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Genetic genealogy of the Piast dynasty and related European royal families

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The Piasts were one of the royal dynasties that shaped the political structure of medieval Europe in the 10th century CE. Despite their importance, as the founders and rulers of the early Polish kingdom, little is known about Piast origin, the conditions of Poland's transformation into a medieval monarchy, and generally about the mechanisms of political entity formation in 10th-century East-Central Europe. Here we present an interdisciplinary investigation of Piast necropolises scattered throughout Poland. Within eight sites, we find 33 sets of skeletal remains likely to belong to the Piasts. Archaeogenomic analyses confirm the identities of ten as Piasts. Based on genomic data obtained for them, we determine the mitochondrial haplogroups of more than 200 historical figures from 10 European royal dynasties. The Y haplogroup lineage identified in the Piasts (R1b-BY3549) is currently rare. The same Y haplogroup lineage in databases of ancient DNA is found in three individuals who lived in North-Western Europe (present-day France, the Netherlands, and England). Together, these findings may suggest that the Piasts were of non-local origin and support the hypothesis that the state-building processes occurring in the 9th-11th centuries in East-Central Europe were induced not only by local elites but also by foreigners.

The tenth century CE is considered a turning point in the history of medieval Christian civilisation, as it marked the political formation of medieval Europe[1–4]. The declining Carolingian Empire in the west was replaced by the rising powers of France and Germany[5–10]. The number of Norman invasions and trade expeditions gradually decreased, whereas in territories beyond the Elbe River, the process of early state formation began to accelerate. One of the key factors contributing to the establishment of the new shape of Europe around AD 1000 was the formation of the early Polish kingdom in the present-day Greater Poland region[4,11–14]. For the next few centuries, this kingdom became the eastern boundary of Latin civilisation that in the culmination point, i.e. at the end of the fourteenth century, spread from the Baltic to Black Seas[15,16].

The founders and rulers of the early Polish state were the members of the House of Piast (Supplementary Fig. 1 and Supplementary Note 1). The first documented Polish ruler was Prince Mieszko I. He transformed the just emerging Polish pagan community into a Christian principality in AD 966, which allowed Poland to participate in the

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politics and society of Latin Europe. As one aspect of this participation, the Piasts often intermarried with other European dynasties[17] which had a significant impact on the political landscape of medieval Europe. For example, Mieszko's daughter, known as Sigrid the Haughty or Gunhild of Wenden, was the Queen of Sweden, Denmark, Norway, and England and the mother of several kings: Olof Skötkonung, Harald II Svensson, and Cnut the Great[18]. Within a matter of decades, the Piasts grew to become one of the largest European dynasties. The Piast monarchy ended in AD 1370 with the death of King Kazimierz III Wielki (Casimir III the Great). However, other Piast branches continued to control duchies, such as Masovia and Silesia, until the last male Piast representative died in AD 1675.

Despite the Piasts' reputation and importance, there are very few documents and little direct information available about the dynasty origin and the process of early Polish state formation. The surviving historical sources, such as Gallus Anonymus' 'Chronica Polonorum' from the early twelfth century[19] provide only a limited perspective on these events. Therefore, various legends and scientific hypotheses have been developed to explain the origin of the Piasts (Supplementary Note 1). Some of them suggest that this family was of local Slavic origin, whereas others hypothesise that the Piasts were of foreign origin, such as Norman or Moravian[15,20,21]. Unfortunately, the origin of the Piast dynasty has remained inconclusive based on previous historical and archaeological methods, and thus, the questions on the mechanisms of early Polish state formation remain open. The same problem concerns other states that have been developing in East-Central Europe at that time. They could be established by the local elites or foreigners.

The recent development of archaeogenomics has transformed the study of human demographic history. To date, the vast majority of studies have focused on groups of anonymous individuals. The latest achievements in ancient DNA (aDNA) analyses have brought high expectations that many issues connected with individual historical figures or families, e.g. the medieval European royal dynasties and the mechanisms of the political formation of modern Europe in the tenth century, would also be answered. However, it turned out that finding royal burial places and the identification of the remains of particular historical figures are extremely difficult. For medieval royal families, a few successful examples include: the last member of the English Plantagenet dynasty, King Richard III[22]; Kings Ladislaus I and Béla III of the Hungarian Árpád dynasty[23–26] and Prince Dmitry Alexandrovich, son of Alexander Nevsky, one of the members of the Rurikid dynasty[27]. In all these cases, the studies have been limited to individual representatives, and one has to remember that considering the unforeseen events which can happen regardless of time and a person's social status (e.g. adultery, rape), it is impossible to prove that genetic data obtained for a single historical figure applies to a whole dynasty. Additionally, for people who lived hundreds of years ago, the unambiguous assignment of skeletal remains to a given historical figure, even to a king or queen, can be challenging. Thus, to create a reliable genetic portrait of any dynasty, it is important to determine the continuity of male (Y-chromosome haplogroup, Y-hg) and female (mitochondrial DNA haplogroup, mt-hg) lineages, as well as the kinship between particular family members, which requires DNA samples from persons representing at least several consecutive generations.

Here, we present a comprehensive genetic analysis of numerous representatives of the Piast royal dynasty who were buried during the twelfth to seventeenth centuries CE. Our aDNA findings, together with historical data, allowed us to identify the skeletal remains of at least 10 Piasts. The genome-wide analyses we performed indicate that the Piasts most likely came from outside of Poland. By tracing both maternal and paternal Piast lineages, we confirmed historically-documented links between the Houses of Piast and Hungarian Árpád. Based on our results, supported by genealogical data, we assigned the mitochondrial and/or Y-chromosomal haplogroups of over two hundred known historical figures from European dynasties and noble families, including 18 kings. The created genetic portrait of the House of Piast against the background of other medieval royal dynasties forms the basis for further studies of the processes that led to the formation of new political entities based on monarchy and self-sufficient economies in the tenth century.

Results

In search of the Piast's burial sites

To determine the origin of the Piasts, we attempted to find skeletal remains of the individuals representing at least several consecutive generations of the dynasty. To this end, we identified the location of over 340 potential burial sites of Piast family members, using available historical and archaeological sources[28–35]. Our closer examination of these sites revealed that the vast majority of them were only symbolic memorials with no human remains inside. However, in eight locations, we found human bones in graves that were attributed to members of the Piast family according to tradition as well as previous historical and archaeological analyses (Supplementary Fig. 2 and Supplementary Note 2). Samples were collected from 33 graves/coffins (30 male graves and 3 female graves) that had been assigned to a single member of the Piast dynasty (Supplementary Data 1). Within the group of 33 Piasts whose graves we identified, a set of samples representing 13 consecutive generations was defined, comprising 22 dynasty members buried in the Płock and Warsaw Cathedrals (Supplementary Fig. 2 and Supplementary Data 2a).

Piast of Płock. The Płock Cathedral is the largest Piast necropolis in Poland, serving as the interment site of 12 generations of Piasts of the main and Masovian lineages, spanning four centuries. According to historical sources, 18 Piast family members (17 males and 1 female) were buried in Płock[28,30,36]. As a result of archaeological and anthropological studies performed in the 1970s, skeletal remains found in the Cathedral Royal Chapel and the crypt beneath it were deposited in 18 separate containers. Each container was labelled with the name of the individual to whom remains were attributed[37,38]. In 2019, we re-examined the contents of all containers and took 2–5 samples from each container for DNA analysis and radiocarbon dating (Supplementary Data 2a, Supplementary Fig. 3a and Supplementary Note 3). Radiocarbon dating results indicated that the ages of the samples overlapped perfectly with the period of the Piasts' reign in Płock (Fig. 1), consistent with earlier historical reports suggesting that human remains deposited in the Płock Cathedral actually belong to the Piast family. However, the dates were often inconsistent with the dates of death of the individuals indicated by the labels assigned to each set of skeletal remains in the 1970s (Fig. 1a). This observation agrees with earlier reports that, at some time in the past, these graves were disturbed, coffins were destroyed, and bones were partially mixed. In addition, some reports have indicated that the remains of the Płock Piasts could have been mixed not only with each other but also with the remains of bishops or noblemen buried in the cathedral[38,39]. As a result, none of the 18 skeletal remains from Płock have been unequivocally attributed to specific historical figures.

