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A BIOCULTURAL PERSPECTIVE ON THE TRANSITION TO AGRICULTURE IN CENTRAL EUROPE

ABSTRACT: This study focuses on the changes in the human skeleton that are associated with the transition to agricultural subsistence. Two populations from the territory of contemporary Poland that differ in terms of their subsistence strategies are compared. An agricultural subsistence strategy is represented by a Lengyel Culture population from Osłonki (5690–4950 BP), whilst the Corded Ware populations from Żerniki Górne and Złota (c. 4160–3900 BP) represent mixed, agricultural-breeding-pastoral economies supplemented with hunting and gathering. The Corded Ware sample consisted of 62 individuals in total, and the Lengyel sample comprised 68 individuals. Health status was examined through skeletal stress indicators, cribra orbitalia*, enamel hypoplasia and Harris lines. The analysis of enamel hypoplasia showed the effect of different adaptive strategies on buffering adverse nutritional factors and diseases. The prevalence and severity of the condition proved significantly higher in the Lengyel sample than in the Corded Ware population (64.7% vs. 43.5%, respectively). It is suggested that agricultural subsistence, associated with a less diversified diet, sedentism, exposure to pathogens, spread of infections and increased population density, caused more frequent and severe stress episodes than the mixed economy of the Corded Ware people. The inverse relationship between enamel hypoplasia and the mean age at death found in the agricultural population clearly shows an effect of adverse living conditions on the biological development of the individuals studied.*

KEY WORDS: Neolithic – Corded Ware Culture – Lengyel Culture – Enamel hypoplasia – Cribra orbitalia – Harris lines – Agricultural subsistence – Mixed subsistence

INTRODUCTION

The transition from food collection to food production is frequently considered from the perspective of new cultural challenges designed to buffer against subsistence and social disruptions. The apparent consequences of agricultural intensification are increased population size and density, which, in connection with other changes of

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a demographic and ecological nature, have an adverse effect on the health status of human groups, by, among other things, creating favourable conditions for the spread of infectious diseases and increasing the risk of parasite infestation (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984). The shift to farming also caused a decline in the quality of nutrition. The diet of foragers, based on a wide range of animal and plant species, high in key nutrients, minerals, protein, vitamins, and trace elements, appears to have been more healthy, than the diet of farmers, typically focused on starchy, highly caloric food of high productivity and storability, a few cereal and legume crops, and, in some areas, root crops (Larsen 2006). The consequences of the adoption of agriculture for the health of human groups can be interpreted in various ways, depending on the given sample set (for some early agricultural groups relatively adequate dietary composition has been reported), but, generally, health measured by skeletal indicators declined rather than improved with the advent of farming (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984). Skeletal studies found hunter-gatherers to be relatively healthy, affected only by seasonal and periodic stress, unlike agriculturalists, who were plagued by severe and chronic physiological stress, as evidenced by among other things increased average mortality rates, high frequencies of porotic hyperostosis and *cribra orbitalia*, a substantial increase in the number and severity of enamel hypoplasias and pathologies caused by infections (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984).

In this paper three indicators of health status have been examined: *cribra orbitalia*, enamel hypoplasia and Harris lines in two Neolithic populations that differed in their adaptive strategies. The term "adaptive strategy" has been used in the meaning of "a pattern of adaptation or adjustment to the environment in a biological or cultural way" (Piontek 1995), but this actually corresponds to only one of the components of the human socio-cultural system, economy, because of the limited prospect of analysing the other factors (Piontek 1995).

Cribra orbitalia is a sieve-like lesion that develops in the orbital roofs, when blood producing bone marrow expands through the diploë, increasing red blood cell production (Stuart-Macadam 1985, Walker *et al.* 2009). The lesion's etiology is diverse, including a variety of anemic conditions, rickets, scurvy, and infectious diseases (Djuric *et al.* 2008, Temple 2010, Walker *et al.* 2009, Wapler *et al.* 2004).

Enamel hypoplasia is a deficiency in enamel thickness, which is macroscopically visible on the surface of the tooth crown, and is caused by disturbances in ameloblast activity during the secretory phase of enamel formation (Skinner, Goodman 1992). The lesion is a nonspecific stress indicator, caused by a range of diseases and nutritional deficiencies (Duray 1996, El-Najjar *et al.* 1978, Goodman, Rose 1990, Larsen 2006), and it can result from any particular insult that affects the growing child (Stuart-Macadam 1985). The metabolic insult affects only the part of the tooth that is just being formed, thus the defect's location on the crown surface enables a reconstruction of age at response to adverse factors (Goodman, Rose 1990, Larsen 1987).

Harris lines (also called lines of arrested growth, transverse sclerotic lines or radiopaque lines) consist of layers of dense bone visible on long bone radiographs. They form when a period of arrested growth, indicated by increased density of bone trabeculae, is followed by a period of growth recovery (Arnay-de-la-Rosa *et al.* 1994, Cohen, Armelagos 1984). The condition has been correlated with a variety of adverse factors, including malnutrition and illness (McHenry 1968, Papageorgopoulou *et al.* 2011).

These stress indicators differ slightly in terms of the information that they provide. Harris lines and enamel hypoplasia develop as a consequence of episodic factors; therefore it is possible to assess the age of an individual at the time of their formation. Information on the chronology of the lesions has proven to be very useful in terms of revealing the ages at which non-adults are particularly sensitive to factors disturbing their metabolism, and also in revealing the pattern of occurrence of stress episodes (e.g. sex differences). It is recognised that information derived from the chronological distribution of these skeletal markers is mutually complementary: enamel hypoplasia reflect episodes that occur in early childhood, while Harris lines, examined in adults, may reveal factors disturbing the individual growth and development in further phases of childhood and even adolescence (Cohen, Armelagos 1984, Huss-Ashmore *et al.* 1982). Remarkably, Harris lines may resorb and disappear within a few years of the time of their formation (Arnay-de-la-Rosa *et al.* 1994, Drenhaus 1991, Hummert, Van Gerven 1985, Garn *et al.* 1968, Garn, Schwager 1967, Jerszyńska, Nowak 1996, Nowak, Piontek 2002a, b, Papageorgopoulou *et al.* 2011). *Cribra orbitalia* is treated as a nonspecific indicator of physiological stress, although based on its presence and context, one can draw inferences about the etiology of this particular stress marker (Ortner 2003). Researchers who focus on the health status of prehistoric populations suggest the use of multiple indicators of stress in order to draw population-based conclusions about disease prevalence (Ribot, Roberts 1996, Wheeler 2012).

The aim of this paper is to address the impacts of different subsistence economies on response to adverse factors facing Neolithic human populations in the territory of contemporary Poland.

MATERIAL

The skeletal material, used in this paper, comes from three Neolithic sites (now villages) located on the territory of Poland (*Figure 1*): Żerniki Górne and Złota (both from Świętokrzyskie Voivodeship) of the Corded Ware Culture (CWC), and Osłonki (Kujawy-Pomorze Voivodeship) of the Lengyel Culture (LC). The subsistence of Corded Ware sample was based on a mixed, agricultural-breeding-pastoral economy, supplemented with hunting and gathering, and the Lengyel sample was a typical, agricultural population (Krenz-Niedbała 1999a).

