



The Early Growth Genetics (EGG) and EARly Genetics and Lifecourse Epidemiology (EAGLE) consortia: design, results and future prospects

Christel M. Middeldorp^{1,2,3}  · Janine F. Felix^{4,5,6} · Anubha Mahajan^{7,8} · EARly Genetics Lifecourse Epidemiology (EAGLE) consortium · Early Growth Genetics (EGG) consortium · Mark I. McCarthy^{7,8,9}

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Abstract

The impact of many unfavorable childhood traits or diseases, such as low birth weight and mental disorders, is not limited to childhood and adolescence, as they are also associated with poor outcomes in adulthood, such as cardiovascular disease. Insight into the genetic etiology of childhood and adolescent traits and disorders may therefore provide new perspectives, not only on how to improve wellbeing during childhood, but also how to prevent later adverse outcomes. To achieve the sample sizes required for genetic research, the Early Growth Genetics (EGG) and EARly Genetics and Lifecourse Epidemiology (EAGLE) consortia were established. The majority of the participating cohorts are longitudinal population-based samples, but other cohorts with data on early childhood phenotypes are also involved. Cohorts often have a broad focus and collect(ed) data on various somatic and psychiatric traits as well as environmental factors. Genetic variants have been successfully identified for multiple traits, for example, birth weight, atopic dermatitis, childhood BMI, allergic sensitization, and pubertal growth. Furthermore, the results have shown that genetic factors also partly underlie the association with adult traits. As sample sizes are still increasing, it is expected that future analyses will identify additional variants. This, in combination with the development of innovative statistical methods, will provide detailed insight on the mechanisms underlying the transition from childhood to adult disorders. Both consortia welcome new collaborations. Policies and contact details are available from the corresponding authors of this manuscript and/or the consortium websites.

Keywords Genetics · Consortium · Childhood traits and disorders · Longitudinal

Background

The full author list for this manuscript, including affiliations, includes all current active members of both consortia and is listed at the end of the paper followed by the membership lists of the EGG and EAGLE consortia as well as the acknowledgments and disclosures of interests.

✉ Christel M. Middeldorp
c.middeldorp@uq.edu.au

✉ Mark I. McCarthy

¹ Child Health Research Centre, University of Queensland, Brisbane, QLD, Australia

² Child and Youth Mental Health Service, Children's Health Queensland Hospital and Health Service, Brisbane, QLD, Australia

³ Department of Biological Psychology, Vrije Universiteit Amsterdam, 1081 BT Amsterdam, The Netherlands

⁴ The Generation R Study Group, Erasmus MC, University Medical Center Rotterdam, 3015 CE Rotterdam, The Netherlands

In countries with a high-sociodemographic index, the major contributors to burden of disease during childhood and adolescence are non-communicable diseases such as obesity,

⁵ Department of Epidemiology, Erasmus MC, University Medical Center Rotterdam, 3015 CE Rotterdam, The Netherlands

⁶ Department of Pediatrics, Erasmus MC, University Medical Center Rotterdam, 3015 CE Rotterdam, The Netherlands

⁷ Wellcome Centre for Human Genetics, University of Oxford, Oxford OX3 7BN, UK

⁸ Oxford Centre for Diabetes, Endocrinology and Metabolism, University of Oxford, Oxford OX3 7LE, UK

⁹ Oxford National Institute for Health Research (NIHR) Biomedical Research Centre, Churchill Hospital, Oxford OX3 7LE, UK

asthma or allergies, and psychiatric disorders. These have a large cumulative impact on individuals, families and society [1]. Moreover, many early-life traits track throughout childhood and adolescence into adulthood. Childhood obesity, for example, is associated with adult obesity and cardiovascular disease [2]. Several childhood psychiatric disorders persist into adolescence and adulthood or precede severe mental illness such as schizophrenia, which usually starts at late adolescence or early adulthood [3, 4]. Low birth weight, as a proxy for a suboptimal intrauterine environment, has been shown to be robustly associated with many later-life non-communicable traits, including cardiovascular, respiratory and psychiatric disorders (see e.g., 5–7). This prompted researchers, including those within the Developmental Origins of Health and Disease (DOHaD) field, to investigate the basis for the early origins of later life differences in health and disease.