Piast of Warsaw. St. John the Baptist Cathedral in Warsaw (hereafter, Warsaw Cathedral) is another important Piast necropolis. Historical records indicate that this is the interment site of the skeletal remains of four Piasts, namely, Janusz I, Bolesław IV, Stanisław and Janusz III[30,40]. The graves of princes Stanisław and Janusz III remained intact until 1953, when they were opened by a group of archaeologists and anthropologists. The investigations carried out at that time confirmed the identities of both princes[41] (Supplementary Note 2). In 2016, we reopened these graves, performed anthropological analyses of the skeletal remains and took two samples from each. The results of

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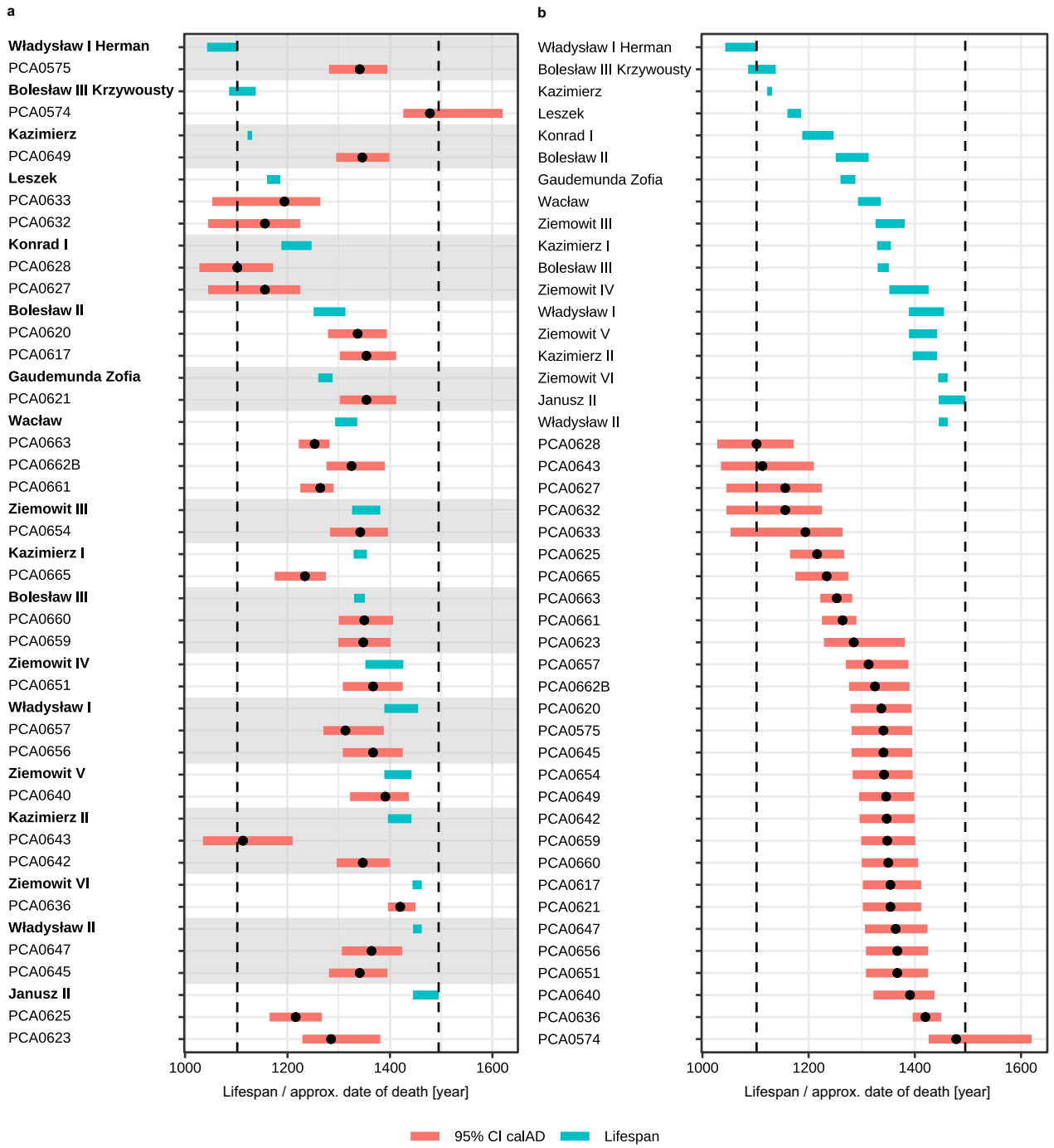

Fig. 1 | Radiocarbon dating of bone samples retrieved from the Płock Cathedral. a Shows the radiocarbon dating results of samples taken from individual containers comprising the remains of supposed Piast family members buried in Płock and the lifespan of the individual whose name was placed on the container. Separate containers are indicated by alternating grey and white areas, with the individual corresponding to the label shown at the top (bold) of each area. **b** Shows (separately) the chronologically ordered lifespans of the Piasts buried in Płock and the radiocarbon dating results. The mean radiocarbon dates are indicated by black dots, and the corresponding 95% confidence intervals are shown with red lines (for details, see Supplementary Fig. 3a). The lifespans of the indicated Piasts are shown with blue lines. Dashed vertical lines mark the period during which Piast dynasty members were buried in the Płock Cathedral. Source data are provided in a Source data file.

anthropological examination and radiocarbon dating confirmed that the skeletons belonged to young people (approximately 25 years old) who died around the same time as one another.

The situation was less clear with regard to the interment of Janusz I and Bolesław IV. We were unable to find reliable information regarding when their graves were opened. The stone sarcophagus on which the names of both princes (Janusz I and Bolesław IV) were carved contained two coffins. In one of them, we found two skeletons from which we took 2–3 samples. Radiocarbon dating revealed that these could not be the skeletal remains of Janusz I or Bolesław IV (Supplementary Data 2a). The second coffin contained one skeleton, from which we collected two samples. The results of the anthropological analyses and radiocarbon dating were consistent with historical information about Prince Bolesław IV (Fig. 2 and Supplementary

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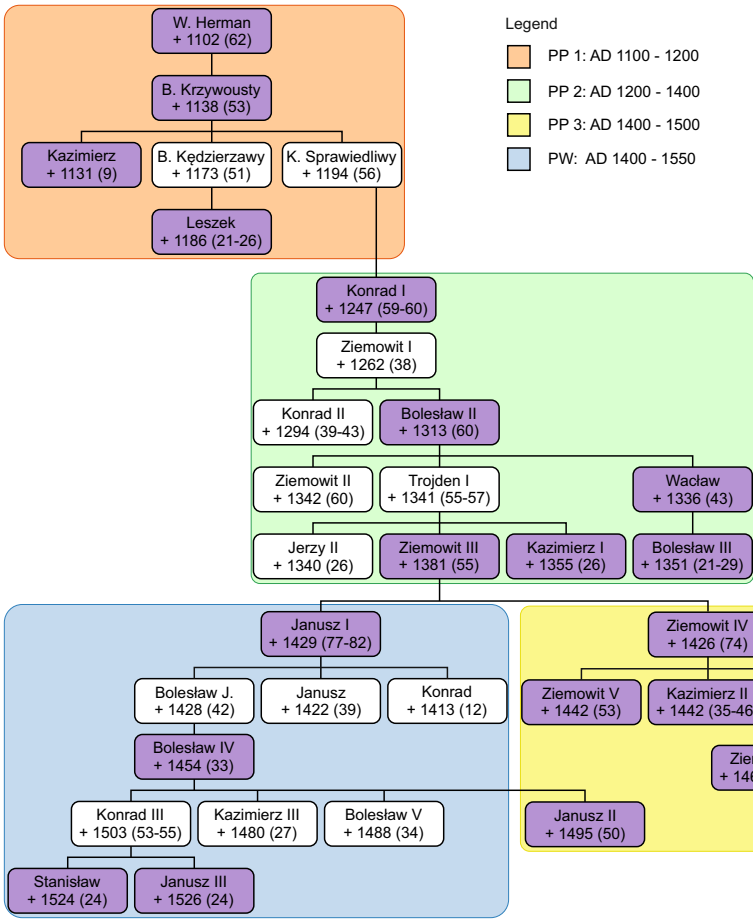
a



b

ID	^{14}C	ESA	mt-hg	Y-hg	Identity
PIAST01	1102	60	T2b4b	R	?
PIAST02	1113	40	H1e8a	R1a1a1b1a1a1c1	?
PIAST03	1156	25	-	R1a1a1b1a2b3~	?
PIAST04	1216	-	-	R1a1a1b1a1a1c1	?
PIAST05	1234	> 40	T2b2b1	R1b1a1b1a1	?
PIAST06	1285	-	H3s	R1b1a1b1a	?
PIAST07	1325	-	H11a	R1	?
PIAST08	1337	-	K1b2a1	R1a1a1b1a1a1c1	?
PIAST09	1341	-	R	R1a1a1b1a2b3a	?
PIAST10	1341	15	T2b4b	-	?
PIAST11	1342	45	B4b1a3a	R1b1a1b1a1a2	?
PIAST12	1346	7	U5b2a5	-	?
PIAST13	1348	-	R	R1b1a1b1a1a	?
PIAST14	1478	50	H11	R1a1a1b1a1a1a	?
PIAST15	1455	30	U5a1b1e	R1	?
PIAST16	1460	25	T2b	R1b1a1b1a1	Stanisław
PIAST17	1484	25	W1	R1b1a1b1a1a	Janusz III

c

Degree of Kinship	Related Individuals
1st	PIAST06 - PIAST11
	PIAST11 - PIAST13
2nd	PIAST05 - PIAST06
	PIAST06 - PIAST09
	PIAST11 - PIAST09
	PIAST17 - PIAST16
3rd	PIAST05 - PIAST11

Fig. 2 | Integration of historical data and results of our anthropological and genomic studies of the Piasts of Płock and Warsaw. a Shows a portion of the Piast family tree with all 21 male members of the dynasty reported to be buried in Płock and Warsaw (purple blocks). The individuals who also belong to this portion of the family tree and were buried elsewhere or at an unknown location are shown as white blocks. For each of the Piasts, his or her historical name, date of death, and age at death (in parentheses) are shown. **b** Presents selected results of our anthropological and genomic analyses of 17 skeletal remains found in Płock and Warsaw. For each individual, we showed the mean radiocarbon date (^{14}C), estimated skeletal age (ESA), mt-hg, Y-hg, and if their name was determined earlier by other researchers, their identity. **c** (Pink) shows the kinships among the 17 examined individuals that we determined on the basis of the obtained genome-wide data. The data in (**a**, **b**) are coloured based on the four subsets of 21 historical Piasts/17 skeletal remains (PIAST01-17) we determined: Piast of Płock-1 (PP-1, orange), Piast of Płock-2 (PP-2, green), Piast of Płock-3 (PP-3, yellow) and Piast of Warsaw (PW, blue).