The skeletal material of the Żerniki Górne village comes from a barrow situated on the southern edge of a loess plateau. The barrow is circular in shape, 26 m in diameter at the base and 3.6 m high. The mound was

FIGURE 1. Map of Poland, with locations of the examined Neolithic sites.

built on top of a natural hill, therefore the height of the mound itself is 1.8 m (Kempisty 1978). In the central part of the barrow, there is extensive evidence of damage caused by laying the foundations of a chapel from the 17th century. The areas under the mound and spreading to the south and east were used as a cemetery toward the end of the Neolithic and in the first two periods of the Bronze Age. The cemetery was used by, in turn, people of the Corded Ware Culture (c. 40 graves), the Chłopice-Veselé and Mierzanowice Cultures (jointly 37 graves) and the Trzciniec Culture (14 graves). The mound was built by the people of the Trzciniec Culture and covered burials from all phases of the cemetery's use. In the years 1965–1968, the barrow; together with the cemetery underneath and the cemeteries adjoining the mound from the south and east were explored (Kempisty 1978, 1979, 1989, Kempisty, Włodarczak 1996). On the basis of a study by Kempisty, as well as data obtained from Wiercińska (pers. comm.), the graves of the Corded Ware Culture were selected for analysis. The dead were generally put in a tightly crouched position, lying on their backs, with their legs bent to the right or left side, but always to the same side as the head. A few skeletons were lying in a sideways position. The graves were mostly single, though twelve graves contained two skeletons. The burials were predominantly equipped with pottery (95% of the goods), usually in a form of clay vessels, mostly amphorae. In addition, stone axes and items made of copper, bone, flint, antler and shell were found. The Corded Ware finds at Żerniki Górne are dated between 4160 ± 50 BP to 3900 ± 55 BP (Kempisty, Włodarczak 1996). Most researchers consider the Corded Ware people to have been pastoralists and nomads (Kruk 1980, Kruk, Milisauskas 1999, Wiślański 1969, 1970, for different opinion see Jankowska 1999, Tunia 1986), but occasional land cultivation is highly probable (Machnik 1979).

A second part of the "Corded Ware" sample comprises skeletal material from the Złota village. In the 19th century on that territory traces of a late-Neolithic settlement and a cemetery were encountered (Krzak 1976). In the excavations pits close to the cemetery were uncovered the remains of half dugouts, rubbish and clay extraction pits. The pits contained numerous fragments of ceramics, bone and flint tools, animal bones and pieces of mud daub, which suggests semi-permanent as opposed to seasonal, inhabitation of the settlement (Machnik 1979). Approximately 200 graves have been unearthed. They usually contained multiple inhumations from different times. The dead were usually put on their sides, rarely on their backs, with legs drawn up, along a north west – south-east axis (similarly as in Żerniki Górne). Males were usually lying on their left sides with their heads oriented toward the south east, and females on their right sides with the heads directed toward the north-west. Faces, independently of sex, were turned to the south, i.e. toward the Wisła river valley. Some skeletons bore the traces of a pigment, likely ochre. The grave inventory was abundant (up to 90 items) and consisted of pottery, flint tools and semi-raw material, bone and antler tools, as well as shell, bone, amber and cooper ornaments. The Złota Culture was initially regarded as a group of the Corded Ware Culture, however later it was defined as a separate archaeological unit (Machnik 1979). The origin of the Złota Culture is a complex and intriguing issue for researchers of the late Neolithic. It is claimed to contain elements of two, or even three cultures, including the Globular Amphorae Culture, Radial Decorated Pottery Culture, and the Corded Ware Culture with its predominant share (Kempisty 1978, Krzak 1973, for different opinion see Ścibior 1991, 1992). According to the archaeological data, the Złota Culture arose on the basis of a local group of Globular Amphorae people, who rapidly came into contact with representatives of the older phase of the Corded Ware Culture. The subsistence of the people of Złota was mixed, based on agriculture and breeding as well as fishing, hunting and gathering (Kruk, Milisauskas 1999, Krzak 1976, Wierzbicki 1999). The cemetery and settlement of Złota is dated between 4260 ± 80 BP to 4070 ± 55 BP (Krzak 1989). A craniometric analysis of the population from Żerniki Górne and Złota found no significant differences in the morphology between the two skeletal series (Krenz-Niedbała 1999a), therefore both datasets were combined for the analysis of stress markers.

The Lengyel Culture is represented by a population from Osłonki, a village lying in Kujawy-Pomorze Voivodeship, in northern central Poland. During the excavations carried out in the years 1989–1994 (Grygiel 1996), a settlement of early Neolithic farmers was discovered, and dated between c. 5690 ± 140 BP to 4950 ± 150 BP (Grygiel, Bogucki 1997). Four characteristic elements were associated with this settlement: big, trapezoidal houses, graves, clay extraction pits and small rubbish pits. A new feature, discovered for the first time in the Polish Early Neolithic is a fortification system at the western edge of the settled area (Grygiel 1996, 2008). One of the most remarkable properties of the Osłonki settlement is the intensity and concentration of occupation, particularly with reference to more diffuse patterns of settlement and less intensive use of natural resources in a period preceding and following the

Lengyel settlement in this region (Grygiel, Bogucki 1997). Numerous animal remains were uncovered, of c. 10,000 specimens. They constitute one of the most abundant Neolithic animal samples from northern central Europe. Preliminary analyses revealed that among domestic species the most numerous were cattle, sheep and goat, then pig (Grygiel, Bogucki 1997). By the end of 1994, 80 graves of the Lengyel Culture had been unearthed, and these are usually very well preserved. The majority of burials contained adults, and there were only a few inhumations of children or adolescents. Two categories of graves were distinguished: firstly "classic" burials, where males were lying on their right sides and females on their left, with heads of both sexes directed toward the south or south east, usually with an abundant equipment inventory, including objects made of copper, shell, bone and antler ornaments and, occasionally, small ceramic vessels. A characteristic feature of the "classic" burial is the decorating of the body of the dead. In the second, less frequent, category of graves, rubbish pits were used, where the dead were put in a random burial position, usually without any grave goods. Based on analogies to Lengyel burials from Brześć Kujawski, it was concluded that the shift in the burial rite from the formal ritual with numerous grave goods to a random pattern with almost no grave offerings occurred in the latest phase of Lengyel occupation (Grygiel, Bogucki 1997: 168–169).

The skeletal material consists of adults recovered from Neolithic graves of the Corded Ware and Lengyel Cultures. In the Corded Ware sample there were in total 62 individuals, 42.5% of young adults, 45.2% of middle adults and 12.3% of old adults; 56.0% of males and 44.0% of females. In the Lengyel sample there were in total 68 individuals, 59.6% of young adults, 29.8% of middle adults and 10.6% of old adults; 54.3% of males and 45.7% of females. The number of individuals examined for *cribra orbitalia*, enamel hypoplasia, and Harris lines is presented in *Table 1*. For enamel hypoplasia, 513 teeth from the Corded Ware sample and 878 teeth from the Lengyel sample were studied.