Insight into the etiology of childhood and adolescent traits and disorders may provide new perspectives, not only on how to improve wellbeing during childhood, but also how to prevent later adverse outcomes. Individual differences in developmental phenotypes, such as body weight and composition, behavioral problems, language skills, and their stability across ages are partly influenced by genetic factors [8–13]. Identifying the specific genetic variants that influence these traits, and the biological pathways through which they operate, can therefore help to unravel etiological mechanisms. Genetic studies can also define whether the relationships between childhood and adult traits, for example, birth weight and cardiovascular disease, are causally mediated by early life exposures. In addition, genetics can support how specific environmental factors contribute to variation in these traits, i.e., whether there is gene-environment

interaction with the increase in risk depending on an individual's genetic risk.

It is increasingly recognized that large sample sizes are essential in genetic research [14] and studies performed in large international consortia have become the norm. Two such consortia with a particular focus on the genetics of early life phenotypes are the Early Growth Genetics (EGG) consortium (<http://egg-consortium.org/>) and the EARly Genetics and Lifecourse Epidemiology (EAGLE) consortium (<http://www.wikigenes.org/e/art/e/348.html>) (Fig. 1). This paper describes these two consortia as they have shared objectives and the participating cohorts partly overlap. We also highlight the results so far and outline the directions of future research.

Description and aims of the EGG and EAGLE consortia

Both consortia arose in 2009 out of the EU-funded European Network for Genetic And Genomic Epidemiology (ENGAGE). The EGG consortium focuses on the genetic basis of growth-related phenotypes spanning from fetal life into adolescence, including birth weight, childhood obesity and pubertal development. EAGLE was established to investigate the genetic basis of the wide range of further phenotypes collected by these cohorts from fetal life into adolescence, such as those relevant to asthma and eczema, childhood psychopathology, cognition, and neurodevelopment. The collective objectives of EGG and EAGLE are:

1. to characterize the genetic background of traits and diseases in fetal life, childhood and adolescence by facilitating collaboration between pregnancy, birth, childhood

Fig. 1 Logo's

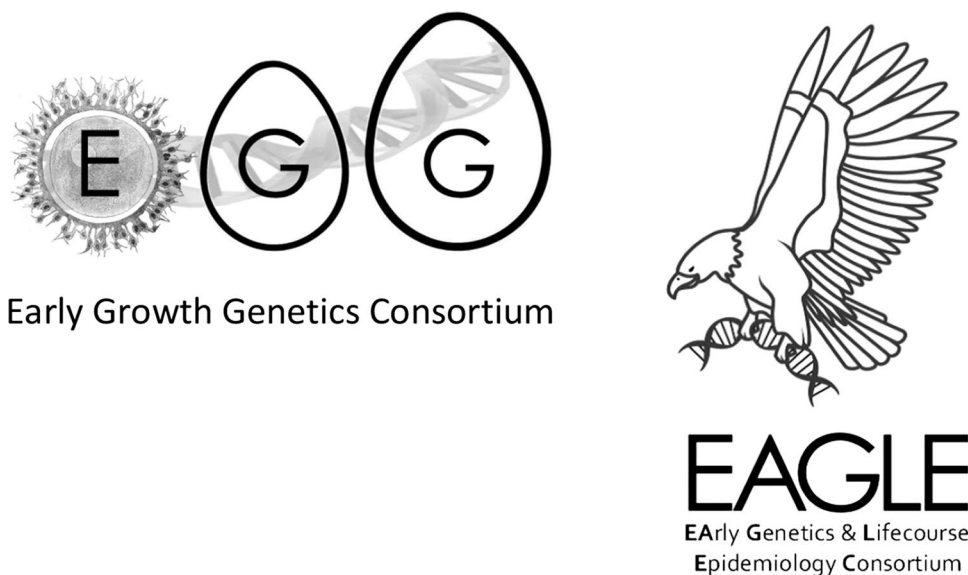


Table 1 (continued)