Data 2a). In summary, in the Warsaw Cathedral, we confidently identified the remains of two representatives of the Piast dynasty, Stanisław and Janusz III, and found remains most likely belonging to Bolesław IV. As we did not identify any skeletal remains that could belong to Janusz I, he was excluded from further analyses.

During the 5-year search, we identified 21 graves containing remains most likely belonging to members of the Piast dynasty. Only for two graves, Stanisław and Janusz III, were the identities of the deceased known.

Genomic analysis of skeletal remains

For genomic analysis, we collected a set of two to five samples from each grave/coffin attributed to a specific member of the Piast dynasty (66 samples in total). For each of the collected sets, we classified the samples into two types: A and B, based on their likelihood of belonging to the same individual. A-type samples were those that definitely corresponded to a single individual, as they were collected either from graves opened for the first time or very recently, such that there was no doubt who was buried there, or from the same bone or skull (e.g. two teeth extracted from the same jaw). B-type samples were those for which we could not be sure that they came from one person, that is, from fragments of different bones taken from graves that had been disturbed in the past (Supplementary Data 2a, b).

The collected materials were examined in a laboratory dedicated exclusively to working with ancient DNA. DNA was extracted from each sample and sequenced as described in 'Materials and Methods'. All analysed DNA exhibited postmortem damage (PMD) patterns characteristic of aDNA (Supplementary Fig. 3b). The sequencing data obtained separately for each of the 66 samples were analysed to determine genetic sex, Y-hg, mt-hg and kinship (Supplementary Data 2–7 and Supplementary Note 4). These analyses revealed that all A-type and 2 B-type samples originated from single individuals (Supplementary Data 2a rows 56 and 57). Additionally, we found B-type samples that were genetically different from their counterparts within a set but identical to samples belonging to another set (Supplementary Data 2a rows 61 and 21; rows 56, 57 and 53). We also identified a set of A- and B-type samples that corresponded to multiple individuals (Supplementary Data 2a rows 17–20). These observations seem to confirm previous speculations that the skeletal remains of some individuals were mixed in the past.

In the next stage, sequencing data obtained for samples from the same individual/skeleton (A-type samples and genetically identical

B-type samples) were combined and analysed to determine their quality. Only samples from 17 skeletons for which we obtained good-quality genome-wide data were used in subsequent studies (for details, see Supplementary Data 2a). These individuals/skeletons were: (i) numbered chronologically, based on the radiocarbon dating results and (ii) marked with identification numbers and historical names if their identities were considered definite. Thus, the final study group included 17 skeletons, each representing one individual (marked as PIAST01–17). The identities of 2 individuals, PIAST16 and PIAST17, were confirmed (Stanisław and Janusz III, respectively), whereas those of the remaining 15 were classified as putative Piasts. Gene-based sex estimates revealed that 15 of the 17 individuals were males and two were females (Supplementary Data 2a). Mt-hgs were determined for 13 male and 2 female samples, and Y-hgs were established for all 15 male samples (Supplementary Data 2a and 7).

Genetic genealogy of the Piast dynasty

To create a genetic portrait of the house of Piast, we aimed to determine the optimal assignment of 17 identified skeletal remains (PIAST01-17) to specific individuals from the group of 21 historical figures who, by existing documents and tradition, were buried in the Płock and Warsaw Cathedrals. To this end, we compared the results of our genetic and anthropological analyses of 17 individuals with the available genealogical data on 21 historical Piasts (Fig. 2 and Supplementary Data 9).

We noticed that further analysis will be much easier if, on the basis of the recorded dates of death (Fig. 2a) and radiocarbon dating results (Fig. 2b), we separate the 21 Piasts and 17 candidate remains (individuals PIAST01–17) into four subsets: three containing Piasts of Płock (PP) PP-1, PP-2 and PP-3 and one containing Piasts of Warsaw (PW). PP-1 included four Piasts who died between 1100 and 1200; three candidate remains dated to the same period (PIAST01–03). PP-2 comprised six Piasts who died between 1200 and 1400, with 10 analogously dated candidate remains (PIAST04–13). PP-3 included seven Piasts who died between 1400 and 1500; only one candidate remains corresponded to this subset (PIAST14). Finally, the PW subset included four Piasts who died between 1400 and 1550 and 3 candidate remains (PIAST15–17) radiocarbon dated to the same period. Next, we tried to match all individuals to historical figures within each subset.

The PP-1 subset included four historical figures, two men who died at age 50–60 years (Władysław I Herman and Bolesław III Krzywousty), one man who died at approximately 21–26 years old (Leszek) and one boy who died at the age of 9 (Kazimierz) (Fig. 2 and Supplementary Fig. 4). Since none of the skeletons found in Płock belonged to a male child, we can conclude that they are not the remains of Kazimierz. PIAST02 and PIAST03 belonged to different R1a Y-hg, and their estimated skeletal ages (ESAs) are 40 and 25, respectively. Thus, these remains could not belong to Herman and Krzywousty, who died at the ages of 62 and 53, respectively. Considering the above, it could be hypothesised that PIAST03 (ESA 25) was Leszek, who died at the age of 21–26; PIAST02 was a person whose identity could not be determined; and PIAST01 (ESA c. 60) may have been either Władysław I Herman (age-at-death 62) or Bolesław III Krzywousty (age-at-death 53) (Supplementary Fig. 4).

The PP-2 subset includes six male historical figures and 10 candidate remains: PIAST04–13 (Fig. 2 and Supplementary Fig. 5). PIAST12 and PIAST10 were females with ESAs of 7 and 15, respectively. Because there was no information about young females from the Piast dynasty buried in Płock, these remains were excluded from further analysis. Taking into account the dates of death of the six historical Piasts and the radiocarbon dating results, we tentatively assigned PIAST05 to Konrad I and PIAST06 to Bolesław II. In the next stage, we tried to match the kinship ties that we determined to particular individuals (see Fig. 2c and Supplementary Note 4). PIAST06, the alleged Bolesław II, showed first-degree kinship with PIAST11. Out of the Piasts buried in Płock, the only person who could have had such a relationship with Bolesław II was his son, Wacław, so the remains of PIAST11 were assigned to him. This assignment is also supported by the ESA and radiocarbon dating determined for PIAST11. At the same time, PIAST11 showed first-degree kinship to PIAST13. Again, the only Piast buried in Płock who could have had this relationship with Wacław was his son, Bolesław III. This assignment is also supported by the radiocarbon dating results obtained for PIAST13. This proposed identification of the skeletal remains was additionally confirmed by the detection of second-degree kinship between PIAST05 and PIAST06 (Konrad I and Bolesław II) and third-degree kinship between PIAST05 and PIAST11 (Konrad I and Wacław) (Supplementary Fig. 5).

We also found second-degree kinship between PIAST06 (Bolesław II) and PIAST09. This finding was not unexpected because two of Bolesław II's grandsons, Ziemowit III and Kazimierz I, were reported to belonged to the group of 18 Piasts buried in Płock; PIAST09 could be one of these individuals. However, PIAST06 (Bolesław II) and PIAST09 belonged to different Y-hgs, R1b and R1a, respectively, indicating that they were not related through the paternal lineage; that is, these findings indicate Bolesław II was not the biological father of Trojden I (not buried in Płock) or that Trojden I was not the biological father of Ziemowit III or Kazimierz I.

Therefore, we sought alternative explanations for the clear second-degree kinship between Bolesław II and one of his grandsons. The key to solving this genetic mystery was Maria of Galicia, the mother of both of Bolesław II's grandchildren. Maria of Galicia was the daughter of Eufemia Kujawska (Supplementary Fig. 6), whose father (Kazimierz Kujawski) and mother (Eufrozyna Opolska) were Piasts. Further examination of the genealogy of the grandmother and great-grandmother of Ziemowit III and Kazimierz I revealed that all male ancestors of Eufemia Kujawska and Eufrozyna Opolska over at least five generations were Piasts, and four of these Piasts were also the ancestors of Bolesław II. In this way, Ziemowit III and Kazimierz I inherited at least one quarter of a Piast genome from their mother. However, we had no information that could be used to determine whether the PIAST09 remains belonged to Ziemowit III or Kazimierz I. Nevertheless, this explanation is very consistent with the proposition that the individuals buried in Płock were actually Piasts and supports the proposed assignment of the skeletal remains to historical figures.

The PP-2 subset also included 3 individuals, PIAST04, PIAST07 and PIAST08, that could not be assigned to any historical figure (Supplementary Fig. 5). Interestingly, two of them, PIAST04 and PIAST08, shared Y-hg lineage R1a–L1029, which was also carried by one individual from the PP-1 subgroup (PIAST02). However, it should be noted that we did not find any closer degree of kinship among these 3 individuals. There was also no higher-degree kinship among PIAST04, PIAST08 and PIAST09 (putative Ziemowit III or Kazimierz I, who belonged to the Y-hg lineage R1a-CTS3402).

The PP-3 subset included seven historical Piasts buried in Płock and only one skeleton (PIAST14) (Fig. 2 and Supplementary Fig. 7) with an ESA of c. 50 years and radiocarbon dated to 1478. Based on these findings, we were able to exclude three of the historical Piasts: Ziemowit VI and Władysław II, who died as teenagers, as well as Ziemowit IV, who lived to 74 and died in 1426. Thus, PIAST14 may be any of the following individuals: Ziemowit V, Kazimierz II, Władysław I or Janusz II.

