Maternal phylogeographic patterns and coalescent times of Arabidopsis thaliana based on chloroplast DNA analyses

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Arabidopsis thaliana, one of the most important model plants, has played an essential role in every biological field including evolutionary biology. Recent population genomic studies have gradually clarified the origin and evolution of this species. Nevertheless, incongruent patterns among gene trees based on cytogenetic data have highlighted the importance of understanding the life history evolution and landscape biogeography of extant A. thaliana populations. Here, we focus on the maternally inherited chloroplast genome in A. thaliana and carry out phylogeographic analyses and coalescent time estimations. The maternal lineage of A. thaliana originated in the European to West and Central Asian regions in the Early Pleistocene. Relicts, the ancient lineages suggested by population genomic data, are not ancestral maternal lineages, but are derived from the European population. Part of the European population then dispersed eastward and spread to the Indian region, and finally extended to the Yangtze River region. The branching patterns and evolutionary time scales of the maternal genealogy are significantly different from those estimated from analyses of autosomal genes, and these cannot be explained by incomplete lineage sorting of the ancestral polymorphisms during the coalescent process due to large differences in the evolutionary time scale involved.

Key words: maternal lineage, Arabidopsis thaliana, Bayesian timetree, chloroplast genome, evolutionary relationship

INTRODUCTION

Arabidopsis thaliana is one of the most important model plants and has played an essential role across all biological fields, especially genetics (Arabidopsis Genome Initiative, 2000) and developmental biology (Tsukaya, 2006; Kawade et al., 2013). This species is also attractive for studies of evolutionary biology, in part because its reproduction system includes self-fertilization (selfing). Because selfing changes the polymorphic patterns of populations (Shimizu and Tsuchimatsu, 2015), it is important to elucidate the phylogeographic history of this species. The origin of A. thaliana has been gradually clarified by recent population genomic studies (1001 Genomes Consortium, 2016; Durvasula et al., 2017). Selfing in this species is thought to have originated in Africa and then subsequently migrated to Eurasia via the Iberian Peninsula (Durvasula et al., 2017). Therefore, several old lineages among non-African populations exist in the Iberian Peninsula as well as its peripheral region. These lineages are called “relicts” (1001 Genomes Consortium, 2016).

Cytogenetic analyses of various organisms have been carried out extensively over the past two decades, and incongruent patterns of species (or population) trees and gene trees have been reported (Roca et al., 2005; Nakagome et al., 2008; Yonezawa et al., 2009; Akihito et al., 2016). These studies suggested that incongruent patterns of gene trees are related to the life histories of the organisms. In particular, discrepancies between the evolutionary histories of maternally inherited genes (e.g., mitochondrial genes or chloroplast (cp) genes) and autosomal genes often reflect complex breeding systems or different behaviors between the sexes (Roca et al., 2005; Nakagome et al., 2008). Therefore, it is important to
compare the different genealogies among cp gene trees and nuclear gene trees to improve our understanding of the complete historical evolutionary landscape of *A. thaliana*. Nevertheless, while several previous studies (e.g., Yin et al., 2010; Tyagi et al., 2015) reported extensive phylogeographic and population genetic analyses of local populations of this species, the maternal history of *A. thaliana* across its geographic distribution areas is little known. Moreover, the evolutionary histories of the chloroplast genomes and the nuclear genomes have seldom been compared. Here, we carry out phylogeographic studies of the maternal history of *A. thaliana* based on cpDNA data, and discuss the different evolutionary histories of the species tree and the maternal lineages.

**MATERIALS AND METHODS**

**Data matrix**  We retrieved 195 complete cp genomes of *A. thaliana* from previous studies (1001 Genomes Consortium, 2016; Zeng et al., 2017). These data comprise all of the reported cp genomic data from relicts (25 individuals) and the Asian population (81 individuals) as well as randomly selected subsamples of the European population (89 individuals). The accession information for these complete cp genome data is shown in Supplementary Table S1.