Short name	Full name cohort	Website	References
NFBC1966 and NFBC1986	Northern Finland Birth Cohort	http://www.oulu.fi/nfbc/	750195; 19060910; 9246691
PIAMA	Preventie en Incidentie van Astma en Mijt Allergie Project Viva	http://piama.iras.uu.nl/ http://daccp.org/viva/	12688626, 23315435 24639442
Qtwin Raine	Queensland Twin Registry The Western Australian Pregnancy Cohort (Raine) Study	http://www.qimrberghofer.edu.au/qtwin/ https://www.rainestudy.org.au/	DOI: 10.1080/00049530410001734865 8105165; 23230915; 233016741; 26169918; 28064197; 28662683
SKOT	Småbørns Kost Og Trivsel	https://skot.ku.dk/om-projektet/engilsh/	28947836
STRIP	Special Turku Coronary Risk Factor Intervention Project	http://stripstudy.uu.fi/english.html	18430753
TCHAD	Twin Study of Child and Adolescent Development	https://ki.se/en/meb/twin-study-of-child-and-adolescent-development-tchad	17539366
TDCOB	The Danish Childhood Obesity Biobank	https://clinicaltrials.gov/ct2/show/NCT00928473	23110994
TEDS	Twins Early Development Study	http://teds.ac.uk/	25431468
TRAILS	TRacking Adolescents' Individual Lives Survey	https://www.trails.nl/	18263651
Young Finns	The Cardiovascular Risk in Young Finns Study	http://youngfinnsstudy.utu.fi/	

- and adolescent cohort studies, as well as adult biobanks (such as UK Biobank) with relevant information;
- to define the causal relationships between early life exposures and related early life phenotypes and major sources of morbidity and mortality in later life;
- to develop and improve statistical methods for analyzing complex, high-dimensional and longitudinal phenotypic data;
- to provide training opportunities for junior researchers to develop in the field of genetic epidemiology.

The EGG and EAGLE consortia started as collaborations of population-based pregnancy and birth cohort studies, each of which has collected longitudinal data across a wide range of developmental phenotypes. As the collaboration developed, cohorts that started data collection during childhood and adolescence were also included. Almost all participating studies have genome-wide genotype data available. In addition, early life data collected through self-report and/or record linkage in adult biobanks, such as UK Biobank or the population based cohorts listed in Table 1 that have an adult counterpart, have been brought into the genome-wide association (GWA) meta-analyses for phenotypes such as birth weight. Both consortia welcome new collaborations, and they are keen to add data from longitudinal cohorts that are currently in the process of obtaining genotype data.

Tables 1 and 2 provides a summary of the participating studies and their design, as of April 2018. Table 3 gives further details on the extensive data available, indicating, per cohort, whether data collection has taken place at least once at preschool, school, adolescent and adult age. However, many cohorts have had multiple follow-up rounds within any given period or follow-up data collection is ongoing, through research clinic assessments, questionnaires or record linkage. The majority of the cohorts have around equal numbers of males and females included.

Most cohorts were established with the aim of investigating risk and protective factors for a broad range of developmental phenotypes. They have collected data on physical traits, cognition, emotional and behavioral problems, as well as on lifestyle and environmental factors, such as smoking during pregnancy and physical exercise. Other cohorts were set up with a specific focus, such as asthma research, but many of these have collected ancillary information on a wider range of phenotypes. Table 2 gives an indication as to whether data collection was focused on a specific phenotype. Additional details on many of these studies will be available from cohort websites and publications (see Table 1).