The PW subset yielded much clearer results (Fig. 2 and Supplementary Fig. 8). PIAST16 and PIAST17 had already been identified by archaeologists and anthropologists as Stanisław and Janusz III, brothers who both died at age of 24, representing the last of the Masovian Piasts. The results of our studies provided further confirmation of the above findings. The ESA values we determined for both were similar (c. 25 years). Genetic analyses revealed that they shared the same Y-hg and presented second-degree kinship. The bone remains of PIAST15 were radiocarbon dated to 1455 with an ESA of 30 years. Based on this

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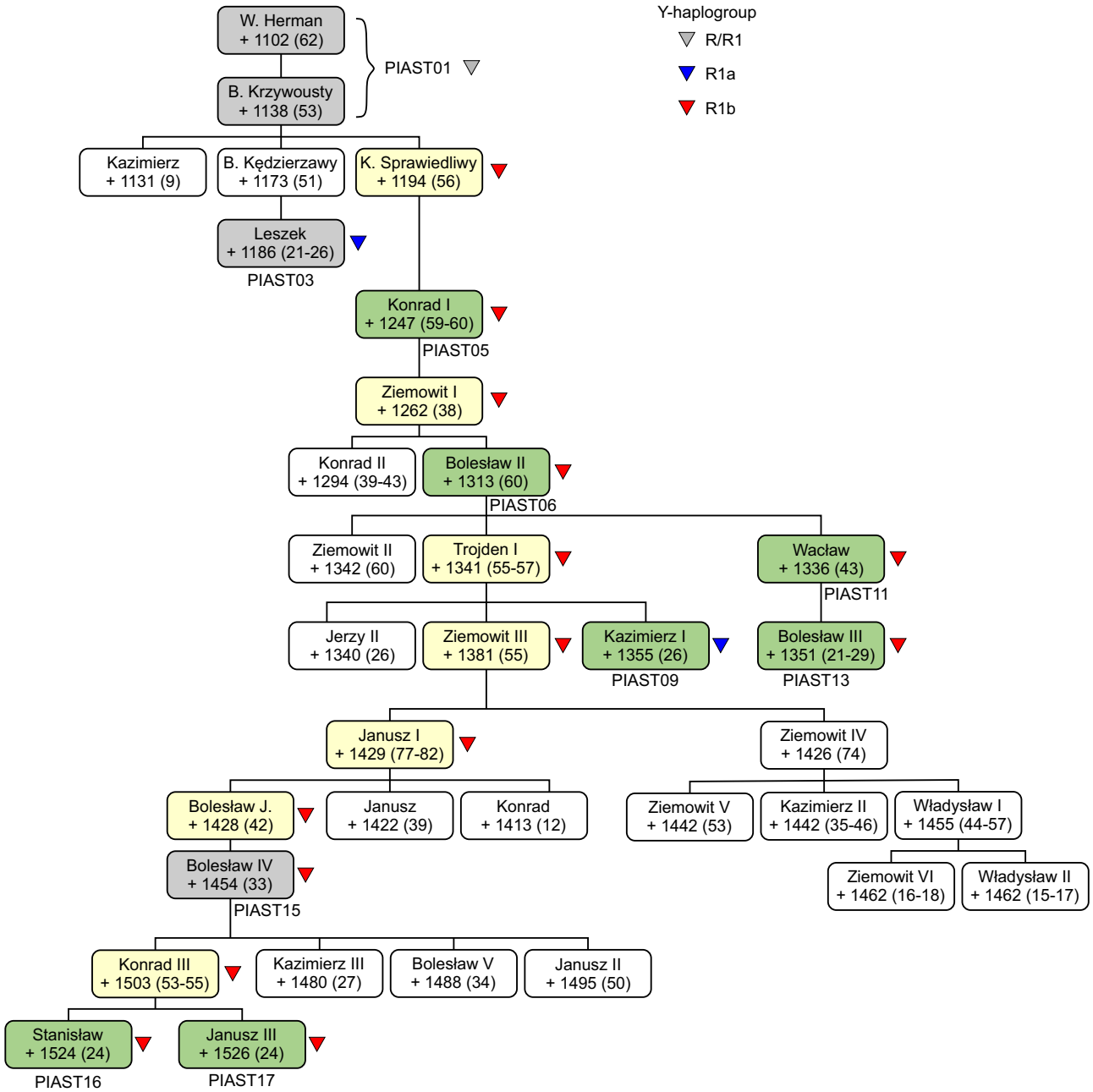

Fig. 3 | Final assignment of the skeletal remains resting in the Płock and Warsaw cathedrals to specific representatives of the Piast dynasty. This figure, similarly to **a** in Fig. 2, presents a portion of the Piast family tree including all of the male members of the dynasty buried in Płock and Warsaw. For each Piast, his historical name, date of death, and age at death (in parentheses) are shown. The ten Piasts to whom we were able to assign skeletal remains with very high probability (assignment confirmed by historical data, ^{14}C, ESA, Y-hg, and kinship) or high probability (assignment confirmed by historical data, ^{14}C, ESA, and Y-hg) are highlighted in green and grey, respectively. The identification numbers of the assigned skeletal remains are shown below each individual's name. Yellow blocks indicate dynasty members who could be assigned the Piast-specific Y-hg lineage because the data obtained for their direct descendants and/or ancestors indicated that the male line was unbroken. Grey, blue, or red triangles next to an individual's name indicate R/R1, R1a, or R1b Y-hg, respectively.

and the available historical and archaeological data, these remains were assigned to Bolesław IV, who died in 1454 at the age of 33.

By combining the results of our genomic analyses of individuals from the PIAST1-17 group with the genealogical data on 21 Piasts buried in Płock and Warsaw, we were able to determine the identity of at least 10 historical figures (Fig. 3 and Supplementary Data 9).

Piast's Y-chromosome lineage identification

To find additional evidence supporting our assumption that a significant proportion of the examined individuals (PIAST1–17) belong to a single family, most likely the Piasts, we focused further analysis on the Y chromosome, which is always passed on from father to son. Depending on the quality of the generated sequencing data, we were able to determine Y-hgs with very different levels of precision for each of the 15 male individuals from the study group. Six individuals identified as Piasts carried R1b haplogroups. The analyses of data generated for individual R1b Piasts suggested that their common ancestor came from the R1b-P312 lineage (Supplementary Data 4a and Supplementary Note 5). Currently, this lineage is most-frequently observed in Great Britain (Fig. 4b). To identify more recent

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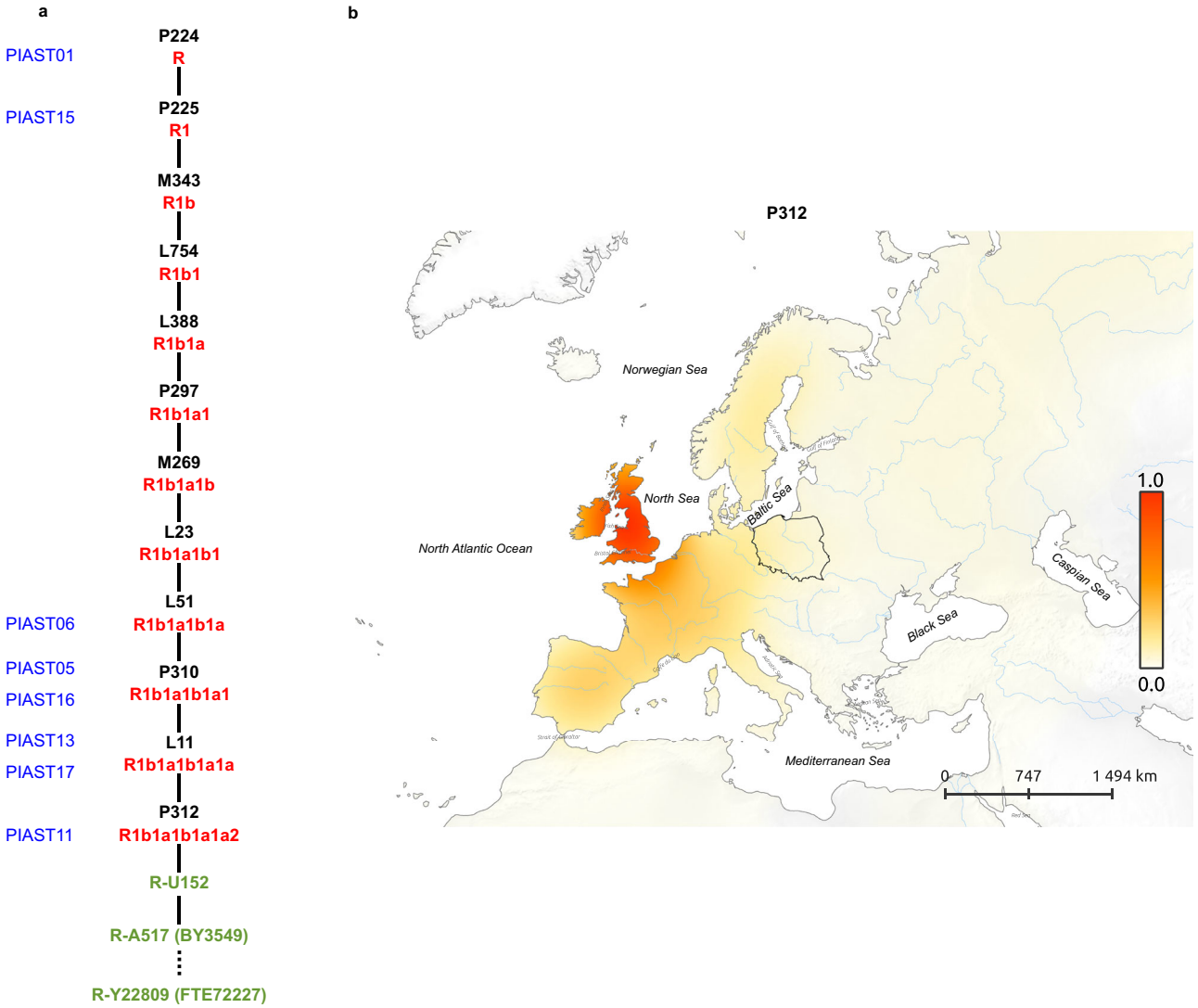