Yin et al. (2010) and Tyagi et al. (2015) carried out phylogenetic and population genetic studies of Chinese and Western Himalayan populations based on 11 cpDNA markers (GenBank accession numbers are GU293237–GU293316, GU293317–GU293396, GU293397–GU293476, GU293477–GU293556, GU293557–GU293636, GU293637–GU293716, GU293717–GU293796, GU293797–GU293876, GU293877–GU293956, GU293957–GU294036, GU294037–GU294116). Therefore, we also retrieved the nucleotide sequence data of 68 *A. thaliana* individuals with these 11 cpDNA markers. The accession information for these cp data is shown in Supplementary Table S2. Finally, these 68 individuals were merged with 195 complete cp genomes, and the full alignment consists of 263 *A. thaliana* individuals with 157,192 bp in total length. Since 68 individuals have only 11 cpDNA markers (~8,742 bp), most of the aligned sites of these individuals were treated as missing data. This complete data matrix consists of sequences from Relicts (25 individuals), the Asian population (149 individuals) and the European population (89 individuals). As discussed below, the individuals distributed in the Western Himalayan to Yangtze River regions form a distinct clade (clade 7) in the phylogenetic tree (Fig. 2). This China–India clade is derived from the European population instead of the Remaining Asia population, which is geographically closer. Therefore, the Asian population was further divided into a “China–India” population (67 individuals) and a “non China–India” population (82 individuals). Hereafter, we refer to this non China–India population as the “Remain-
Fig. 2. Timetree of *Arabidopsis thaliana* and its related species. The timetree is divided into seven clades marked with different symbols (circle, cross, triangle, rectangle, pentagram, diamond and asterisk). The branch lengths are proportional to the time scale and the concentric circles are at intervals of 1.6 million years. *Arabidopsis lyrata, A. halleri, A. suecica* and *Capsella grandiflora* were used as the outgroups, and these are not colored.
ing Asia population", and this population is mainly distributed in Central Asia and its peripheral regions, including Russia, Ukraine, Uzbekistan, Tajikistan, Armenia and Xinjiang (China) (Fig. 1). *Arabidopsis lyrata*, *A. halleri*, *A. suecica* and *Capsella grandiflora* were also used as outgroups.

**Demographic analysis** Tajima’s D (Tajima, 1989) was estimated by MEGA version 6 (Tamura et al., 2013). Since there are many missing data in our matrix, we conducted the analysis with (1) complete deletion, (2) pairwise deletion and (3) partial deletion (50%, 60%, 70%, 80% and 90%).

**Haplotype network** A haplotype network of the 263 *A. thaliana* individuals was constructed by the MJ (median-joining) method (Bandelt et al., 1999) using Network version 5.0.0.3 (http://www.fluxus-engineering.com/sharenet.htm). In this analysis, only 11 chloroplast DNA markers were used for inferring the phylogenetic network. The MJ network was further refined using the maximum parsimony criterion, and a clear tree-like network structure was obtained.

**Phylogenetic inference and coalescent time estimation** To estimate detailed phylogenetic relationships and coalescent times for *A. thaliana*, we used 195 complete cp genomes as well as 68 accessions that shared the same 11 cp DNA markers. A phylogenetic tree was inferred using the RAxML program v8.2.10 (Stamatakis, 2014) with the GTR + I + Γ model. The bootstrap method was applied to evaluate the confidence of the internal branches with 1,000 replications using the rapid bootstrap algorithm (Stamatakis et al., 2008). Coalescent times were estimated by the Bayesian method using BEAST version 1.8.0 (Drummond et al., 2005). For taking account of rate variation among lineages, coalescent times were estimated under a relaxed molecular clock using the hierarchical Bayesian method (Thorne et al., 1998).

MCMC was conducted with $2 \times 10^6$ generations, and trees were sampled every 20,000 generations. Four coalescent demographic models (constant size, exponential growth, logistic growth and expansion growth) were compared with AICM using Tracer 1.6.0. (http://beast.community/tracer), and the logistic growth model was selected as the most suitable model for this data matrix. The initial 1,000 trees were discarded as burn-in, and the remaining 9,000 trees were used for reconstructing the Bayesian timetree using TreeAnnotator 1.6.1 (http://beast.community/treeannotator). The timetree with the maximum node credibility was visualized using FigTree 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/). We repeated these analyses three times with different MCMC conditions and confirmed the stability of our estimates.

To minimize the computational burden, we selected the simplest nucleotide model using the following procedures. Our saturation plot analysis shows that the effect of homoplasy is limited within the framework of the intra- and interspecies analyses (Supplementary Fig. S1). Although the selection of different nucleotide substitution models (e.g., JC69 model, K80 model, TN93 model) had nearly no effect on the estimation of genetic distances, the selection of models for rate heterogeneity among sites (with and without Γ model) resulted in a small effect. Therefore, we applied the simpler nucleotide substitution model, but took rate heterogeneity among sites into account; subsequently, the HYK + I + Γ model (Hasegawa et al., 1985; Yang, 1994) was employed using the empirical base frequency data.

The following two divergence times were applied for the calibration points: first, 15 million years ago (Mya) for the divergence time between the genus *Capsella* and the genus *Arabidopsis*; second, 9.2 Mya for the divergence time between *A. lyrata* and *A. thaliana*. These divergence times were estimated within the comprehensive framework of angiosperm evolution based on 334 orthologous single-copy genes examined in our previous studies (Zeng et al., 2017). The uncorrelated log normal relaxed clock was used for the clock model.

**Ancestral reconstruction of geographic distribution** Ancestral geographic distributions were reconstructed by parsimony and likelihood methods using MESQUITE software version 3.40 (http://mesquiteproject.org). Tree topology of the timetree was inferred by the BEAST program. The following three sets of geographic classifications were applied: (1) Relicts, Europe, Remaining Asia and China–India division; (2) Europe to Remaining Asia division; and (3) Relicts to Non-Relicts division.