Participating cohorts have obtained DNA from blood samples, saliva or buccal swabs. A variety of different genotyping arrays have been used over the years, but meta-analysis has been facilitated by imputation of directly genotyped data using reference panels such as those generated by 1000

Genomes or the Haplotype Reference Consortium [15, 16]. Moreover, an increasing number of cohorts have, or plan to get, additional ‘omics data including parental genotypes, DNA methylation profiles, RNA expression levels, metabolomics and/or microbiome data.

Results of the genetic studies performed in the EGG and EAGLE consortia

The implementation of GWA meta-analyses for each of the phenotypes of interest to EGG or EAGLE has usually been championed and organized at the level of a working group, formed by a subset of motivated investigators and analysts, who have assumed responsibility for assembling, combining and interpreting the genetic data. The wide range of phenotypes available to study across these consortia has provided fertile ground for many such working groups and has resulted in a large number of peer-reviewed papers across this wide range of phenotypes [17–45]. These are typically GWA meta-analyses, focusing on the effects of individual genetic variants, but increasingly now extend to multivariate, polygenic analyses, that evaluate the joint effects of multiple associated genetic variants and apply this information to address questions of causality.

Amongst the many GWA analyses led by EGG and EAGLE, the traits for which the largest numbers of genetic loci reached genome-wide statistical significance ($p < 10^{-8}$) have been birth weight (65 loci), atopic dermatitis (31), childhood BMI (15), allergic sensitization (10), and pubertal growth (10) [17, 19, 23, 26, 28, 36]. For other phenotypes with a large number of genome wide hits, such as age at menarche (108 loci) or ADHD (16 loci), the association analysis has involved collaborations with other consortia [25, 37]. The summary statistics for many of the genome-wide association studies undertaken by EGG and EAGLE investigators can be found on consortium websites (<http://egg-consortium.org/>; <http://www.wikigenes.org/e/art/e/348.html>) or are available from corresponding authors.

As with adult phenotype GWA studies, the number of association signals recovered by these studies is influenced heavily by sample size ($N = 182,416$ for age at menarche, $N = 153,781$ for birth weight) and, to a lesser extent, by phenotype characteristics (somatic or behavioral traits, continuous or binary outcomes).

In addition to cross-sectional GWA analyses, there have been many examples of projects that have investigated genetic relationships within childhood traits or between childhood traits and related adult phenotypes, often revealing shared genetic factors. For example, genetic overlap was found among related atopic conditions during childhood, and between atopic conditions and auto-immune disorders

[19, 36]; among puberty-related phenotypes, and between puberty-related phenotypes and BMI [23, 24, 37]; between childhood and adult blood pressure [41]; between preschool internalizing symptoms and adult psychiatric disorders [18]; and between childhood and adult anthropometric traits [21, 26, 40, 44]. The development of statistical methods that support the calculation of genetic correlations from summary GWAS results [46] and the easy availability of such data from a growing number of GWA meta-analyses for adult traits have enabled these analyses to be undertaken with adequate statistical power.

Figure 2 shows genetic correlations, calculated exclusively from GWAS data, between birth weight and a range of continuous and disease phenotypes [28], generated using the linkage disequilibrium score regression approach [46] as implemented in the LDHub web utility [47]. For many cardiometabolic and anthropometric traits measured in late adult life, there is evidence of substantial sharing of genetic variation with birth weight. In line with the wider epidemiological data, the genetic correlations between birth weight and adult cardiometabolic traits (including type 2 diabetes, blood pressure, and coronary artery disease) tend to be negative. These data indicate that a substantial proportion of the observed covariance between birth weight and cardiometabolic disease predisposition is likely to be driven by genetic rather than environmental factors. However, the potential for more complex causal relationships (such as those that connect fetal genotype to adult disease via the correlation with maternal genotype and altered maternal environment) also needs to be considered. Full characterization of these complex relationships requires the application of statistical methods that enable partitioning of genetic effects into maternal and fetal components both at the level of individual SNPs [48] and genome-wide [49]. Using the M-GCTA method [49], for example, it has been reported that maternal genotypes contribute more to gestational weight gain in the mother, while offspring genotypes contribute more to birth weight [45].