METHODS

Age and sex estimates of the examined individuals were carried out according to standard methods (Buikstra, Ubelaker 1994, White, Folkens 2005). Sex determination was based on the morphology of the pelves and skulls. To estimate age at death a multivariate approach was used, mainly based on assessments of age-related changes of the pubic symphyses and auricular surfaces of the ilia, which were then combined with supplementary data on cranial suture closure, and tooth wear. Stress indicators were estimated macroscopically and recorded using standard methods.

Cribra orbitalia was recorded in individuals with at least one orbital roof and, when possible, for both the right and left orbits, as authors mostly regard this phenomenon as bilateral and symmetric with regard to the type and localisation (Stuart-Macadam 1992, Wapler *et al.* 2004). For the Corded Ware group the occurrence of *cribra orbitalia* was originally estimated according to Hengen's scale (Hengen 1971). However, the data for the Lengyel sample were provided by Garłowska (unpublished PhD thesis), who used Bergman's classification (Bergman 1986). This system follows Hengen's scale, but with the first category excluded, as this is claimed to be a physiological condition. Therefore, the data for the Corded Ware sample was transformed following Bergman's classification system to enable comparisons between the two populations.

For the examination of enamel hypoplasia the individuals qualified only if it was possible to observe at least three different tooth types. Teeth of considerable attrition were excluded from the analysis. Hypoplasias were scored on incisors, canines, and premolars, according to the recommendations of Goodman and Rose (1990), and Buikstra and Ubelaker (1994). All forms of the condition were recorded. The position of linear enamel hypoplasias on the crown surface was measured from the upper limit to the cemento-enamel junction with a digital caliper calibrated to the nearest 0.01 mm. The measurements were then converted to the

TABLE 1. Number of individuals examined for skeletal stress indicators.

	Cribra orbitalia			Enamel hypoplasia				Harris lines			
Sample	M	F	Total	M	F	?	Total	M	F	?	Total
CWC	26	23	49	30	25	7	62	12	23	3	38
LC	26	19	45	25	21	22	68	23	21	4	48

CWC, Corded Ware Culture; LC, Lengyel Culture.

age of formation using the most common method (Krenz-Niedbała, Kozłowski 2013), based on the chart of enamel development for the permanent teeth, constructed by Massler *et al.* (1941), then modified by Swärdstedt (1966) and presented in a form of regression equations by Goodman and Rose (1990).

Harris lines were estimated on X-rays of tibiae. Tibial bones were found most useful in examining transverse lines, on account of high reactivity, clear visibility of lines and reliability of their recording (Hunt, Hatch 1981). Most of the authors use only tibiae or tibiae and femora in the analysis of Harris lines (Clarke 1982, Hummert, Van Gerven 1985, Hunt, Hatch 1981, McHenry, Schulz 1976). The X-rays of the tibiae in anteroposterior view were taken using Fotopan X-S1 films. The exposures were taken at 0.1 seconds at 1 m. The voltage was 45–50 mV and the power was 17 mAs. Harris lines were recorded at both ends of all bones, and counted only when they were a minimum of 5 mm long (Garn *et al.* 1968). According to many authors, lines of incomplete formation are as important as lines that totally cross the transverse axis of the bone (Vyhnánek, Stloukal 1988). Both right and left bones were analysed. Examination of bilateral symmetry of lines brought different results (Drenhaus 1991, Garn, Baby 1969). The distance of the Harris lines to the proximal and distal end of the tibiae were measured with an electric caliper, and used then to calculate the ages of formation (Byers 1991).

To examine differences in the occurrence of *cribra orbitalia*, enamel hypoplasia and Harris lines between the Corded Ware and Lengyel samples, chi-square tests were applied and to check whether there is a relationship between longevity and stress level, *t*-tests were used. The calculations were performed using Microsoft Excel 2007 and StatSoft STATISTICA 10.0 software.

RESULTS

Three skeletal stress indicators, *cribra orbitalia*, enamel hypoplasia, and Harris lines, were examined in two Neolihic samples from contemporary Poland, CWC – Corded Ware Culture (mixed subsistence economy) and LC – Lengyel Culture (agricultural subsistence). The prevalence of these markers are presented in *Table 2*. The frequency of *cribra orbitalia*, estimated according to Bergman's scale (first Hengen's category excluded) is similar in both populations: in the Corded Ware sample 20.4% (males 23.1%, females 17.4%) and in the Lengyel sample 20.0% (males 23.1%, females 15.8%). The slight

TABLE 2. Frequencies of skeletal stress indicators in the examined Neolithic samples.

	Cribra orbitalia									Enamel hypoplasia									Harris lines								
	Males			Females			Total			Males			Females*			Total**			Males			Females			Total		
	N	*n*	%	*N*	*n*	%	*N*	*n*	%	*N*	*n*	%	*N*	*n*	%	*N*	*n*	%	*N*	*n*	%	*N*	*n*	%	*N*	*n*	%
CWC	26	6	23.1	23	4	17.4	49	10	20.4	30	14	46.7	25	9	36.0	62	27	43.5	12	8	66.7	23	14	60.9	38	25	65.8
LC	26	6	23.1	19	3	15.8	45	9	20.0	25	17	68.0	21	14	66.7	68	44	64.7	23	15	65.2	21	10	47.6	48	26	54.2

CWC, Corded Ware Culture; LC, Lengyel Culture.
* $P = 0.04$; ** $P = 0.02$ (*P*-values indicate comparisons of proportions between CWC and LC sample).

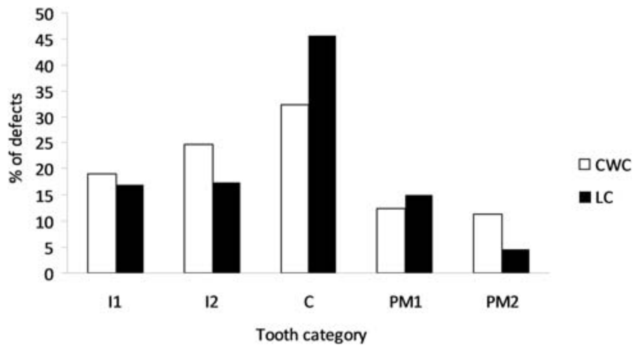

FIGURE 2. Frequencies of enamel hypoplasias by tooth type. CWC, Corded Ware Culture; LC, Lengyel Culture.

difference in the frequencies between the sexes is not significant. The severity of *cribra orbitalia* differs in both groups, but, again, nonsignificantly. In the Corded Ware population first and second stages of the lesion were recorded, while in the Lengyel population there is also third stage of the condition. Moreover, in the former group half of the defects were categorised to the first stage and the other half to the second, while in agriculturalists the majority of defects correspond jointly to second and third stage of severity.