**RESULTS**

**Evolutionary relationships among chloroplast haplotypes** A total of 118 haplotypes were detected from 263 individuals. The China–India population spanning from the Western Himalayan to the Yangtze River regions shows the highest haplotype diversity, having 51 haplotypes out of 70 individuals.

The Bayesian timetree, the MJ network and the Maximum Likelihood tree are shown in Fig. 2, Fig. 3 and Supplementary Fig. S2, respectively. These results are essentially consistent, and the China–India population is directly derived from the European population instead of the Remaining Asia population.

Twenty-five Relicts accessions have 14 haplotypes and are nested within the Europe population, which covers wide areas of the European continent spanning Sweden, Germany, Spain and Italy. Forty-three haplotypes were detected out of 74 individuals.
Compared with other groups, the Remaining Asia population shows the lowest haplotype diversity: 80 Asian individuals only have 15 haplotypes. European populations and the Remaining Asia population are partially intermingled on the phylogenetic tree and several haplotypes are shared by these populations.

**Bayesian timetree** The Bayesian timetree of *A. thaliana* and its related species, based on cpDNA data and estimated by the BEAST program, is shown in Fig. 2, and the detailed result of tMRCA (time of the most recent common ancestor) determinations is summarized in Table 1.

The tMRCA of *A. thaliana* is estimated to be 2.41 Mya (HPD = 0.42–5.39 Mya). The timetree (Fig. 2) shows that the oldest lineages of *A. thaliana* are from North Europe. Subsequently, most of the Asian population, the Relicts and most of the European population diverged in this order, and finally the China–India population emerged.

The tMRCA of the remaining Asian population (2.41 Mya, HPD = 0.43–5.39 Mya),
European population (2.41 Mya, HPD = 0.42–5.37 Mya), Relicts (1.17 Mya, HPD = 0.19–2.66 Mya), and China–India population (0.93 Mya, HPD = 0.17–2.07 Mya).

**Ancestral reconstruction of the geographic distribution** Based on the topology of the Bayesian timetree (Fig. 2), the ancestral geographic distribution areas of *Arabidopsis thaliana* were reconstructed. Nodes weakly supported (<50% posterior probability) were treated as multifurcations. Ancestral geographic distributions of important nodes estimated by the maximum parsimony method are shown in Fig. 4. Ancestral reconstruction by the maximum likelihood method was consistent with this result (data not shown). Our analysis shows that the common ancestor of *Arabidopsis thaliana* was distributed in Central Asia (Remaining Asia) and Europe. The China–India region and the region of the Relicts (Iberian Peninsula and its peripheral region) were not assigned to the ancestral distribution area.

**DISCUSSION**

Our phylogeographic analysis suggests that the ancestral distribution areas of *Arabidopsis thaliana* were in Central Asia (Remaining Asia) or Europe excluding Relicts (Fig. 4). Since larger numbers of geographic categories seem to have lower resolution for reconstructing ancestral geographic distribution areas (Yonezawa et al., 2017), we also carried out reconstruction of ancestral geographic distribution areas based on two geographic categories. The results of these analyses using the maximum parsimony method are shown in Supplementary Fig. S3 (Relicts vs. Non-Relicts) and S4 (Europe including Relicts vs. Asia including Remaining Asia and China–India). Ancestral reconstruction by the maximum likelihood method was consistent with these results (data not shown). These results also suggest that the Relicts are not included in the ancestral populations of the extant *Arabidopsis thaliana* populations. The comparison of two geographic categories (Europe including Relicts vs. Asia including Remaining Asia and China–India) has no power to further resolve the detailed ancestral geographic distribution areas of this species (Supplementary Fig. S4).

Taking these results together, we can use these ancestral geographic distribution areas and the coalescent (and divergence) times to suggest the following evolutionary scenario for the maternal history of extant *Arabidopsis thaliana* populations. The first evolutionary event was the emergence of the earliest extant *Arabidopsis thaliana* population itself. After the branching from other *Arabidopsis* species during the Late Miocene (8.49 Mya), the most recent common ancestor of the maternal lineage of the modern population emerged at 2.41 (0.42–5.38) Mya. The emergence of this species corresponds to the Gelasian stage of
the Early Pleistocene, and, if HPD is taken into account, it corresponds to the Pliocene to Middle Pleistocene. Ice sheets are known to have expanded in the northern hemisphere during this time (Zachos et al., 2001). It has been suggested that global cooling events resulted in increased terrestrial aridity, which can cause the spread of savannah and open scrublands (Yonezawa et al., 2007). It is possible that *A. thaliana*, seen in undisturbed rocky sites and forest openings in natural habitats (Mitchell-Olds, 2001), emerged in such an arid environment. The geographic origin of this species seems to be Central and West Asia (the distribution areas of the Remaining Asia population) and Europe. A more detailed resolution of the region of origin could not be determined based on the phylogenetic ancestral reconstructions in this study (Fig. 4 and Supplementary Fig. S3 and S4). Therefore, we subsequently undertook the coalescent time-based approach (Zeng et al., 2017). If there are two populations (A and B), and population A is derived from population B, then the tMRCA of population B will be equal to the tMRCA of (population A + population B). In addition, the tMRCA of population A will be younger than the tMRCA of (population A + population B). The tMRCA of the Remaining Asia population (West Asia and Central Asia) and the European population were estimated to be 2.41 (0.43–5.39) Mya and 2.41 (0.42–5.37) Mya, respectively (Table 1). These estimates are consistent with the estimate for the entire extant *A. thaliana* population itself. This finding suggests that the European population and the Remaining Asia population are not ancestrally related by descent, but rather that they differentiated by vicariance.