Another critical advantage of genetic studies is the potential to characterize causal relationships using Mendelian randomization approaches [50]. Tyrrell et al. [42] found evidence of a positive causal effect of maternal BMI and fasting glucose levels on offspring birth weight but inverse effect of maternal systolic blood pressure on offspring birth weight. Despite bringing together the largest number of studies at the time with relevant data, there was insufficient power to dissect how the opposing effects of maternal glucose and systolic blood pressure are reflected in the maternal BMI effect (one reason why we are keen to extend the collaboration to any new cohorts). Crucially, however, appropriate application and interpretation of studies that seek to elucidate the mechanisms underlying associations between maternal and offspring phenotypes require investigators to

Table 2 Study designs

Cohort	Study design	Years of recruitment	Country
ABCD	Population based pregnancy cohort	2003–2004	The Netherlands
ALSPAC	Population based birth cohort	1990–1992	UK
B58C	Population based birth cohort	1958	UK
BAMSE	Population based cohort	1994–1996	Sweden
BMDCS	Multi-center observational cohort	2002–2009	United States
Breathe	Population based cohort	2002–2006	Spain
CATSS	Population based twin birth cohort	1992–ongoing	Sweden
CHOP	Population based cohort	1988–Present	USA
CHS	Community based children cohort	1993–2002	United States
CLHNS	Population based birth cohort	1983–1984	Philippines
COPSAC-2000	Asthma risk birth cohort	From 2000-	Denmark
COPSAC-2010	Population based birth cohort	Ongoing From 2010	
COPSAC-REGISTRY	Severe asthma cases (children)	Ongoing	
DNBC-GOYA	Population based pregnancy cohorts	From 1997	Denmark
DNBC-PTB		Ongoing	
EFSOCH	Community-based pregnancy cohort of parent–offspring trios	2000–2004	United Kingdom
Finntwin12	Population-based twin-family cohort	1983–1987	Finland
Gen3G	Population based birth cohort	2010–2013	Canada
Generation R ^a	Population-based birth cohort	2002–2006	The Netherlands
GINIplus	Population based birth cohort	1995–1998	Germany
GLAKU	Population-based birth cohort	1998	Finland
HBSC	Population-based birth cohort	1934–1944	Finland
Health2006	General population study	2006–2008	Denmark
INMA	Population-based birth cohort	1997–2008	Spain
Inter99	Population-based randomized intervention study	1999–2006	Denmark
LISA	population based birth cohort	1997–1999	Germany
MAAS ^a	Population-based birth cohort	1996/1997	UK
MOBA	Population based birth cohort	1999–2008	Norway
MUSP	Pregnancy general population	1981–1984	Australia
NTR ^a	Birth general twin population	From 86—ongoing	Netherlands
NFBC1966 and NFBC1986	longitudinal birth cohort	1966 and 1986	Finland
PIAMA	Population based birth cohort, enriched for high risk allergy children (allergic mother)	1996–1997	Netherlands
Project Viva ^a	Population based birth cohort	1999–2002	USA
Qtwin	Longitudinal twin study	1980–2004	Australia
Raine	Longitudinal pregnancy cohort study	1989–1991	Australia
SKOT	Observational cohort study, monitoring healthy young children from 9 to 36 months of age.	2006–2007 (SKOT I); 2011–2013 (SKOT II)	Denmark
STRIP	Prospective randomized life-style intervention trial	1990–1992	Finland
TCHAD	Birth general twin population	1985–1987	Sweden
TDCOB	Case–control study	Children and adolescence with obesity: 2007–2013; Population-based sample: 2010–2013	Denmark
TEDS	Population based twin birth cohort	From 1994—Ongoing	UK
TRAILS-pop	Population based	2001/2002	Netherlands
TRAILS-CC	High risk	2004	Netherlands
Young Finns	Population based follow-up from childhood to adulthood	1980	Finland