In the case of enamel hypoplasia, a statistically significant difference in the frequencies of the condition was found to exist between the two populations (Corded Ware sample 43.5%; Lengyel sample 64.7%; $P = 0.02$). Also significant is the difference in teeth affected; 20.5% in the Corded Ware sample versus 29.4% in the Lengyel group ($P = 0.0003$). Moreover, in the Corded Ware group incidence is most often restricted to one hypoplastic event per individual (in 59.6% of individuals), more rarely two or three defects (18.5% and 22.2%, respectively), while in the affected Lengyel individuals one, two or three defects were relatively evenly distributed (in 38.6%, 27.3% and 29.5% of individuals, respectively), and two individuals with a higher number of defects were observed: one with four and one with five defects. The difference in severity of enamel hypoplasia between the samples, measured by the total number of hypoplastic defects in affected individuals, is highly significant ($P = 0.0001$). Corded Ware males do not differ significantly from the Lengyel males in hypoplasia prevalence (46.7% vs. 68.0%, respectively), while the females do (36.0% vs. 66.7%, respectively, $P = 0.04$). In both samples, no statistically significant sex differences in hypoplasia frequency were revealed. Within tooth types the pattern of hypoplasia prevalence is similar (*Figure 2*), with the highest frequency found for canines (Corded Ware 32.4%; Lengyel 45.7%), then second incisors (24.8% and 17.4%, respectively), and first incisors (19.0% and 17.0%, respectively). A higher incidence was reported for the mandibular teeth (62.1% and 57.0%, respectively) than maxillary teeth (37.9% and 43.0%, respectively).

Estimated ages of enamel hypoplasia formation in the total examined samples and by sex are presented in *Figures 3–5*. The peak of defects in the Lengyel sample occurs in the age category 3.6–4.0 years for the whole group, and for the male and female subgroups. The peak of hypoplasias in the Corded Ware sample is not as clear, but in general it occurs in the earlier age categories (2.6–3.0 years for the whole sample and males; 3.1–3.5 for females) than in the Lengyel group.

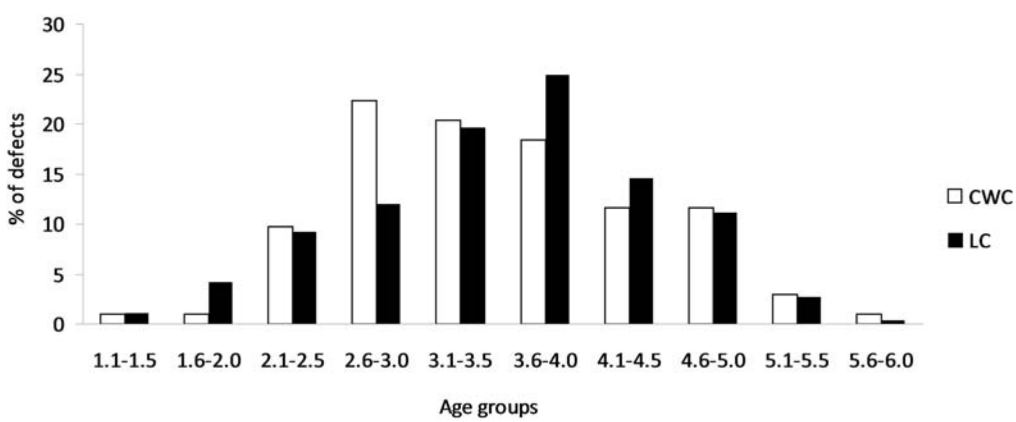

FIGURE 3. Frequencies of enamel hypoplasias by age category. CWC, Corded Ware Culture; LC, Lengyel Culture.

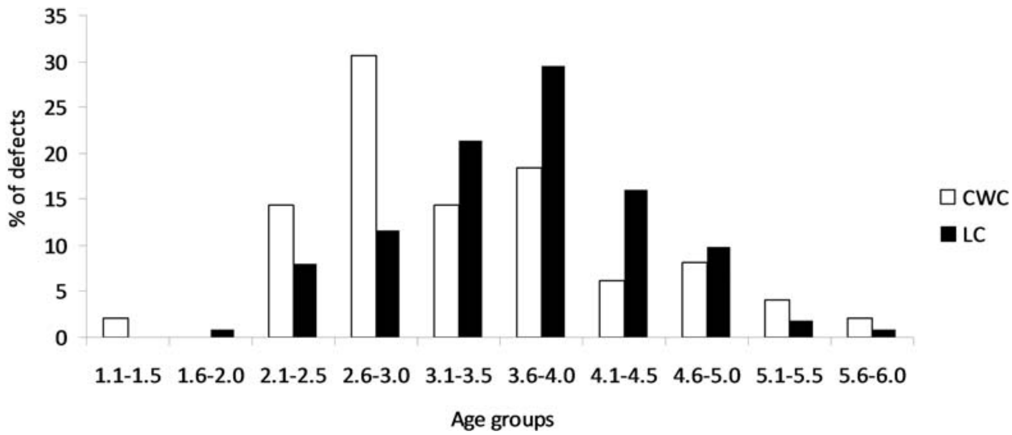

FIGURE 4. Ages of enamel hypoplasia formation in males of the examined Neolithic samples. CWC, Corded Ware Culture; LC, Lengyel Culture.

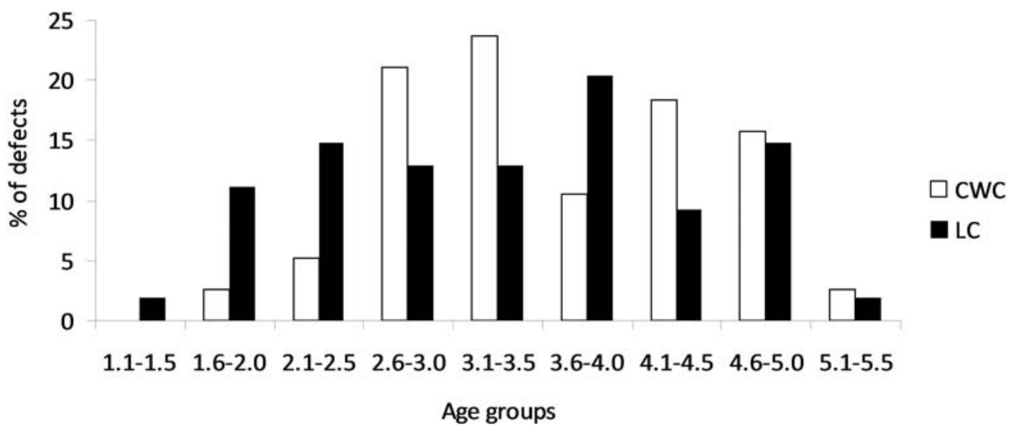

FIGURE 5. Ages of enamel hypoplasia formation in females of the examined Neolithic samples. CWC, Corded Ware Culture; LC, Lengyel Culture.