The second evolutionary event was the emergence of the Relicts. The Relicts were derived from the European population (Fig. 4), and their tMRCA was estimated to be 1.17 (0.19–2.66) Mya (Table 1). This timing corresponds to the Calabrian stage of the Early Pleistocene (Fig. 2).

The third evolutionary event was the emergence of the China–India population. This population is also derived from the European population in the Calabrian stage (Fig. 2, Fig. 4). Although this population is the youngest population, it has the highest haplotype diversity. This is most likely a signature of recent population expansion. If this population is further divided into the Chinese subpopulation and the Indian subpopulation, the tMRCA of the Chinese subpopulation is 0.69 (0.09–1.63) Mya and that of the Indian subpopulation is 0.93 (0.17–2.07) Mya (Table 1), suggesting that the Chinese subpopulation is derived from the Indian subpopulation. Thus, the ancestors of the China–India population most likely migrated from the European region, and then some portions of this population continued to further migrate eastward and finally reached the Yangtze River region.

The maternal evolutionary scenario described above largely contradicts the scenario suggested by recent population genomic studies regarding historical biogeographic patterns (origin and migration routes) (1001 Genomes Consortium, 2016; Durvasula et al., 2017; Zeng et al., 2017) as well as the evolutionary time scale (Durvasula et al., 2017; Zeng et al., 2017). Previous nuclear genomic analyses suggested that the African population or the Tibetan population was the most ancestral lineage (Durvasula et al., 2017; Zeng et al., 2017), but these populations were not included in the present study. However, we show that the Relicts (1001 Genomes Consortium, 2016) clearly have a derived maternal lineage in this study (Fig. 2 and Fig. 4). There is a considerable difference in the tMRCA estimated from whole genomic data (about 140 thousand years ago (Kya) by Durvasula et al. and 126–149 Kya by Zeng et al.) (Durvasula et al., 2017; Zeng et al., 2017) and from cpDNA data (2.41 Mya: this study). If there are considerable numbers of multiple substitutions per site in comparisons between the cp genomes of *A. thaliana* and those of other species, this would result in the overestimation of the coalescent times among *A. thaliana* accessions because the lengths of the internal branches near the root were underestimated and the nodes near the root were used as calibration points. However, since there are very limited numbers of multiple substitutions per site among Arabidopsis species or between genus Arabidopsis species and genus Capsella (Supplementary Fig. S1), the old tMRCA of the cp genome of *A. thaliana* is not an analytical artifact caused by saturation of the genetic distances.

This remarkable discrepancy of the time scale cannot be explained by incomplete lineage sorting of ancestral polymorphism. Zeng et al. (2017) and Durvasula et al. (2017) estimated the tMRCA of the nuclear genomes, and obtained very similar ages (about 150 Kya). Since these estimates are based on multiple nuclear genes at the whole-genome level, about 150 Kya can be interpreted as the mean tMRCA of the nuclear genes. Because the expected tMRCA and their standard deviations are $4N_e \pm 4N_e$ generations ago, tMRCA of more than 99% of the genes are principally younger than 600 Kya. Moreover, considering that the effective population size of cp genes is 1/4 of the autosomal genes, the expected tMRCA of cp genes should be about 1/4 of that of autosomal genes, which is about 37.5 Kya. Even taking account of the standard deviations, the tMRCA of the cp genome should be younger than 150 Kya. However, the tMRCA of the cp genome was estimated to be 2,410 Kya. Thus, the estimated tMRCA of cpDNA in this study is clearly outside this range even taking account of the large standard deviation of the tMRCA.

Accordingly, it can be interpreted that this discrepancy of the time scale is caused by the different evolutionary history of the cp genome and the nuclear genome. One possible explanation is a balancing selection of the cp genome. However, since the Tajima’s D of the cp genome
is negative (−2.65 to −2.85), balancing selection of the cp genome is unlikely. Another possible explanation is a recent very strong selective sweep of the nuclear genome but not of organelle genomes in the modern A. thaliana population. A recent origin for self-compatibility in A. thaliana has been suggested (Shimizu and Tsuchimatsu, 2015). It is possible that the maternal lineage of A. thaliana has retained older phylogeographic structures that existed prior to when the capacity for self-compatibility spread in this species, thereby revealing a maternal history suggested by this study that contradicts the evolutionary scenario suggested by recent population genomics studies (1001 Genomes Consortium, 2016; Durvasula et al., 2017; Zeng et al., 2017). To examine this hypothesis further, we have initiated extensive population genomic analyses that are now in progress.