Fig. 4 | Piast-specific Y-hg R1b lineage. a A portion of the Y-hg R/R1b phylogenetic tree with annotations indicating Y-R/R1b lineages determined for seven skeletal remains buried in Płock and Warsaw (R/R1b lineages are shown in black/red and Piast identification numbers are shown in blue). The lineages resulting from the analysis of the consensus Y-chromosome haplogroup are shown in green. One could postulate that not R1b-BY3549 but R1b-FTE72227 is the most recent lineage; however, this claim is not fully supported by the collected data (Supplementary Data 4b and Supplementary Note 5). **b** Presents a heatmap showing the frequency of the Y-hg R1b-P312 lineage across modern Europe. The map was created using QGIS v3.40.15. Country boundaries for Europe, Poland, and river data were sourced from https://www.naturalearthdata.com/. Data for creating the heatmap was sourced from https://www.yfull.com/ (accessed April 2024).

ancestors of R1b Piasts, we determined their consensus Y chromosome haplogroup. The collected data indicated that all of the R1b Piasts could share the same Y-hg lineage, R1b-BY3549 (Fig. 4a, Supplementary Data 4b, Supplementary Fig. 9 and Supplementary Note 5). It means that they could be male ancestors/descendants of each other within one family. Two individuals identified as likely Piasts (Leszek−PIAST03 and Ziemowit III/Kazimierz I−PIAST09) and four unidentified individuals (PIAST02, PIAST04, PIAST08, and PIAST14) belonged to three distinct R1a lineages (L1029, L260, and CTS3402; Supplementary Fig. 10). Therefore, they could not be male ancestors/descendants of each other within one family. For two individuals, we were only able to determine that they belonged to the R1 Y-hg. One of these individuals is most likely Bolesław IV (PIAST15), whose two grandsons, Stanisław (PIAST16) and Janusz III (PIAST17), carry R1b Y-hg. It can therefore be assumed that Bolesław IV belonged to the same haplogroup. Unfortunately, we were unable to determine the identity of the second individual with the R1 haplogroup (PIAST07). Thus, among the 10 individuals identified as Piasts with a very high probability, seven belonged to R1b Y-hg (from one branch containing the lineages R1b, L754, L761, L389, P297, M269, L23, L51, L52, PF6538, L151, P312, U152 and BY3549), and two carried R1a Y-hg (from two lineages, L1029 and CTS3402). For one individual, PIAST01, we were not capable of determining whether he belonged to R1a or R1b Y-hg.

Given the identification of R1b Y-hg in members of the Piast dynasty across 13 generations, we were able to infer that the intervening members of this male lineage, i.e. two Warsaw Piasts (Janusz I and Bolesław IV) and five Piasts either buried in Płock or Warsaw (Kazimierz Sprawiedliwy, Ziemowit I, Trojden I, Jerzy II, and Konrad III), also belonged to R1b Y-hg. Ziemowit III (the above-mentioned grandson of Bolesław II, son of Trojden I, and great-great-great-grandfather of Stanisław and Janusz III) also must have been a carrier of R1b Y-hg (Fig. 3). Therefore, the remains marked PIAST09 (Y-hg R1a) could not belong to Ziemowit III. As a result, PIAST09 must be Kazimierz I, who could not have been the biological son of Trojden I because the latter was carrying R1b Y-hg. Ultimately, on the basis of our findings, we

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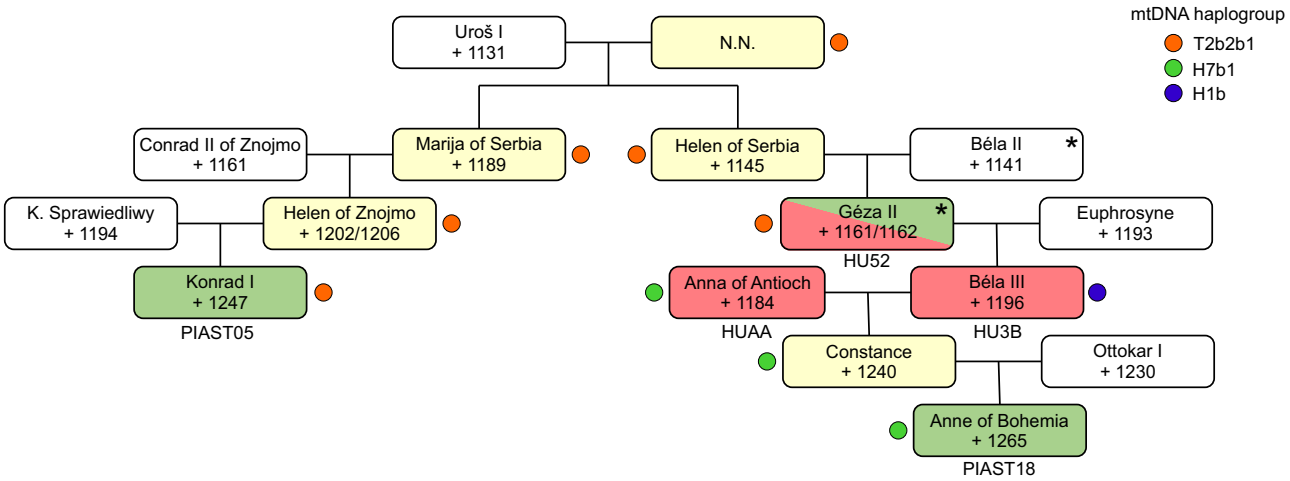

Fig. 5 | The family tree showing the connections between the house of Piast and the Hungarian royal house of Árpád. The Piasts whose identity was confirmed in our studies are shown in green blocks. Representatives of the Árpád family identified by Nagy et al.[24] are shown in pink blocks. The representatives of the Piast and Árpád dynasties whose mt-hgs could be determined based on the basic inheritance rules (mitochondrial DNA is always inherited from a mother) are shown in yellow blocks. The circle symbolising the identified mt-hg is placed next to the name of the corresponding historical figure (T2b2b1—orange circle, H7b1—green circle and H1b—blue circle). The identification numbers of the assigned skeletal remains are shown below the individual's name. The asterisks mark two historical figures who, in Nagy's opinion, could have been buried next to Béla III (his father or grandfather). The block coloured in green/pink corresponds to Géza II whose identity was determined based on our and Nagy et al.[24] results.

managed to assign Y-hgs to 17 Piasts (3 from the main lineage and 14 from the Masovian branch, Fig. 3).

These findings are generally consistent with what would be expected for multiple generations of one family. Most representatives of the male lineage share the same Y-hg (in this case, R1b). However, due to adultery or other unpredictable events, there may also be family members belonging to other, usually different Y-hgs (in this case, two or even three lineages of R1a).

The evidence presented above indicates that all individuals classified as R1b Piasts belonged to one family and shared the same Y-hg R1b-BY3549 lineage, which is currently rare in Europe. Among the samples dated to the period before the Piast state formation, the same lineage was found in three ancient samples: CGG_023713 (dated to 770–540 BCE) from present-day France[42], CGG_107766 (dated to 20–200 CE) from present-day Netherlands[42], and VK177 (dated to 880–1000 CE) from present-day England[43]. Thus, our data revealed that the Piasts belonged to the R1b-BY3549 lineage, suggesting that they were migrants of non-Slavic origin.

Piast relations with the Hungarian Árpád dynasty

To find independent evidence supporting the above-proposed assignment of the skeletal remains (PIAST01–PIAST17) to specific historical figures, we sought to determine whether there were other genetic data available for any individuals related to the Piast dynasty. We found that the remains of King Béla III of Hungary and his wife Anna of Antioch were recently examined[23–25]. Béla III belonged to the Árpád dynasty, which ruled Hungary from the ninth century to the beginning of the fourteenth century. Another as yet unidentified representative of the Árpád dynasty was found in the grave located next to the sarcophagus of Béla III and his wife. This individual carried the same Y-hg as Béla III and an mt-hg different from that of both Béla III and Anna of Antioch[24]. Thus, the unidentified Árpád could be neither Béla III's son nor his brother. He could be a male ancestor of Béla III, i.e. his father (Géza II) or his grandfather (Béla II). Alternatively, the unidentified Árpád could be, other than a son, a descendant of Béla III in the male lineage, e.g. his grandson or great-grandson.

In the second half of the tewlfth century, two sisters, Helena of Serbia and Marija of Serbia were particularly closely connected to the Árpád and Piast dynasties. Helena of Serbia was the mother of Géza II and the grandmother of Béla III. Marija of Serbia was the grandmother (in the maternal lineage) of Płock Piast Konrad I. If the unidentified Árpád is Géza II, then he must have shared an mt-hg with his mother, Helena of Serbia, and her sister, Marija of Serbia. This means that Konrad I and Géza II must have had the same mt-hg. Indeed, the individual we identified as Konrad I (PIAST05) carried an mt-hg (T2b2b1) identical to that of the unidentified Árpád (Fig. 5). Deeper analysis showed that all the mutations determining mt-hg and a private mutation detected in unidentified Árpád were also present in the mtDNA of Konrad I (PIAST05) (Supplementary Data 8). This discovery provides an additional line of evidence indicating that (i) the unidentified Árpád is Géza II, (ii) the remains of PIAST05 belong to Konrad I, and (iii) the individuals buried in Płock are Piasts.