No significant differences in Harris lines prevalence were found between the studied samples (*Table 2*). However, Harris lines are slightly more frequent in the Corded Ware group when compared to the Lengyel sample (65.8% and 54.2%, respectively). Both males and females do not differ in the frequency of the condition (males: Corded Ware 66.7%, Lengyel 65.2%; females: Corded sample 60.9%, Lengyel 47.6%). There are no significant sex differences in the frequency of lines in either group. The mean number of Harris lines per individual was no significantly higher in the Lengyel sample than in the Corded Ware population (8.6 and 6.7, respectively). The highest number of lines per individual is 15 in the Corded sample and 25 in the Lengyel population. Harris lines in both populations formed symmetrically, i.e. they matched in the left and right bone, as well as in similar pattern, as at distal ends of right and left tibiae the lines were more than twice as frequent when compared to the proximal ends. In the Corded Ware sample, in the right tibiae 50 lines in total were formed at the proximal ends and 120 at the distal ends, and in the left tibiae 55 and 109 lines, respectively. In the Lengyel sample in the right tibiae 76 lines were recorded at the proximal ends and 174 at the distal ends, and in the left bones 52 and 168 lines, respectively. From this, the chronological distributions of Harris lines in the total sample were examined, and this was also undertaken for the male and female subsamples (*Figures 6–8*). In the Corded Ware population and in males in particular, the peak of Harris line formation falls in the 11th year. In females the peak is more extended, to between 9 and 12

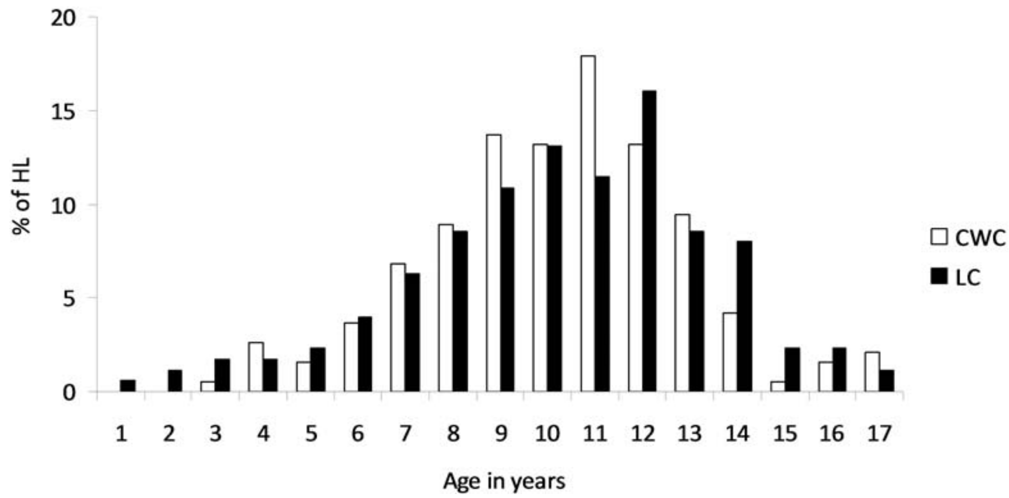

FIGURE 6. Ages of Harris line formation in the examined Neolithic samples. CWC, Corded Ware Culture; LC, Lengyel Culture.

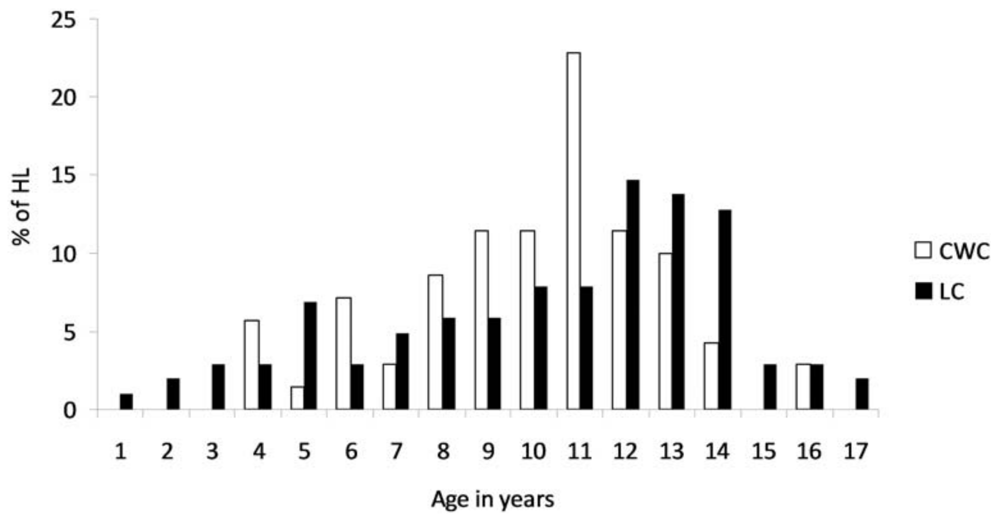

FIGURE 7. Ages of Harris line formation in males of the examined Neolithic samples. CWC, Corded Ware Culture; LC, Lengyel Culture.

years of age. In the Lengyel total sample and in males the peak falls more or less in the 12th, and in females in the 10th year.

The relationship between longevity and stress level was tested with *t*-tests (*Table 3*). Limited numbers of observations, when dividing the individuals into those with and without the particular stress markers by mean age at death, is likely to be one of the reasons why an independent two-sample *t*-test produced statistically significant results only for enamel hypoplasia occurrence in the Lengyel population ($t = -2.84$, $P = 0.007$, one-tailed). The affected individuals died on average at younger ages (mean age at death = 33.1) than unaffected individuals (mean age at death = 43.2).

DISCUSSION

In prehistoric populations stress cannot be directly measured, but may be inferred from skeletal indicators,

TABLE 3. Summary statistics of age at death according to presence of skeletal stress indicators.

	Cribra orbitalia						Enamel hypoplasia						Harris lines					
	Present			Absent			Present			Absent			Present			Absent		
	N	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*	Mean	SD
CWC	22	36.7	10.1	25	44.5	15.6	23	35.4	9.4	31	37.4	10.3	21	37.6	10.1	7	35.4	7.7
LC	9	36.7	12.1	36	38.6	13.1	33	33.1*	9.5	14	43.2*	13.5	26	38.0	14.3	20	37.0	14.1

CWC, Corded Ware Culture; LC, Lengyel Culture.
* $P = 0.007$ (*P*-value indicates comparison of mean age-at-death between individuals with and without enamel hypoplasia).

such as enamel hypoplasia, porotic hyperostosis, *cribra orbitalia*, Harris lines, short stature, sexual dimorphism reduction, and cortical bone loss (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984). The causes of bone lesions are often impossible to identify, but population-based studies of osteological pathologies may still provide the general view on the frequency and severity of stress, and also allow researchers to establish how socio-economic transitions in a population affect changes in health status (Cohen, Armelagos 1984). In such research the effects of nutrition and diseases cannot be separated, because of their synergistic relations (Cohen, Armelagos 1984, Larsen 2006, Nowak, Piontek 2002b). In the case of malnutrition, the organism is less resistant to infectious diseases, which in turn lower the nutritional status, e.g. through increased need for certain nutrients associated with decreased absorption (Goodman 1992). The malnourished individual is more susceptible to diseases than the well-nourished individual and this is one of the reasons why indicators of physiological stress are widely accepted as measures of the nutritional status of a population (Cohen, Armelagos 1984). The intensity and duration of the individual response to adverse living conditions are a function of the degree of environmental and cultural constraints on one hand, and the adequacy of the cultural buffering system and individual resistance on the other (Goodman 1992, Ribot, Roberts 1996, Wheeler 2012).