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Supplementary material

Supplementary Fig. S1. Saturation plot analysis. The y-axis indicates the pairwise genetic distances corrected by the MCL (maximum composite likelihood: Tamura et al., 2004) with the TN93+Γ model (Tamura and Nei, 1993). The x-axis indicates the pairwise genetic distances (the p-distances, the JC69 model, the K80 model, the K80+Γ model, the MCL with the TN93 model: Jukes and Cantor, 1969; Kimura, 1980). The shape parameter (α) of the Γ distribution (Yang, 1994) was estimated by the maximum
likelihood method. These distances and parameters were estimated by MEGA v. 6 (Tamura et al., 2013). **(A) Saturation plot analysis based on 11 cpDNA markers with 267 sequences. (B) Saturation plot analysis based on cp genomes with 199 individuals.** Since the shape parameter ($\alpha$) based on the cp genome data could not be estimated by the MEGA v. 6 program due to computational issues, we used the ModelFinder program implemented in the IQ tree v.1.6.9 program (Kalyaanamoorthy et al., 2017) for these data in order to estimate the shape parameter, which was estimated to be 0.02. However, since MEGA v. 6's minimal value for the shape parameter is 0.05, we applied this value.

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Supplementary Fig. S2. Maximum likelihood tree. The maximum likelihood tree as inferred from the cpDNA data consists of the whole chloroplast genome (195 unique sequences) and 11 cpDNA markers (68 unique sequences). The tree is also divided into seven clades. The branch lengths are proportional to the number of substitutions and the nodal numbers indicate bootstrap probabilities with 1,000 replications. The compressed China–India group is shown separately due to limited space. (A) Whole cpDNA tree of Arabidopsis thaliana. The China–India clade is compressed in this figure. (B) Detailed structure of the China–India clade.
Supplementary Fig. S3. Ancestral geographical distribution areas of *Arabidopsis thaliana*
reconstructed by the maximum parsimony method. This figure indicates the phylogenetic
relationships of the seven major clades shown in Fig. 2. Relationships within each clade are
compressed and branch lengths are proportional to the time scale. All individuals were divided into
Relicts and Non-Relicts, and clades are colored in accordance with each category.
Supplementary Fig. S4. Ancestral geographical distribution areas of Arabidopsis thaliana reconstructed by the maximum parsimony method. This figure indicates the phylogenetic relationships of the seven major clades shown in Fig. 1. Relationships within each clade are compressed and branch lengths are proportional to the time scale. All individuals were divided into Europe (pink, including Europe and Relicts groups) and Asia (green, including Remaining Asia and China–India groups).
Supplementary Table S1. Accessions retrieved from 1001 Genomes Consortium (2016) and Zeng et al. (2017)