Further analysis of the Piast and Árpád family trees brought our attention to Constance, daughter of Anna of Antioch and Béla III. She married King Ottokar I of Bohemia from the Přemyslid dynasty. One of the nine children born from this union was Anne of Bohemia (1204–1265), the wife of Henryk II Pobożny (High Duke of Poland), belonging to the Silesian branch of the Piast dynasty. Anne of Bohemia was therefore the granddaughter of Anna of Antioch in the maternal lineage and must have shared the same mt-hg (Fig. 5). Anne of Bohemia died in 1265, and her grave has survived to this day in Wrocław. We opened her grave, determined the ESA of the remains and sampled two skeletal fragments. Analyses performed in the same way as for PIAST01-17 confirmed the identity of Anne of Bohemia and showed that she carried the same mt-hg (H7b1) as Anna of Antioch (Supplementary Data 2b).

The fact that the results of our genomic analyses are consistent with the historical data describing the relations between the Polish and Hungarian royal dynasties is another important piece of evidence that the remains PIAST01-17 indeed belong to the Piasts.

Piast relations with other European dynasties

The genetic data presented in this article can be a rich source of information on Y-hgs and mt-hgs in many figures who played crucial roles in European history. Therefore, in the last stage of our studies, we tried to determine Piast's contribution to the genetic portrait of other European royal dynasties. In all our predictions, we have assumed that the official legal status of a given family/individual is consistent with

their biological history recorded in DNA; this assumption is usually well justified in the case of mt-hgs inherited in the maternal line but much less certain in the case of Y-hg lineages inherited in the paternal line. For these reasons, we made both Y-hg and mt-hg predictions only for two Polish kings, Władysław I Łokietek and Kazimierz III Wielki, whose skeletal remains were interred at the Wawel Cathedral in Cracow. King Władysław I Łokietek was a grandson of the duke of Masovia Konrad I Mazowiecki and the father of King Kazimierz III Wielki (Supplementary Fig. 1). Assuming that the paternal and maternal lines of both kings were unbroken, we predict that they shared the same Y-hg (R1b-BY3549 lineage) but had different mt-hgs. Władysław Łokietek should have inherited the mt-hg (R) from his mother, Eufrozyna Opolska, a member of the Piast family. Kazimierz III Wielki should have had an mt-hg (B4b1a3a) identical to that of the wife of Władysław I Łokietek, Jadwiga Kaliska, who also came from the Piast family (Supplementary Fig. 11 and Supplementary Data 3).

Many of Piast's daughters and the women who married into the Piast family were also representatives of famous European dynasties; hence, the genetic data we collected for the Piast dynasty members allow us to predict mt-hgs for over 200 well-known historical figures. Within this group, there are 108 Piasts, 32 Rurikids, 12 Giediminids, 23 Árpáds, 15 Přemyslids, 13 Hohenzollerns, 10 Habsburgs, 8 Wettins, 5 Angevins, and 4 Wittelsbachs (for details, see Supplementary Fig. 11 and Supplementary Data 3). The information collected here constitutes a wide range of data enabling further searches and genealogical analyses across a large group of individuals related to the abovementioned families.

Discussion

The main goal of these studies was to expand our knowledge about the processes that shaped the political structure of modern East-Central Europe. Since the tenth century, Poland has become one of its important elements. Therefore, we sought to elucidate the mechanism by which the Piast state, the cradle of Poland, was created. To answer this question, we tried to determine the origins of the state's founders, whether they were a local elite or came from outside. The results obtained indicate that the Piasts were not of Slavic origin, and therefore suggest that external forces played a key role in the process of Poland formation.

In our studies, we focused on two Piast necropolises (in Płock and Warsaw) whose authenticity was previously postulated by archaeologists and anthropologists, and where a significant number of skeletal remains were found. Here, we provide a range of evidence that at least some of the examined remains belonged to representatives of the Piast dynasty. First, radiocarbon dating confirmed that the examined skeletal remains in Płock and Warsaw came from the period of Piast rule. Second, the kinship identified between particular individuals was fully consistent with that expected on the basis of historical documents, including for one individual born out of wedlock, who as we showed, inherited Piast genes from his grandmother and great-grandmother rather than his father. Third, 7 out of 10 individuals identified as Piasts exhibited the same R1b Y-hg haplotype. It can, therefore, be assumed that they all shared the same R1b-P312 lineage, which is still rare in Central and Eastern Europe (Fig. 4). This R1b Y-hg lineage was also found in the last two representatives of the Masovian Piast dynasty, whose identities were certain. Further analysis of Piast consensus Y-hg showed that in fact they could share R1b-BY3549 lineage.

This view is further confirmed by the consistency between our results and those obtained by Nagy et al.[24] for representatives of the Árpád dynasty. It is very unlikely that all the relationships we observed between the examined individuals, as well as the coincidence of our findings with historical documents, occurred by chance. Therefore, based on the results presented in this work, we can clearly confirm the identity of at least 10 examined remains, and there is no doubt that our subjects are members of the Piast family (Fig. 3).

The origin of the Piast dynasty has been the subject of extreme controversy for years (and for the origins of Czechia, Hungary and Rus' royal dynasties too)[44]. According to centuries-old tradition, the Piasts were Slavs living in present-day western Poland. In the last years, information has emerged that challenges this traditional Polish national myth. Notably, a recent study indicated that the main source of Piast income was the slave trade[21,45], leading to the suggestion that they were Vikings, who dominated the slave trade at that time, rather than Slavs. According to another hypothesis, Piasts were refugees from the principality of Nitra, in modern-day Slovakia, which was conquered at the beginning of the 9th century by Mojmir I, the Prince of Great Moravia[15].

Our results are consistent with the hypothesis that the Piasts were of foreign, i.e. non-Slavic, origin. In 2023, we published a paper in which we analysed the changes in the genetic structure of the population living in Central and Eastern Europe in the first millennium CE[46]. Our studies focused on the populations living in the area of present-day Poland before the Migration Period (between 375 and 568 CE) and during the formation of the Piast state. Interestingly, we did not detect the Piast R1b-BY3549 lineage in any of the more than 150 males examined. This result demonstrates that the Piast Y-hg lineage was relatively rare in this region of Europe at that time, as it is today. Considering this rarity, it can be concluded that the Piasts were outsiders who subjugated the people living in the region.

The analysis of the prevalence of the Piast Y-hg lineage in Europe provides additional indications of the dynasty's origin. In modern-day populations, the Y-hg R1b-BY3549 lineage is very rare. In ancient DNA databases, this lineage was identified in three individuals who lived before or during the period of the Piast state formation in the territory of present-day France[42], the Netherlands[42], and England[43]. According to archaeological analyses, the first individual (from c.a. 650 BCE) represented the Western Hallstatt Culture, the second individual (from c.a. 115 CE) was buried in a Roman cemetery, and the third individual (from c.a. 940 CE) was most likely Viking.

Our findings, indicating the non-local roots of the Piast dynasty, point to directions that still have not been fully addressed in the study of the early stages of Polish kingdom formation. This is particularly true of the Piasts' close connections with families ruling at that time in north-western Europe. During this period, there were intense interactions between the first Polish rulers (Mieszko I and Bolesław I Chrobry) and the Holy Roman Emperors. According to the chronicle of Widukind of Corvey[47], Mieszko I was involved in struggles for the Emperor's throne after the death of Otto I (AD 973-4) and Otto II (AD 984). In both cases Mieszko I supported Henry II of Bavaria as a candidate for Emperor. Moreover, the chronicle of Thietmar[18] clearly shows that Bolesław I Chrobry rivalled Emperor Henry II (also known as Saint Henry) for Lusatia and Meissen between AD 1002 and 1018. It is also worth noting the marriage of the Mieszko I's daughter, Sigrid the Haughty, to the powerful European ruler Eric the Victorious, king of Sweden, and later (after Eric's death) to Sweyn Forkbeard, king of Denmark, Norway and England. Based on the written sources one can assume that both of Sigrid's marriages were political and intended to consolidate power in the Baltic States and the British Isles. The non-local origin of the Piasts should also prompt researchers to reconsider the relations of the first Polish dynasty with the Vikings[48]. This issue has been widely discussed for many years now[49,50]. All the above facts show the importance of the Piast family in North-Central Europe and seem to be consistent with our findings suggesting the non-local origin of Piasts. It is hard to imagine that the just-emerging local leaders of a small, newly established Slavic principality would be such influential players in pan-European political games. However, the questions of when and how the Piast ancestor migrated to Central Europe still remain open.

Our study also provides genetic information about other European dynasties related to the Piasts. We confirmed the results of

earlier genetic analyses of Anna of Antioch and her husband Béla III from the Árpád family[24]. Moreover, our findings suggest that the unidentified representative of the Árpád dynasty, whose grave, as indicated by Olasz et al.[23], Nagy et al.[24] and Varga et al.[26], has been located next to the sarcophagus of Béla III and Anna of Antioch, is Géza II. There is, however, one report suggesting that the unidentified Árpád is not Géza II (Béla III's father) but prince Anderas (Béla III's grandson)[26]. The authors of the article, Gergely I B Varga and colleagues[26], have drawn this conclusion based on the kinship analysis between the unidentified Árpád and the royal couple, Béla III and Anna of Antioch. Importantly, they do not provide any other evidence to support such a scenario. The skeletal remains of unidentified Arpad have not been radiocarbon dated. The postulated skeletal age of this individual is 20–30 years and fits well to all: Andreas, Géza II and Béla II. There are no historical records suggesting that Andreas was buried in the same place as his grandparents. What is more, the data we have collected, including the results of kinship analyses, do not substantiate the hypothesis put forward by Gergely I B Varga and colleagues[26]. Therefore, further studies are indispensable to unequivocally prove to which historical figure the examined remains should be assigned.