^aIncludes individuals from non-European descent

Table 3 Data collected

Cohort	N genotyped children ^a	Phenotypes	Age periods data available				
			Pregnancy	Pre-school	School	Adolescence	Adult
ABCD	1192	Broad	x	x	x	x	
ALSPAC	10,000	Broad	x	x	x	x	x
B58C	6491	Broad	x	x	x	x	x
BAMSE	2500	Broad	x	x	x	x	x
BMDCS	1885	Broad		x	x	x	x
Breathe	1667	Broad			x		
CATSS	13,576	Broad, focus on psychiatry	x, information from registers		x	x	x
CHOP	43,320	Broad		x	x	x	
CHS	3986	Broad, focus on respiratory and metabolic health			x	x	
CLHNS	1779	Broad		x	x	x	x
COPSAC-2000	411	Broad	x	x	x	x	x
COPSAC-2010	700	Broad	x	x	x		
COPSAC-REGISTRY	1240	Broad	x	x			
DNBC	1500	Broad	x	x	x	x	
-GOYA	1500						
DNBC-PTB							
EFSOCH	812	Anthropometric and glycemic traits	x	x			Parents only
Finntwin12	1264	Broad	Retrospective	Retrospective	x	x	x
Gen3G	582	Broad, focus on metabolic/adiposity	x	on-going			
Generation R	5731	Broad	x	x	x	x	
GINIplus	835	broad	x	x	x	x	Ongoing
GLAKU	357	Broad	x	x	x	x	x
HBCS	1566	Broad		x	x	x	x
Health2006	2802	Cardiovascular disease, type 2 diabetes, and other lifestyle related diseases					x
INMA	1517	Broad	x	x	x	Ongoing	
Inter99	6184	Cardiovascular disease, type 2 diabetes, other lifestyle related diseases, glucose tolerance					x
LISA	674	Broad	x	x	x	x	Ongoing
MAAS	919	asthma and allergy focused	x	x	x	x	Ongoing
MOBA	17,000	Broad	x	x	x	x	x
MUSP	1200	Broad	x	x	x	x	x
NTR	7750	Broad	x	x	x	x	Ongoing
NFBC1966 NFBC1986	5402	Broad	x	x	x	x	x
	3743						
PIAMA	2113	Broad, focus on respiratory health	x	x	x	x	
Project Viva	1580	Broad	x	x	x	x	
Qtwin	4500	Broad			x	x	x
Raine	1500	Broad	x	x	x	x	Ongoing

Table 3 (continued)

Cohort	N genotyped children ^a	Phenotypes	Age periods data available					
			Pregnancy	Pre-school	School	Adolescence	Adult	
SKOT I	260	Dietary intake, growth, cognitive development, overweight and lifestyle related diseases		x				
SKOT II	112							
STRIP	666	Broad	x	x	x	x	x	
TCHAD	990	Broad			x	x	x	
TDCOB	1771	Overweight and Obesity		x	x	x	x	
TEDS	10,346	Broad		x	x	x	x	
TRAILS-pop	1354	Broad	Retrospective	Retrospective	Retrospective	x	x	
TRAILS-CC	341							
Young Finns	2442	Broad	x	x	x	x	x	