| No. | Name     | Geographic origin* | Group |
|-----|----------|--------------------|-------|
| 1   | Cvi-0    | CPV                | Relict|
| 2   | Can-0    | ESP                | Relict|
| 3   | IP-Cem-0 | ESP                | Relict|
| 4   | IP-Fun-0 | ESP                | Relict|
| 5   | IP-Gra-0 | ESP                | Relict|
| 6   | IP-Her-12| ESP                | Relict|
| 7   | IP-Hum-2 | ESP                | Relict|
| 8   | IP-Iso-4 | ESP                | Relict|
| 9   | IP-Lso-0 | ESP                | Relict|
| 10  | IP-Mar-1 | ESP                | Relict|
| 11  | IP-Sne-0 | ESP                | Relict|
| 12  | IP-Vim-0 | ESP                | Relict|
| 13  | IP-Vis-0 | ESP                | Relict|
| 14  | IP-Cat-0 | ESP                | Relict|
| 15  | IP-Con-0 | ESP                | Relict|
| 16  | IP-Moj-0 | ESP                | Relict|
| 17  | IP-Nac-0 | ESP                | Relict|
| 18  | IP-Per-0 | ESP                | Relict|
| 19  | IP-Pun-0 | ESP                | Relict|
| 20  | IP-Ven-0 | ESP                | Relict|
| 21  | Don-0    | ESP                | Relict|
|   | Location   | Country | Region       |
|---|------------|---------|--------------|
| 22| Ped-0      | ESP     | Relict       |
| 23| LDV-18     | FRA     | Europe       |
| 24| Doubravnik7| CZE     | Europe       |
| 25| Kar-1      | KGZ     | Remaining Asia|
| 26| Sus-1      | KGZ     | Remaining Asia|
| 27| Dja-1      | KGZ     | Remaining Asia|
| 28| Zal-1      | KGZ     | Remaining Asia|
| 29| Neo-6      | TJK     | Remaining Asia|
| 30| Ale-Stenar-64 | SWE   | Europe       |
| 31| Aledal-6-49 | SWE   | Europe       |
| 32| Tos-95-393 | SWE     | Europe       |
| 33| MNF-Riv-21 | USA     | Remaining Asia|
| 34| UKSW06-207 | UK      | Europe       |
| 35| UKSW06-360 | UK      | Europe       |
| 36| UKID11     | UK      | Europe       |
| 37| Dra-3      | SWE     | Europe       |
| 38| DraIV 1-8  | CZE     | Europe       |
| 39| Fly2-1     | SWE     | Europe       |
| 40| T1000      | SWE     | Europe       |
| 41| T1110      | SWE     | Europe       |
| 42| T620       | SWE     | Europe       |
| 43| T990       | SWE     | Europe       |
| 44| TAA 04     | SWE     | Europe       |
| 45| TL 03      | SWE     | Europe       |
|   | Site  | Country | Region     |
|---|-------|---------|------------|
| 46 | TDr-9 | SWE     | Europe     |
| 47 | TEDEN 03 | SWE | Europe |
| 48 | Tottarp-2 | SWE | Europe |
| 49 | TR01 | SWE | Europe |
| 50 | ANH-1 | GER | Europe |
| 51 | CIBC-5 | UK | Europe |
| 52 | Kondara | TJK | Remaining Asia |
| 53 | Kz-9 | KAZ | Remaining Asia |
| 54 | Ms-0 | RUS | Remaining Asia |
| 55 | Sorbo | TJK | Remaining Asia |
| 56 | Tamm-2 | FIN | Europe |
| 57 | Ct-1 | ITA | Europe |
| 58 | Chat-1 | FRA | Europe |
| 59 | Co | POR | Europe |
| 60 | El-0 | GER | Europe |
| 61 | Er-0 | GER | Europe |
| 62 | Gd-1 | GER | Europe |
| 63 | Kas-1 | IND | Remaining Asia |
| 64 | Kl-5 | GER | Europe |
| 65 | Li-7 | GER | Europe |
| 66 | Nw-0 | GER | Europe |
| 67 | Or-0 | GER | Europe |
| 68 | Petergof | RUS | Europe |
| 69 | Rubezhnoe-1 | UKR | Remaining Asia |
|   | Code  | Country | Region        |
|---|-------|---------|---------------|
| 70| Si-0  | GER     | Europe        |
| 71| Sp-0  | GER     | Europe        |
| 72| Tscha-1| AUT     | Europe        |
| 73| Db-1  | GER     | Europe        |
| 74| Lp2-6 | CZE     | Europe        |
| 75| PHW-2 | ITA     | Europe        |
| 76| In-0  | AUT     | Europe        |
| 77| Is-0  | GER     | Europe        |
| 78| Ost-0 | SWE     | Europe        |
| 79| Per-1 | RUS     | Remaining Asia|
| 80| Sanna-2| SWE     | Europe        |
| 81| Kelsterbach-4| GER | Europe        |
| 82| Kas-2 | IND     | Remaining Asia|
| 83| Xan-5 | AZE     | Europe        |
| 84| Lerik2-1| AZE    | Europe        |
| 85| Nar-3 | AZE     | Europe        |
| 86| Istisu-5| AZE  | Europe        |
| 87| Lag1-4| GEO     | Europe        |
| 88| Geg-14| ARM     | Remaining Asia|
| 89| Yeg-2 | ARM     | Remaining Asia|
| 90| Yeg-4 | ARM     | Remaining Asia|
| 91| Yeg-5 | ARM     | Remaining Asia|
| 92| Yeg-7 | ARM     | Remaining Asia|
| 93| Yeg-8 | ARM     | Remaining Asia|
|   | Name     | Code | Region   |
|---|----------|------|----------|
| 94| Grn 12   | SWE  | Europe   |
| 95| Nyl 13   | SWE  | Europe   |
| 96| Spro 2   | SWE  | Europe   |
| 97| IP-Rei-0 | POR  | Europe   |