The transition to agriculture is a frequently studied context for assessing how past populations developed new approaches to buffer against disturbances in prehistoric lifeways (Cohen, Armelagos 1984, Gleń-Haduch 1995, Huss-Ashmore *et al.* 1982, Larsen 2006, Meiklejohn, Zvelebil 1991, Piontek 1999a, b, Piontek, Vančata 2012, Temple 2010). Direct consequences of the adoption of agriculture for the nutritional status of human

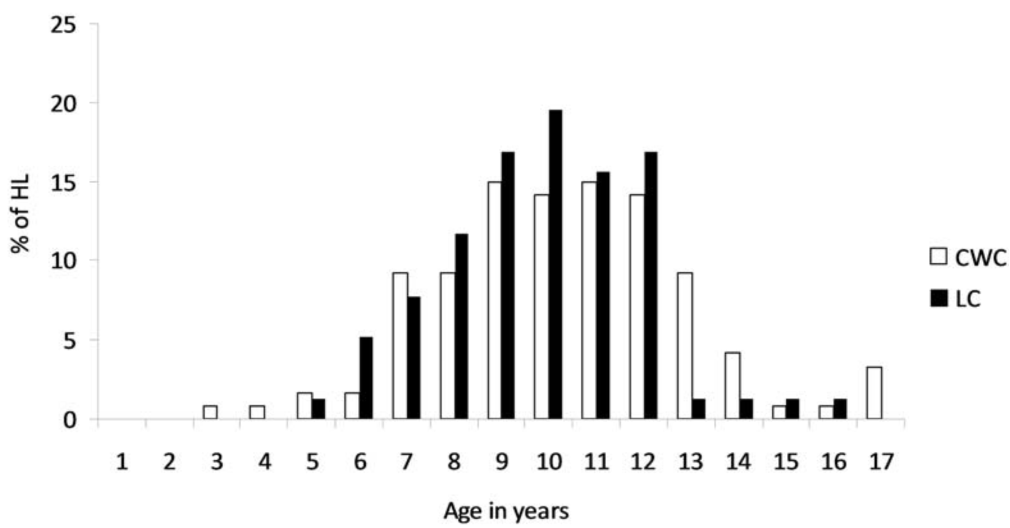

FIGURE 8. Ages of Harris line formation in females of the examined Neolithic samples. CWC, Corded Ware Culture; LC, Lengyel Culture.

samples are differently interpreted, depending on a given population, but an undoubted and invariable element associated with agricultural intensification is higher population density, which in connection with other demographic and ecological changes adversely influenced the health status of human populations, e.g. by promoting the spread of infections and parasite infestation (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984, Goodman 1992). Hence, dynamically developing cultural systems act in two ways: through buffering adverse phenomena (here: low predictability of food acquisition in pre-agricultural groups, see Larsen 2006) and creating new limitations (e.g. greater population density, insufficient quantity of certain nutrients in the diet), which may lead to a decrease in health status (Bocquet-Appel, Bar-Yosef 2008, Goodman 1992, Larsen 2006).

This study was aimed at answering the question of whether Neolithic populations varied in their adaptive strategies (i.e. a mixed agricultural-breeding-pastoral economy supplemented with hunting and gathering versus a "typical" farming economy) responded to adverse environmental factors in the same/similar, or in different ways. The analysis was based on three nonspecific skeletal stress indicators, *cribra orbitalia*, enamel hypoplasia and Harris lines (Krenz-Niedbała 1999b, c). The use of multiple markers may at least partly help to avoid the "non-survivor" problem in skeletal studies (Bocquet-Appel, Bar-Yosef 2008, Goodman 1992). Due to limited sample sizes, amongst other factors, studies of stress indicators in European Neolithic non-agricultural populations are scarce, slightly more numerous are the studies on farmers. As seen in *Table 4*, the frequencies of skeletal markers considerably vary among the samples. Comparable data on *cribra orbitalia* in the populations from contemporary Poland come from a composite Corded Ware sample of Małopolska (south-eastern Poland) and an agricultural Funnel Beaker Culture population of Bronocice (Gleń-Haduch 1995). The frequencies of the condition in both examined samples are similar, and while different in the study of Gleń-Haduch, the prevalence is lower in the group of mixed economy than in farmers (16.7% vs. 38.5%, respectively). In this study, the tendency toward a higher frequency of *cribra orbitalia* in agricultural samples when compared with groups exploiting hunting-gathering or mixed economies has not been highlighted. Several studies on the transition to agriculture have found statistically higher frequencies of *cribra orbitalia* in farmers (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984). In many studies it was observed that *cribra orbitalia* in periods prior to Neolithic was not common, but in the Neolithic, or generally after the transition to agriculture, this became more prevalent (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984), though the range of frequency of the condition is very wide, and it happens to be quite low in farmers (Cohen, Armelagos 1984, Larsen 2006). The increase in the frequency of *cribra orbitalia* with the introduction of agriculture has been explained through growing population size and density, sedentism and low hygiene, which is contrasted to the living conditions of preagricultural groups: mobility, lower density, lower possibility to contact with soil pathogens (Larsen 2006, Stuart-Macadam 1992).

Cribra orbitalia

Cribra orbitalia was first believed to be an indicator of nutritional stress (iron-deficiency anemia), but the results of further studies have made this claim controversial (Djuric *et al.* 2008, Stuart-Macadam 1992, Temple 2010, Walker *et al.* 2009, Wapler *et al.* 2004). Populations that mainly lived on cereal grains rather than a meat-based diet were supposed to become iron-deficient. The lack of iron would lead to reduced iron absorption in the intestines, and then to the formation of orbital perforations. Later on, the impact of diet on the development of iron-deficiency anemia ceased to be regarded as being so important (Kent, Dunn 1996, Klepinger 1992, Stuart-Macadam 1992). *Cribra orbitalia* has been found in skeletal populations from around the world, coming from different time periods, geographical locations, and cultures, and this suggests that there must be a variety of causal factors. The involvement of parasites in the etiology of *cribra orbitalia* was proposed as an alternative explanation (Stuart-Macadam 1992), though Hengen, as early as 1971 suggested a synergistic relationship between iron-deficiency anemia and infectious and parasitic diseases. Stuart-Macadam (1992) proposed that mild iron-deficiency is an adaptive mechanism against disease, since lowering of the serum iron would inhibit micro-organism reproduction (Stuart-Macadam 1992). Now *cribra orbitalia* is regarded as a nonspecific indicator of stress.

In the examined samples no significant sex difference in the frequency of *cribra orbitalia* was observed (Corded sample: males 23.1%, females 17.4%; Lengyel sample: 23.1% and 15.8% respectively), and this is similar to other studies (El-Najjar *et al.* 1976, Walker 1986). However, some authors have found *cribra orbitalia* to be more frequent in females than males (Armelagos,

TABLE 4. Frequencies of *cribra orbitalia* and enamel hypoplasia in selected European Neolithic agricultural samples.