A further valuable result of our search is the collection of mt-hg data for over 200 representatives of 10 great European dynasties. These data constitute an excellent starting point for further historical, archaeogenomic, and genetic studies on the origins of the most important European royal dynasties and their mutual relations. At this point, it is worth noting that the mt-HGS data presented here provide a large amount of information on the role of women in shaping the political structure of Europe. There is no doubt that the role of women, although profound, was often omitted or downplayed in official documents and historical studies.

Despite yielding information on the 13 generations of the first Polish royal dynasty, our studies could not provide definitive answers to several questions related to the Piasts' origin and their relations with other European noble families. Although the observations we made for a number of representatives of the main and Masovian Piast branches seem to be consistent, we still cannot unequivocally prove the continuity of the male lineage for the whole period of the Piast rule. We cannot, therefore, say with certainty whether Mieszko I, Bolesław I Chrobry, and their ancestors, similarly to the majority of the examined representatives of the dynasty, belonged to the Y-hg R1b-BY3549 lineage. The same problem applies to other branches of the Piasts.

Moreover, the data we collected did not allow us to determine the basic phenotypic features of the studied members of the Piast family, such as the colour of their eyes, hair, or skin complexion. Additionally, one should remember that genomic analyses provide only information on the biological history of particular individuals and do not say anything about their legal status. Therefore, further interdisciplinary research is necessary, as there is no doubt that for great royal dynasties, the biological history and the official history recorded by chroniclers may be different.

To sum up, here we provide a large set of genetic data characterising one of the most powerful medieval European dynasties, which at the turn of the first and second millennium CE created independent political entities in East-Central Europe. So far, analogous, but much smaller sets of data concerning single representatives have been obtained for the Árpád and Rurik dynasties. Our findings support the hypothesis that the state-building processes observed in the ninth to eleventh centuries in East-Central Europe were induced largely by foreigners. Similar scenarios were proposed for Rus' and Hungary, ruled by the Rurikids and Árpáds, respectively. It suggests that the model of state development emerging from our research could be typical at that time for this region of Europe. Thus, our findings contradict the common stereotypes assuming the involvement of mythical local elites in the state-building process. We therefore believe that this article will inspire further multidisciplinary research on the history of the House of Piast as well as many other European royal families.

Methods

Ethics

According to Polish law, in the case of historical human remains that are the objects of archaeological/archaeogenomic studies, there is no requirement for the bioethics committee to issue consent or any kind of permission for the use of these human remains in scientific research e.g. ancient DNA analyses. The compliance of the proposed study protocol with the principles of ethics was checked during the evaluation process by the governmental institution financing this project (National Science Centre). Our studies were performed according to five globally applicable guidelines for DNA research on human remains[51] as well as to the document elaborated by the Committee of Pra- and Protohistorical Sciences of Division I of the Polish Academy of Sciences on 24 October 2003, entitled 'Zbiór zasad postępowania i norm etycznych środowiska archeologów w Polsce' (transl. A set of rules of conduct and ethical norms of the archaeological community in Poland). We obtained all other permissions required in Poland to open the graves and collect bone materials for any kind of studies, including aDNA analyses (for details see reporting summary). In the case of human remains, as a rule, after samples were taken for testing, the bone material was returned to the burial sites (see Supplementary Note 2), from where it can be re-sampled and used for future research after obtaining the appropriate permits. Permits are issued by the church authorities managing the churches in which the Piast necropolises are located, and by the provincial conservators of monuments who supervise these buildings.

Radiocarbon dating

Radiocarbon dating of the bone samples was conducted at the Poznan Radiocarbon Laboratory (Foundation of the A. Mickiewicz University). The detailed analysis procedure is described in the Supplementary Note 3.

DNA isolation

Bone samples, primarily teeth and in some cases, petrous bones, were obtained from 33 individuals from 8 burial sites. The bone material was transported to a specialised aDNA laboratory (Institute of Human Biology and Evolution, Adam Mickiewicz University Poznan) maintaining all the rules of working with aDNA (e.g. proper clothing, UV lights, filters and positive air pressure) and physically separated from modern DNA laboratories. The bone samples were cleaned with 5% NaOCl, rinsed with sterile water, and then exposed to UV irradiation (254 nm) for 1 h per side or plane. The teeth and bones were drilled using Dremel® drill bits. Bone powder (approximately 250 mg) was then digested overnight with proteinase K, and the extract containing DNA was purified using a silica-based method, following the procedure described by Yang et al.[52] and Svensson et al.[53].

Library preparation

Genomic libraries were prepared using the protocol described by Meyer and Kircher[54] except for the initial sonication step, which was omitted due to the natural fragmentation of aDNA. After adaptor ligation, six separate PCR reactions were set up for each library to amplify and barcode DNA fragments. The reactions were performed in 25 μl solution, containing 3 μl of the DNA library template, 12.5 μl of 1× AmpliTaq Gold® 360 Master Mix (Life Technologies), 0.5 μl of indexing primer (10 μM), and 0.5 μl of PCR primer IS4 (10 μM). The PCR profile included an initial denaturation at 94 °C for 12 min, 12–16 cycles of amplification (94 °C for 30 s, 60 °C for 30 s, and 72 °C for 45 s), followed by a final extension at 72 °C for 10 min. The PCR reactions performed for the same aDNA template were pooled and purified using AMPure® XP beads (Agencourt-Beckman Coulter)[55]. High Sensitivity DNA or DNA 1000 kits and

the 2100 Bioanalyzer system (Agilent) were used to verify the quality and size distribution of the libraries. DNA concentration was determined using a Qubit fluorimeter and Qubit dsDNA HS Assay Kit (ThermoFisher Scientific) according to the manufacturer's protocols.

Library screening (shallow sequencing)

To quantify the human DNA content, all of the obtained barcoded libraries were initially subjected to shallow (low-depth) sequencing using the Illumina GAIIx, NextSeq 550, or HiSeq 2500/4000 platforms, with single-end (75–100 bp) or paired-end (2 × 100 bp) sequencing runs. On average, 1–5 million reads per library were obtained.

Human DNA enrichment

Library enrichment was performed using in-solution hybridisation capture, regardless of what type of DNA they were enriched with. The procedure was conducted with myBaits target capture kits from MYcroarray (now Daicel Arbor Biosciences, Michigan, USA) following the in-solution hybridisation capture method recommended by the manufacturer (v.3.0). Libraries with human DNA content lower than 1% were subjected to mitochondrial DNA enrichment (MTE) with the baits representing the complete human mitochondrial genome. Whole genome enrichment (WGE) was performed with the use of baits representing the complete human genome for libraries with human DNA content between 1 and 15% (libraries with higher human DNA content were not enriched). Samples from individuals with an identified male genetic sex were separately subjected to Y-chromosome enrichment (YCE) with the use of baits complementary to selected regions of the Y-chromosome and targeting a set of additional SNPs. When the starting library amount was limited, MTE and YCE were combined in a single reaction.

Whole genome enrichment

WGE was mainly carried out using the myBaits Human WGE kit (Daicel Arbor Biosciences). The kit contained reagents and hybridisation capture probes that target over 2 million sites in the human genome that are known to be polymorphic in both contemporary and ancient populations. The kit was developed and tested in collaboration with experts in ancient human population genetics. A single round of enrichment was applied, followed by 14 cycles of amplification.

Mitochondrial DNA enrichment

MTE was done using the myBaits Mito-Human rCRS kit (Daicel Arbor Biosciences). The kit contained reagents and a set of 80-bp-long tiling probes that were designed based on the revised Cambridge Reference Sequence (rCRS). Two rounds of enrichment were applied, with the first round followed by 14 cycles of amplification, and the second round followed by 10 cycles of amplification.

Y-chromosome enrichment

YCE was done using the custom myBaits Human SNPs kit (Daicel Arbor Biosciences). The kit included universal reagents and custom probes that were specifically designed for the selected regions of the Y chromosome and additional SNPs located on other human chromosomes. Two rounds of enrichment were applied, the first round followed by 14 cycles of amplification, and the second round followed by 10–11 cycles of amplification.

Deep sequencing

Based on initial screening results, libraries were either immediately subjected to deep sequencing (whole genome sequencing—WGS) if human DNA content was greater than 15%, or further processed to enrich for human DNA (as described above). The final deep sequencing was done using either the Illumina HiSeq 4000 or HiSeq X Ten platforms. The depth of sequencing varied depending on the quality of the library and the effectiveness of the DNA enrichment.

Data pre-processing

The raw sequencing data from various library types were processed separately. Initially, AdapterRemoval[56] v.2.1.7 was applied to eliminate adaptor sequences from reads, trim bases with a quality score below 30, and collapse overlapping reads. Subsequently, reads were trimmed and three nucleotides were removed from both ends using fastx_trimmer from fastx-toolkit v.0.0.14. Only reads with a minimum length of 25 nucleotides were retained. The processed data were then aligned to both the hg19 and rCRS reference genomes using BWA[57] aln v.0.7.10, with seeding blocked via the -l 1000 option.

Data integration

Data integration was carried out at both library and individual level (type-A samples) using samtools[58] merge v.1.3.1. Following this integration, duplicates were removed with picard-tools v.2.9.2. The final data integration was conducted based on the analysis of genetic traits such as sex, mitochondrial haplogroup, Y-chromosome haplogroup, and kinship. In addition, the radiocarbon dating of the samples that were merged had to overlap. Data from the same individual were then combined, and duplicates were removed for the second time.