| 98| IP-Bea-0 | ESP  | Europe   |
| 99| IP-Cdc-3 | ESP  | Europe   |
|100| IP-Fue-2 | ESP  | Europe   |
|101| IP-Mot-0 | ESP  | Europe   |
|102| IP-Rel-0 | ESP  | Relict   |
|103| IP-Stp-0 | ESP  | Europe   |
|104| Aitba-1  | MAR  | Relict   |
|105| Panik-1  | RUS  | Remaining Asia |
|106| Karag-2  | RUS  | Remaining Asia |
|107| Adam-1   | RUS  | Remaining Asia |
|108| Lesno-4  | RUS  | Remaining Asia |
|109| Lesno-1  | RUS  | Remaining Asia |
|110| Lesno-2  | RUS  | Remaining Asia |
|111| Parti-1  | RUS  | Remaining Asia |
|112| Krazo-1  | RUS  | Remaining Asia |
|113| Karag-1  | RUS  | Remaining Asia |
|114| Basta-1  | RUS  | Remaining Asia |
|115| Basta-2  | RUS  | Remaining Asia |
|116| Basta-3  | RUS  | Remaining Asia |
|117| Chaba-2  | RUS  | Remaining Asia |
|   |井号 | 地理区域 | 国家 |
|---|---|---|---|
| 118 | Kolyv-2 | RUS | Remaining Asia |
| 119 | Kolyv-3 | RUS | Remaining Asia |
| 120 | Kolyv-5 | RUS | Remaining Asia |
| 121 | Kolyv-6 | RUS | Remaining Asia |
| 122 | K-oze-1 | RUS | Remaining Asia |
| 123 | K-oze-3 | RUS | Remaining Asia |
| 124 | Lebja-1 | RUS | Remaining Asia |
| 125 | Lebja-2 | RUS | Remaining Asia |
| 126 | Lebja-4 | RUS | Remaining Asia |
| 127 | Masl-1 | RUS | Remaining Asia |
| 128 | Nosov-1 | RUS | Remaining Asia |
| 129 | Noveg-1 | RUS | Remaining Asia |
| 130 | Noveg-2 | RUS | Remaining Asia |
| 131 | Noveg-3 | RUS | Remaining Asia |
| 132 | Panke-1 | RUS | Remaining Asia |
| 133 | Rakit-1 | RUS | Remaining Asia |
| 134 | Rakit-2 | RUS | Remaining Asia |
| 135 | Rakit-3 | RUS | Remaining Asia |
| 136 | Sever-1 | RUS | Remaining Asia |
| 137 | Aiell-1 | ITA | Europe |
| 138 | Mitterberg-3 | ITA | Europe |
| 139 | Dolen-1 | BUL | Europe |
| 140 | Epidauros-1 | GRC | Europe |
| 141 | Stiav-3 | SVK | Europe |
|   | Location    | Country | Region   |
|---|-------------|---------|----------|
| 142 | Ulies-1    | ROU     | Remaining Asia |
| 143 | Sij 1-96   | UZB     | Remaining Asia |
| 144 | Altai-5    | CHN     | Remaining Asia |
| 145 | Westkar-4  | KGZ     | Remaining Asia |
| 146 | IP-Bae-0   | ESP     | Europe |
| 147 | IP-Cha-0   | ESP     | Europe |
| 148 | IP-Pad-0   | ESP     | Europe |
| 149 | GEN-8      | FRA     | Europe |
| 150 | Aitba-2    | MAR     | Relict |
| 151 | Agu-1      | ESP     | Europe |
| 152 | Kly-1      | RUS     | Remaining Asia |
| 153 | Kly-4      | RUS     | Remaining Asia |
| 154 | Koz-2      | RUS     | Remaining Asia |
| 155 | Stepn-2    | RUS     | Remaining Asia |
| 156 | Stepn-1    | RUS     | Remaining Asia |
| 157 | Borsk-2    | RUS     | Remaining Asia |
| 158 | Shigu-1    | RUS     | Remaining Asia |
| 159 | Shigu-2    | RUS     | Remaining Asia |
| 160 | Kidr-1     | RUS     | Remaining Asia |
| 161 | Sij-1      | UZB     | Remaining Asia |
| 162 | Sij-2      | UZB     | Remaining Asia |
| 163 | Sij-4      | UZB     | Remaining Asia |
| 164 | Yeg-1      | ARM     | Remaining Asia |
| 165 | Istisu-1   | AZE     | Europe |
|   | Location | Continent  |
|---|----------|------------|
| 166 | Xan-1    | AZE        | Europe |
| 167 | Ara-1    | AFG        | Remaining Asia |
| 168 | Petro-1  | SRB        | Europe |
| 169 | Kos-1    | RUS        | Remaining Asia |
| 170 | Kos-2    | RUS        | Remaining Asia |
| 171 | Radk-1   | RUS        | Remaining Asia |
| 172 | Radk-2   | RUS        | Remaining Asia |
| 173 | Shu-1    | RUS        | Remaining Asia |
| 174 | Shu-2    | RUS        | Remaining Asia |
| 175 | Valm     | RUS        | Remaining Asia |
| 176 | OOE3-2   | AUT        | Europe |
| 177 | Pien     | RUS        | Remaining Asia |
| 178 | Samm     | RUS        | Remaining Asia |
| 179 | Bur-0    | IRL        | Europe |
| 180 | Col-0    | USA        | Europe |
| 181 | Edi-0    | UK         | Europe |
| 182 | Kn-0     | LTU        | Europe |
| 183 | Ler-0    | GER        | Europe |
| 184 | No-0     | GER        | Europe |
| 185 | Oy-0     | NOR        | Europe |
| 186 | RSCH-4   | RUS        | Remaining Asia |
| 187 | Sf-2     | ESP        | Europe |
| 188 | Tsu-0    | JPN        | Remaining Asia |
| 189 | Wil-2    | LTU        | Europe |
|   | Code | Country | Region  |
|---|------|---------|---------|
| 190 | Wu-0 | GER | Europe |
| 191 | Zu-0 | SUI | Europe |
| 192 | IP-Cor-0 | ESP | Europe |
| 193 | IP-Alm-0 | ESP | Europe |
| 194 | Etna-2 | ITA | Europe |
| 195 | Qar-8a | LBN | Europe |