				Enamel hypoplasia						
	Cribra orbitalia			Individual			Teeth			
Sample	*N*	*n*	%	*N*	*n*	%	*N*	*n*	%	Author
Poland, Osłonki	36	9	20.0	68	44	64.7	878	258	29.4	This paper
Poland, Bronocice	26	10	38.5							Gleń-Haduch (1995)
Czech Republic, Vedrovice	48	7	14.6							Lillie (2008)
Czech Republic, Moravia, LBK[a]	28		77.8	52	7	13.5	246	10	4.1	Smrčka, Tvrdý (2009), Jarošová, Dočkalová (2008)
Czech Republic, Moravia, LC[b]	12	5	41.7	16	3	18.8	62	5	8.1	Smrčka, Tvrdý, 2009, Jarošová, Dočkalová (2008)
Italy, Western Liguria				22	18	81.8				Formicola (1986–1987)
Hungary, composite	31	5	16.1				626	9	1.4	Ubelaker *et al.* (2006)
Greece, Alepotrypa Cave	35	21	60.0	15	2	13.3	436	36	8.3	Papathanasiou (2005), Papathanasiou *et al.* (2000)

[a] LBK, Linear Pottery Culture.
[b] LC, Lengyel Culture.

Goodman 1991, Cohen, Armelagos 1984, Cybulski 1977, Hengen 1971), which was attributed to the exposure of females to blood losses during menstruation and childbirth amongst other factors, as well as to a decrease in iron during pregnancy and lactation.

Enamel hypoplasia

Enamel hypoplasia is an indicator most frequently used in studies of socio-economic transitions (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984) and was called the most important stress indicator in paleopathological research (Bocquet-Appel, Bar-Yosef 2008, Goodman 1992, Wittwer-Backofen, Tomo 2008). Undoubtedly, the specific features of tooth enamel development are the main reason for enamel hypoplasia's widespread usage. Tooth enamel forms in a rhythmic and regular manner and is sensitive to nutritional and disease factors (Goodman *et al.* 1987, Krenz-Niedbała, Kozłowski 2013, Sarnat, Schour 1941). It does not undergo remodelling once formed and therefore retains the episodes of developmental disturbances during the childhood of the individual (Buikstra, Ubelaker 1994, Goodman, Rose 1990, Skinner, Goodman 1992). Moreover, clinical and experimental research (e.g. Goodman *et al.* 1987) has contributed to a widely accepted idea that individuals with hypoplasia are less adapted to living conditions than those without the defects (Goodman 1991).

In contrast to the *cribra orbitalia* expression discussed above, significant differences in the frequencies of enamel hypoplasia were found between the samples examined. The prevalence of affected individuals in the Corded Ware group is lower than in the Lengyel population (43.5% and 64.7%, respectively). This difference seems to result from the significant differences in the response of rather females than males. The frequencies of affected teeth also differ significantly between the samples. Additionally, it was found that the Corded Ware and the Lengyel groups also differ in the severity of the condition. It seems that the Lengyel population was exposed to more frequent and more severe stress episodes than the Corded Ware people. Some other studies found significant differences in the prevalence of enamel hypoplasia in populations that underwent economic transition from hunting-gathering to agriculture (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984, Goodman *et al.* 1980, Larsen 2006). The available data on the frequency of the condition in preagricultural populations suggests that prevalence ranges between 20% and 40%, while for the farming groups 50–60% (Lanphear 1990, Skinner, Goodman 1992). The increase in hypoplasia frequency after the transition to agriculture, detected in numerous studies on different populations, from various geographic regions and temporal periods (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984) has been attributed to unfavourable changes in diet (greater reliance on cereal products, lesser variety of food), temporary quantitative food limitations, consequences of increased sedentism, greater population density and conditions favouring the spread of pathogens, etc. (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984, Larsen 2006).

In the present paper no significant sex differences in the proportion of enamel hypoplasias were detected, similarly to other studies (Cohen, Armelagos 1984, Goodman *et al.* 1980, Lanphear 1990, Tomczyk *et al.* 2012). However, some authors did find sex-dependent prevalence of the condition (Bocquet-Appel, Bar-Yosef 2008, Cohen, Armelagos 1984, El-Najjar *et al.* 1978, Huss-Ashmore *et al.* 1982). The higher frequency of hypoplasia in males was attributed to, among other factors, greater susceptibility to developmental disturbances of growing boys than girls, caused by lower energy resources at birth in boys associated with their greater caloric needs (Huss-Ashmore *et al.* 1982). Greater hypoplasia incidence in females is explained through a lower degree of cultural buffering of adverse environmental factors (Goodman *et al.* 1980), reflected in, among other factors, weaning practices. It seems that the pattern of sex differences strictly relates to a given socio-cultural situation of a human population.

Estimation of the timing of hypoplasia occurrence has revealed that in the Lengyel series the peak age of occurrence occurs between 3.6 and 4.0 years, both for the whole sample and for both sexes, while in the Corded sample occurrence is recorded at earlier age categories, 2.6–3.0 years for the whole sample and males; 3.1–3.5 for females. Peak frequency of hypoplastic defects formed in childhood in a given sample is usually explained through weaning stress, bearing a variety of unfavourable consequences for the child's health, e.g. loss of nutrients provided by the mother's milk, or a decrease in organism immunity (Cohen, Armelagos 1984, Huss-Ashmore *et al.* 1982, Krenz-Niedbała, Kozłowski 2013, Lanphear 1990, Larsen 1987, comp. Katzenberg *et al.* 1996). Goodman *et al.* (1984) found the peak age at stress at 3.0–3.5 years for hunter-gatherers and 2.5–3.0 years for agriculturalists. Earlier weaning in farmers than in pre-agriculturalists corresponds to cultural factors, as suggested by ethnographic research (Goodman, Armelagos 1989). However, the importance of weaning in explaining peak frequency of hypoplasias was later questioned. Studies of contemporary non-industrial human groups found weaning to occur around c. 2 years of age (Skinner, Goodman 1992), while the research on chronological distribution of hypoplastic defects in prehistoric populations has brought a wide range of peak ages, between 2 and 4 years (Lanphear 1990, Skinner, Goodman 1992, Swärdstedt 1966). Such an extended period of the peak frequency of enamel hypoplasias was suggested to be due to methodological bias. Enamel development stages of particular teeth overlap, and the highest number of defects corresponds to the period when the greatest amount of enamel is formed (Skinner, Goodman 1992). Bone chemistry, historical evidence, and ethnographic analogy suggest that the average age at weaning for non-industrialised societies is by 2–3years of age (Stuart-Macadam 1995). The later age peak of enamel hypoplasia in farmers than in the mixed-economy population, found in this study, seems to partly result from the applied methodology and partly from the fact that weaning stress acts together with a variety of other factors to result in disturbed enamel growth (Ritzman *et al.* 2008).