Following data integration, each sample's DNA quality was assessed such that a sample had to have all the necessary information assigned (i.e. mt-haplogroup, Y-haplogroup, and genetic sex) in order to pass. Samples were also excluded if there was no radiocarbon dating available or if they did not overlap the individual's lifespan. Finally, DNA contamination eliminated samples with contamination on either the mtDNA or chromosome X above 5%. This process resulted in our final sample set (Supplementary Data 2a, b).

Genetic sex estimation

The genetic sex of each individual was estimated using the Ry method[59]. This method calculates the ratio of sequences mapped to the Y chromosome to the total number of sequences mapped to both the X and Y chromosomes. The analysis involved all reads with a minimum mapping quality of 30, except for YCE sequences, which were excluded. Finally, results with at least 1000 reads aligned to the sex chromosomes were kept.

Y-chromosome haplogroup assignment

Y-chromosome haplogroups were determined with two versions of Yleaf software[60] (v2.1 and v3.2.1). Before analysis, sequencing reads were trimmed by 7 nucleotides at the 5′ and 3′ ends to eliminate sequencing errors that could result from post-mortem DNA damage. The resulting BAM files were used as input to Yleaf software, with parameters set to a minimum read depth of 1, base quality threshold of 30, and at least 90% base agreement at each position. Output files from each sample were manually reviewed to identify mutations potentially affected by post-mortem damage (C- > T or G- > A transition) and to evaluate the consistency of haplogroup assignments. If a C- > T or G- > A transition appeared in the 7-nt trimmed reads and was not the terminal SNP, but rather supported the overall haplogroup placement, it was retained. Finally, haplogroups were assigned based on the most derived mutation confidently identified in each sample.

Consensus Y-chromosome haplogroup

To increase the resolution of our analyses, we merged BAM files from all samples identified as Piasts and belonging to haplogroup R1b. We then analysed the combined data using Yleaf v3.2.1 and the extended SNP database (Yleaf database supplemented with entries from the YFull[61] and FamilyTreeDNA[62] databases; see Supplementary Note 5).

Estimation of deamination rates

We used mapDamage[63] v.2.0 to assess deamination patterns in the untrimmed reads.

Mitochondrial DNA contamination estimates

To assess the extent of modern human contamination in the ancient samples, we employed the Schmutzi software[64]. This tool utilises a database of allele frequencies from European and Asian populations to calculate contamination rates and identify the closest matching contaminant mtDNA sequences in the database.

Mitochondrial DNA haplogroup assignment

We assigned mitochondrial DNA haplogroups using two tools: haplocheck[65] v.1.3.2 and haplogrep[66] v.3.2.1. Assigning haplogroups with haplocheck from BAM files required an additional variant calling step. For this, we used mutserve v.2.0.0-rc7, a component of the haplocheck package, with default settings. The resulting variant call VCF files were then used as input for haplocheck to determine haplogroups, using default parameters. Haplogroups with a score above 0.8 were considered true. Since haplocheck does not output the list of private mutations, we separately ran haplogrep on the same VCF files generated by mutserve to obtain such a list.

X-chromosome contamination in males

We utilised the software ANGSD[67] v.0.929 to calculate X-chromosome contamination. In male individuals, who are haploid for the X-chromosome, discrepancies at polymorphic sites could be a result of either contamination or sequencing errors. To take into account the latter, polymorphic sites and their adjacent bases were screened for discrepancies, as sequencing errors should be observed at consistent frequencies throughout the genome. The analysis was carried out using default parameters. We only considered bases with a base quality ≥20 and mapping quality ≥30, which limited the analysis to unique regions of the X-chromosome and HapMap X-chromosome polymorphisms. Results from method 2 were used to infer possible contamination. Samples exceeding the 5% threshold were excluded from downstream analysis.

Kinship analysis

We performed kinship analysis on samples obtained from Płock and Warsaw separately. We restricted the analysis to positions overlapping the Allen Ancient DNA Resource[68] (1240k AADR) v.54.1 dataset. Samples collected in Płock needed to cover a minimum of 10,000 SNPs each to qualify for analysis, mainly to address concerns regarding potential bone mixing. Conversely, samples from Warsaw were not subject to this requirement, as their identity was indisputable.

We used two methods for kinship estimation that were specifically designed for aDNA data: READ[69] and KIN[70] v.3.1.3. Our kinship analysis comprised two rounds. In the first round, we were interested only in identifying samples originating from the same individual. The remaining relationships were ignored at this stage. After merging data originating from the same individual we ran the analysis again (second round) to identify potential family relationships. The relationship between pairs of individuals was considered true if the following criteria were met: $|Z| > 1$ (READ method), log-likelihood ratio >1 (KIN method), there were at least 1000 overlapping SNPs between the pair of individuals, and the same pair was indicated by both methods (except for the pair PIAST06—PIAST05, where only the READ method showed kinship). If one method showed a different degree of kinship from the other, we chose the one that best fit the genealogy.

READ. The READ software uses pseudo-haploid genotype data as input and estimates kinship up to second-degree based on the proportion of non-matching genotypes (P0). BAM files were prepared as described above. Variant calling was performed using bcftools[58] v.1.9 separately for each individual. Vcf files were then converted to plink format with plink[71] v.1.90 and merged. A pseudohaploid genotype was assigned at each heterozygous SNP by randomly sampling one out of two detected alleles at that site. Finally, the data were converted and transposed with plink and used as input. READ was run with default parameters.

KIN. The KIN software was used for verification and improvement of the results obtained by the READ method. KIN was designed to accurately classify individuals up to third-degree of relationship. Moreover, it also differentiates first-degree relationships as siblings and parent-offspring. Pre-processed BAM files were filtered for reads overlapping positions on the 1240k AADR. Estimating kinship with KIN is a two-stage process. First, we used KINgaroo, a software to generate input files for KIN directly from bam files. KINgaroo was run with default parameters and without contamination correction. Then, we run KIN also with default parameters.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The raw sequencing data generated in this study have been deposited at the European Nucleotide Archive (ENA) project PRJEB78346 under the accession numbers ERS20610255-ERS20610512. The sequencing data published by other authors are available at the ENA under the accession number PRJEB51515 (Árpáds). All source data on radiocarbon dating and DNA damage analysis are provided with this paper in a Source Data file. All other data are included in the Supplementary Data. The human remains we analysed were returned to the institutions that provided them to us, and to gain access to them, permission must be sought from their authorities. The following authorities issued permissions: (i) Bishop of Warsaw and Office of the Monument Conservator in Warsaw for the remains of Janusz I Stary, Boleslaw IV, Janusz III and Stanislaw buried in the Cathedral of St. John the Baptist in Warsaw; (ii) Bishop of Płock for the remains of Władysław I Herman, Kazimierz, Bolesław III Krzywousty, Leszek, Konrad I, Gaudemunda Sophia of Lithuania, Bolesław II, Wacław, Bolesław III, Kazimierz I, Ziemowit III, Ziemowit IV, Kazimierz II, Ziemowit V, Władysław I, Władysław II, Ziemowit VI and Janusz II buried in the Płock Cathedral; (iii) Superior of the Ursuline Sisters Congregation in Wrocław for the remains of Anne of Bohemia buried in the church of the Saint Clare and Saint Jadwiga in Wrocław; (iv) Provincial of the Franciscan Order in Cracow for the remains of Bolesław V Wstydliwy buried in the church of St. Francis of Assisi in Cracow; (v) Chancellor of the Wrocław Curia for the remains of Jarosław Opolski and Konrad IV Starszy buried in the Cathedral of St. John the Baptist in Wrocław; (vi) The Museum of the First Piast at Lednica for the remains of Bolesław Mieszkowic and Władysław III Laskonogi; (vii) Conservator of monuments of the Curia in Opole for the remains of Jan II Dobry buried in the church of Holy Cross in Opole; (viii) Lower Silesian Voivodeship Conservator in Wrocław Legnica Branch for the remains of Chrystian, Jerzy IV Wilhelm and Louise of Anhalt-Dessau buried in the church of St. John the Baptist in Legnica; (ix) Chancellor of the Wrocław Curia and the parish priest of the Holy Cross church in Brzeg for the remains of Jan Chrystian buried in the church of St. John the Baptist in Brzeg. Source data are provided with this paper.

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Author contributions

M.Z. participated in sample collection, extracted DNA, prepared NGS libraries, participated in bioinformatics analysis design, performed all bioinformatics analyses, participated in data interpretation, discussed the results, participated in the draft writing, created all figures and supplementary materials, and reviewed the final version of the manuscript L.H., participated in the study design and sample collection, planned and performed NGS sequencing, participated in data interpretation, discussed the results, participated in the draft writing and reviewed the final version of the manuscript M.M-S. participated in sample collection, NGS libraries preparation, NGS sequencing and figures preparation, discussed the results and reviewed the final version of the manuscript I.S. participated in bioinformatics analysis design, discussed the results and reviewed the final version of the manuscript M.G. participated in bioinformatics analyses of Y-chromosome haplogroups, discussed the results and reviewed the final version of the manuscript A.J. participated in sample collection and design of molecular experiments, provided access to the specialised aDNA laboratory A.D., M.M. and H.K-K. participated in sample collection, provided archaeological context descriptions, and discussed the results D.T., M.Ch. and A.W. participated in sample collection, provided anthropological context descriptions, and discussed the results A.L.-S. participated in sample collection, and provided historical context descriptions T.J. and J.D. provided historical context descriptions, and discussed the results A.B.L. participated in sample collection and discussed the results M.F. conceived the overall idea of the study, obtained funding, participated in the study design, data interpretation, and discussion, wrote the draft, and prepared the final version of the manuscript All of the authors read and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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