*AFG, Afghanistan; ARM, Armenia; AUT, Austria; AZE, Azerbaijan; BUL, Bulgaria; CHN, China; CZE, Czech Republic; ESP, Spain; FIN, Finland; FRA, France; GEO, Georgia; GER, Germany; GRC, Greece; IND, India; IRL, Ireland; ITA, Italy; JPN, Japan; KAZ, Kazakhstan; KGZ, Kyrgyzstan; LBN, Lebanon; LTU, Lithuania; MAR, Morocco; NOR, Norway; POR, Portugal; ROU, Romania; RUS, Russia; SRB, Serbia; SUI, Switzerland; SVK, Slovakia; SWE, Sweden; TJK, Tajikistan; UK, United Kingdom; UKR, Ukraine; USA, United States of America; UZB, Uzbekistan.*
| No. | Name  | Geographic origin* | Group       |
|-----|-------|--------------------|-------------|
| 1   | Chi-1 | IND                | China-India |
| 2   | Chi-2 | IND                | China-India |
| 3   | Chi-25| IND                | China-India |
| 4   | Chi-33| IND                | China-India |
| 5   | Chi-35| IND                | China-India |
| 6   | Chi-37| IND                | China-India |
| 7   | Chi-38| IND                | China-India |
| 8   | Chi-4 | IND                | China-India |
| 9   | Deh-1 | IND                | China-India |
| 10  | Deh-13| IND                | China-India |
| 11  | Deh-17| IND                | China-India |
| 12  | Deh-25| IND                | China-India |
| 13  | Deh-3 | IND                | China-India |
| 14  | Deh-35| IND                | China-India |
| 15  | Deh-37| IND                | China-India |
| 16  | Deh-5 | IND                | China-India |
| 17  | Dha-03| IND                | China-India |
| 18  | Dha-04| IND                | China-India |
| 19  | Dha-06| IND                | China-India |
| 20  | Dha-07| IND                | China-India |
| 21  | Dha-09| IND                | China-India |
|   |   |   |   |
|---|---|---|---|
| 22 | Dha-10 | IND | China-India |
| 23 | Dha-12 | IND | China-India |
| 24 | Dha-15 | IND | China-India |
| 25 | Kok-03 | IND | China-India |
| 26 | Kok-07 | IND | China-India |
| 27 | Kok-08 | IND | China-India |
| 28 | Kok-09 | IND | China-India |
| 29 | Kok-20 | IND | China-India |
| 30 | Kok-21 | IND | China-India |
| 31 | Kok-22 | IND | China-India |
| 32 | Kok-25 | IND | China-India |
| 33 | Mun-1  | IND | China-India |
| 34 | Mun-11 | IND | China-India |
| 35 | Mun-14 | IND | China-India |
| 36 | Mun-2  | IND | China-India |
| 37 | Mun-3  | IND | China-India |
| 38 | Mun-5  | IND | China-India |
| 39 | Mun-8  | IND | China-India |
| 40 | Mun-9  | IND | China-India |
| 41 | San-1  | IND | China-India |
| 42 | San-18 | IND | China-India |
| 43 | San-19 | IND | China-India |
| 44 | San-2  | IND | China-India |
| 45 | San-25 | IND | China-India |
|   |   |   |   |
|---|---|---|---|
| 46 | San-28 | IND | China-India |
| 47 | San-29 | IND | China-India |
| 48 | San-3  | IND | China-India |
| 49 | AHthx  | CHN | China-India |
| 50 | AHyxx  | CHN | China-India |
| 51 | CQbbq  | CHN | China-India |
| 52 | CQtlx  | CHN | China-India |
| 53 | GSwex  | CHN | China-India |
| 54 | GZyjx  | CHN | China-India |
| 55 | HBhax  | CHN | China-India |
| 56 | HBwcq  | CHN | China-India |
| 57 | Hirokazu | JPN | Remaining Asia |
| 58 | HNylx  | CHN | China-India |
| 59 | HNZijj | CHN | China-India |
| 60 | JSnjs  | CHN | China-India |
| 61 | JXjgs  | CHN | China-India |
| 62 | JXnfx  | CHN | China-India |
| 63 | SXegx  | CHN | China-India |
| 64 | SXmix  | CHN | China-India |
| 65 | XJalt  | CHN | China-India |
| 66 | XJqhx  | CHN | China-India |
| 67 | ZJdys  | CHN | China-India |
| 68 | ZJjds  | CHN | China-India |

*CHN, China; JPN, Japan; IND, India.*