^aSome cohorts also have genotype data on parents

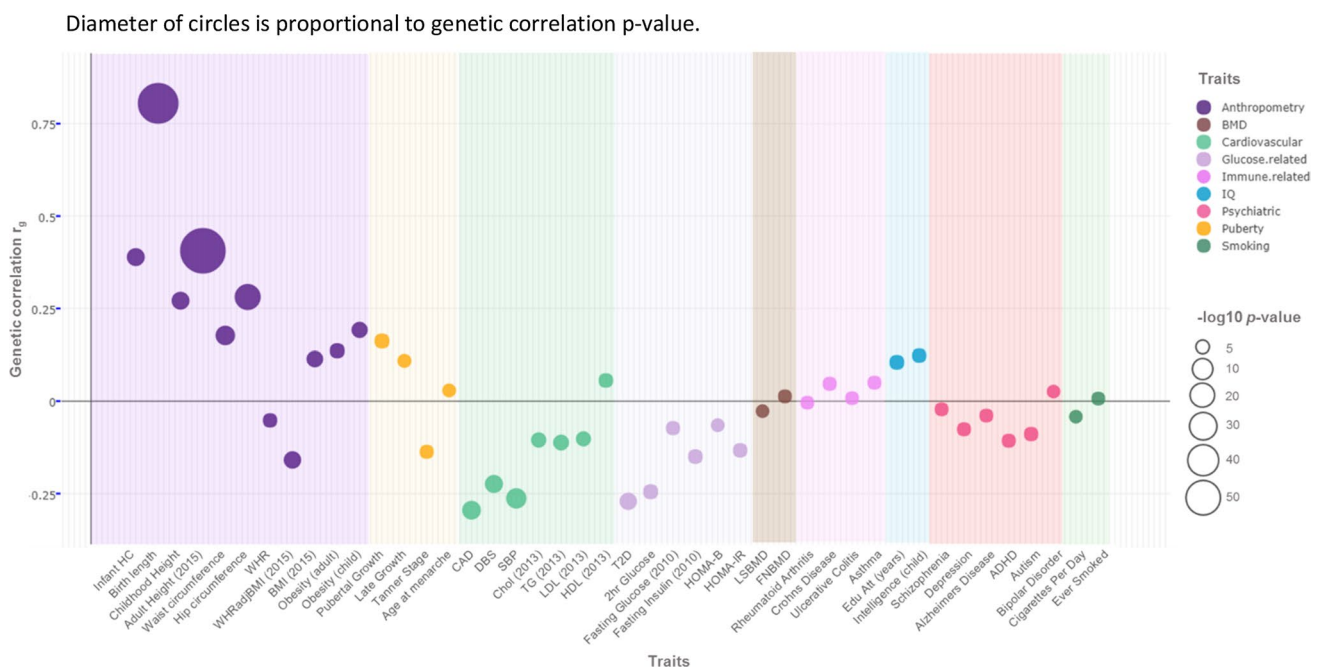


Fig. 2 Genome-wide genetic correlation between birth weight and a range of traits and diseases in later life. Genome-wide genetic correlations between birth weight and traits and diseases evaluated in later life. The figure (adapted from Horikoshi et al. 2016 [28] with permission of the authors) displays the genetic correlations between birth weight and a range of traits and diseases in later life as estimated using LD Score regression. Traits selected were those for which genome-wide association summary statistics were available in suitably large sample sizes, and the analyses were typically performed

on the largest meta-analyses available as of early 2016. The genetic correlation estimates (r_g) are colour coded according to phenotypic area. Allelic direction of effect is aligned to increased birth weight. Size of the circle denotes the significance level for the correlation (per the key). Correlations with a lower significance level are not depicted. Further detail on the methods and studies involved is available in Horikoshi et al. 2016 [28]. Diameter of circles is proportional to genetic correlation p value

consider diverse complicating factors including the correlation between maternal and fetal genetic instruments, and to account for these sources of potential bias in the Mendelian randomization analyses wherever possible [51].

The longitudinal data collected in EGG and EAGLE cohorts provide the means to investigate whether the influence of genetic variants changes over time. This has only recently been explored given the need for large numbers

of studies with repeated measures. We have found that genetic variation in FTO, one of the first BMI increasing genetic variants to be identified in GWAS and one of the variants most strongly associated with mean BMI (in adults) is inversely associated with BMI in infancy only becoming positive in later childhood and adult [38], indicating the value of research that explores gene-by-age interactions. On a genome-wide scale, using meta-regression methods, polygenic risk scores generated from adult schizophrenia data yielded associations with variation in childhood and adolescent psychiatric symptom scores, which strengthened in magnitude with increasing age [52].

