposium, Helsinki. The Finnish Antiquarian
389 Society, *Iskok.* 21, 85-100.

390 Maicher, C., Bleicher, N., Le Bailly, M., 2019. Spatializing data in paleoparasitology:
391 Application to the study of the Neolithic lakeside settlement of Zürich-Parkhaus-

392 Opéra, Switzerland. *The Holocene* 29, 1198–1205.
393 <https://doi.org/10.1177/0959683619838046>.

394 Maigrot, Y., 2014. Bone tools from Neolithic settlement Serteya II (Smolensk region, Russia),
395 in: Mazurkevich A., Polkovnikova M., Dolbunova E. (Eds.), *Archaeology of Lake*
396 *Settlements IV – II Mill. BC: Chronology of Cultures, Environment and*
397 *Palaeoclimatic Rhythms. Presented at the Archaeology of lake settlements IV – II*
398 *mill. BC: chronology of cultures, environment and palaeoclimatic rhythms, Saint-*
399 *Petersburg*, pp. 214–220.

400 Mazurkevich, A., 2016. Северо-Западной археологической экспедиции
401 Государственного Эрмитажа о раскопках и подводных исследованиях памятника
402 Сертея II в 2015 году (*Rapport de fouilles archéologiques*). Musée de l’Hermitage,
403 Saint-Petersburg.

404 Mazurkevich, A., Dolbunova, E., 2011. Underwater Investigations in Northwest Russia:
405 lacustrine archaeology of Neolithic pile dwellings, in: *Submerged Prehistory*. Oxbow
406 Books, pp. 158–172.

407 Mazurkevich, A., Dolbunova, E., Kittel, P., Fassbinder, J.W.E., Maigrot, Y., Mroczkowska,
408 A., Płóciennik, M., Sikora, J., Słowiński, M., Sablin, M., Shirobkov, I., 2017. Multi-
409 disciplinary research on the Neolithic pile-dwelling Serteya II site (Western Russia)
410 and the landscape reconstruction, in: *Nie Tylko Krzemienie – Not Only Flints*. Instytut
411 Archeologii Uniwersytetu Łódzkiego, Łódzka Fundacja Badań Naukowych,
412 Stowarzyszenie Naukowe Archeologów Polskich Oddział w Łodzi, Łódź, pp. 103–
413 128.

414 Mazurkevich, A., Dolbunova, E., Maigrot, Y., Hook, D., 2010. The results of underwater
415 excavations at Serteya II, and research into pile-dwellings in northwest Russia.
416 *Archaeologia Baltica* 14, 47–64.

417 Mazurkevich, A., Dolbunova, E., Zaitseva, G., Kulkova, M., 2018. Chronological timeframes
418 of cultural changes in the Dnepr-Dvina region (7th to 3rd millennium BC). *Doc.*
419 *Praehist.* 44, 162–175. <https://doi.org/10.4312/dp.44.10>.

420 Mazurkevich, A., Sablin, M., Dolbunova, E., Kittel, P., Maigrot, Y., Kazakov, E. 2020.
421 Landscape, seasonality and natural resources use in the 3rd millennium BC by pile-
422 dwelling communities (NW Russia). In: *Settling waterscapes in Europe. The*
423 *Archaeology of Neolithic and Bronze-Age pile-dwellings.* OSPA 1: 17 -36.

424 Measures, L.N., 2008. *Dioctophymatosis*, in: Samuel, W.M., Pybus, M.J., Kocan, A.A. (Eds.),
425 *Parasitic Diseases of Wild Mammals.* Iowa State University Press, pp. 357–364.

426 Nozais, J.-P., Datry, A., Danis, M., 1996. *Traité de parasitologie médicale.* Pradel, Paris,
427 France.

428 Paridon, B.J. van, Gilleard, J.S., Colwell, D.D., Goater, C.P., 2017. Life Cycle, Host
429 Utilization, and Ecological Fitting for Invasive Lancet Liver Fluke, *Dicrocoelium*
430 *dendriticum*, Emerging in Southern Alberta, Canada. *J. Parasitol.* 103, 207–212.
431 <https://doi.org/10.1645/16-140>.

432 Sablin, M., Syromyatnikova, E.V., 2009. Animal Remains from Neolithic Sites in
433 Northwestern Russia, in: *The East European Plain on the Eve of Agriculture.* Oxford:
434 Archaeopress, Oxford, pp. 153–158.

435 Savinetsky, A.B., Khrustalev, A.V., 2013. Paleoparasitological investigations in Mongolia,
436 Middle Asia and Russia. *Int. J. Paleopathol.* 3, 176–181.
437 <https://doi.org/10.1016/j.ijpp.2013.09.004>.

438 Slepchenko, S., Reinhard, K., 2018. Paleoparasitology and pathoecology in Russia:
439 Investigations and perspectives. *Int. J. Paleopathol.* 22, 39–44.
440 <https://doi.org/10.1016/j.ijpp.2018.03.005>.

- 441 Soulsby, E.J.L., 1982. Helminths, Arthropods and Protozoa of domesticated animals. 1982,
442 7th ed. Baillière Tindall, London.
- 443 Taylor, M.A., Coop, R.L., Wall, R., 2007. Veterinary parasitology, third ed. Blackwell Pub.,
444 Oxford, UK.
- 445 Tokiwa, T., Harunari, T., Tanikawa, T., Akao, N., Ohta, N., 2011. *Diectophyme renale*
446 (Nematoda: Dioctophymatoidea) in the abdominal cavity of *Rattus norvegicus* in
447 Japan. *Parasitol. Int.* 60, 324–326. <https://doi.org/10.1016/j.parint.2011.03.003>.
- 448 Tolar, T., Galik, A., 2019. A Study of Dog Coprolite from Late Neolithic Pile-Dwelling Site
449 in Slovenia. *Archaeol. Discov.* 20–29. <https://doi.org/10.4236/ad.2019.71002>.
- 450