In this paper it was found that teeth of different categories are not uniformly susceptible to metabolic insults, which is a well established fact (Goodman, Rose 1990, Huss-Ashmore *et al.* 1982, Krenz-Niedbała-Kozłowski 2013, Larsen 1987). The canines turned out the most affected teeth, followed by the incisors and lastly – premolars. This pattern may result from two phenomena: duration of enamel development (the longest for canines) and different degree of genetic determination of development of particular tooth types (Goodman, Rose 1990, Huss-Ashmore 1982).

A significant inverse relationship between mean age at death and the prevalence of enamel hypoplasias in the Lengyel population was found. The affected individuals died on average at younger ages. A similar relationship was revealed by Duray (1996) and Miszkiewicz (2012). This finding proves the reliability of the marker, as claimed in other studies (Bocquet-Appel, Bar-Yosef 2008, Miszkiewicz 2012, Wittwer-Backofen, Tomo 2008) and provides evidence for the severity of the factors that cause disturbances during enamel development.

Harris lines

Harris lines are considered non-specific as they occur in response to a range of adverse nutritional or disease factors (Cohen, Armelagos 1984, McHenry 1968, Papageorgopoulou *et al.* 2011, Wells 1967). The lines form in long bones until they stop growing, therefore they may complete the information provided by enamel hypoplasia with stress events in late childhood and adolescence. Additionally, they were found to be more prevalent in skeletal material than enamel hypoplasias (McHenry, Schulz 1976), as the skeleton is more susceptible to adverse factors of low intensity and short duration (Cohen, Armelagos 1984, Larsen 1987). However, on account of interpretative difficulties (e.g.

resorptive processes), these researchers clearly recommend using Harris lines as a component of multiple marker research design (Cohen, Armelagos 1984, Huss-Ashmore *et al.* 1982). Between the examined human samples no significant differences in the frequency of Harris lines and their mean number per individual were found. These results agree with some other studies on hunter-gatherers and agriculturalists (Cohen, Armelagos 1984). These authors also observed a nonsignificant decrease in the lines frequency after the transition to agriculture, while the frequency of enamel hypoplasia was two and even three times as high. Such a discrepancy in the results of analysis of Harris lines and enamel hypoplasia provokes a question regarding the reliability of Harris lines as a measure of the biological status of a population (Alfonso-Durruty 2011, Cohen, Armelagos 1984, Huss-Ashmore *et al.* 1982, Nowak, Piontek 2002a, Wittwer-Backofen, Tomo 2008), however, some studies showed the usefulness of this indicator for an assessment of health status of human samples, for example inverse relationships between the lines prevalence and body height and mean age at death in adults were found (McHenry 1968, Nowak, Piontek 2002b, Wells 1967). Cohen and Armelagos (1984) emphasised different aetiology of Harris lines and enamel hypoplasia and claimed that minor, regular famine periods in hunter-gatherers could have changed into more intense and irregular episodes in farmers, associated with severe infectious diseases. Cohen and Armelagos (1984) also stressed that enamel hypoplasia seems to be a more reliable indicator of metabolic disorders, taking into account Harris lines resorption and the fact that lines actually do not reflect the cessation of bone growth, but rather its further, compensatory acceleration (in farmers lower frequency of lines may actually reflect a lack of such acceleration). These authors cited the results of experimental studies, supporting this hypothesis. On the basis of those considerations it seems probable that a slightly lower frequency of Harris lines in agriculturalists of Osłonki in comparison with the people of mixed economy does not conflict the results provided by enamel hypoplasia and may even indicate that in the studied Lengyel group new, i.e. different kinds of disturbances might have been occurring, and that these were generally more irregular and more severe in expression. However, it should also be noted that some studies have found no correlation between Harris lines and illnesses (Alfonso-Durruty 2011, Clarke 1982, Garn *et al.* 1968, McHenry, Schultz 1976, Ribot, Roberts 1996).

In both examined samples, there are no statistically significant sex differences in the lines frequency, similarly to some other studies (Arnay-de-la-Rosa *et al.* 1994, Cohen, Armelagos 1984, McHenry 1968, Papageorgopoulou *et al.* 2011). Higher prevalence of the condition in males has been frequently reported (Cohen, Armelagos 1984, Garn, Schwager 1967, Hojo 1981, Jerszyńska, Nowak 1996), and attributed to greater susceptibility of boys than girls to unfavourable environmental factors (Cohen, Armelagos 1984, Wells 1967). By contrast, other studies have found a greater frequency of lines in females (Cohen, Armelagos 1984).

In the present paper, a widely observed pattern of occurrence of Harris lines within the human skeleton has been revealed, as in both populations at the distal ends of the tibias more than twice as many lines formed than at the proximal ends (Garn *et al.* 1968, Hojo 1981, Papageorgopoulou *et al.* 2011). Moreover, the observed lines are characterised by symmetrical and bilateral arrangement in the right and left bones (similarly to the study of McHenry 1968, comp. Garn, Baby 1969, Garn, Schwager 1967).

In the total Corded Ware population and in the male subgroup the peak of Harris lines occurs in the 11th year, and 9–12 years of age in females. In the total Lengyel population and in the male subgroup the peak falls in the 12th year of age and in the 10th year in females. In other studies of the chronology of Harris lines there are usually two periods in the peak of occurrence: a more obvious incidence around c. 2–3 years of age and a less marked occurrence at c. 11–14 years of age (Cohen, Armelagos 1984). It was found that the second peak falls in the lower age categories in females when compared to males, and that this probably results from their earlier growth spurt (Arnay-de-la-Rosa *et al.* 1994, Jerszyńska, Nowak 1996). The present results agree with those findings. From the chronological distribution it may be inferred that some Harris lines, that occurred in early childhood, had disappeared, since it is rather unlikely that the examined individuals were not exposed to adverse factors in infancy.

In summary, the results obtained in this study confirmed the exceptional value of enamel hypoplasia among skeletal stress markers, as claimed in other studies (Bocquet-Appel, Bar-Yosef 2008, Miszkiewicz 2012, Wittwer-Backofen, Tomo 2008). Enamel hypoplasia appears to be a more reliable and sensitive skeletal stress indicator than *cribra orbitalia* and Harris lines. The pattern of occurrence of developmental enamel defects clearly differentiated the examined populations that presumably truly differed in health status.

CONCLUSIONS

Among the analysed skeletal stress indicators in two Neolithic samples enamel hypoplasia proved a useful tool in revealing the effect of different subsistence economies in buffering against adverse nutritional and disease factors. It seems that the agricultural Lengyel population was exposed to more frequent and severe stress episodes, with regard to higher population size and density, sedentism, low hygiene, and less diversified diet than the population of the Corded Ware Culture who adopted mixed, agricultural-breeding-pastoral economy supplemented with hunting and gathering, characterised by mobility, better nutrition, lower population size and density. For the Lengyel population it was found that individuals affected by enamel hypoplasia died on average at younger ages than the unaffected individuals did. This finding demonstrates the reliability of the marker and highlights the severity of the factors disturbing enamel development.

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