Strengths and weaknesses

The aggregation of data in consortia such as EGG and EAGLE provides vastly improved sample sizes and a powerful way to overcome the major weakness of many of the early GWAS, which were, in hindsight, underpowered to detect the generally small genome-wide significant associations. This has brought multiple robust association signals across many traits, and provided a valuable basis for dissecting the, often complex, causal relationships between epidemiologically-correlated traits.

A clear strength of the EGG and EAGLE consortia is the wealth of data available. This encompasses not only repeated measures for physical and behavioral traits, but also copious information on lifestyle and environmental circumstances. Moreover, some of the cohorts have collected data for several decades, and now provide repeated measures well into adulthood. This enables developmental research as well as analyses of the interplay between genes and environment.

To date, one of the limitations has been that the majority of participating cohorts have data based on European-ancestry populations (see Table 2 for exceptions). There is a clear need for equivalent data to be generated in samples from other ethnic groups, so that the genetic contribution to reproducible ethnic differences in the distribution of early life phenotypes can be explored and the implications for adult disease risk quantified.

Since the cohorts are population-based and lack a particular disease-focus, the consortia are not so well-suited to investigate conditions with a low prevalence. They are better-placed to analyze common traits, particularly those that can be measured on continuous scales and analyzed as quantitative measures, such as blood pressure instead of hypertension and ADHD symptom score instead of ADHD diagnosis [32, 34]. Power analyses demonstrate that identification of a genetic variant is, in most circumstances, more powerful for continuous traits than for dichotomous variables based on clinical cut-offs [53].

Future

Considerable progress is to be expected from ongoing increases in sample sizes, especially for traits such as childhood aggression, ADHD-related traits and internalizing symptoms, where the number of identified genetic variants has been limited so far. Access to new data sets can motivate efforts to tackle phenotypes that have not hitherto been subject to detailed genetic analysis.

The results emerging from many of these studies provide a timely reminder that analysis of early life phenotypes often requires researchers to consider the joint impacts of multiple genomes (e.g., those of the fetus and the mother) together with the web of environmental influences as potential contributors to individual variation. They also highlight the need to take into account the changes happening throughout development. This is now possible because of large, rich and complex datasets that support use of novel statistical methods for the analysis of causality or gene-by-age interaction [48, 49, 51, 54]. There have already been several examples of papers performing such analyses and this will only increase with the number of identified genetic variants. In addition, existing gender differences in the associations between early life and adult factors (such as cardiometabolic risk) suggest a need for more thorough analysis of the effects of gender on these early acting mechanisms. The focus to date on the role of maternal and offspring GWAS information indicates a failure to properly consider the contribution of genetic variation in the father that will be remedied as more data from complete trios and pedigrees becomes available.

We are also planning to expand these consortia to accommodate access to the increasing amount of ‘omics data now becoming more available. Combining the results from EGG and EAGLE GWA analyses with those from DNA methylation analyses performed by the Pregnancy And Childhood Epigenetics (PACE) consortium [55] and with the pregnancy/child cohorts in the Consortium of METabolomic Studies (COMETS; <https://epi.grants.cancer.gov/comets/>) will shed further light on the biological mechanisms underlying associations of early-life risk factors and childhood, adolescent and adult health outcomes.

The focus on translating this knowledge to clinical and public health settings represents a major motivation. Insight into genetic factors underlying stability in traits such as obesity and psychiatric disorders may aid in providing targeted interventions to the groups at highest need. A more complete understanding of the contributions of genetic and non-genetic factors in the relationships between early life and later life traits may focus attention on the most effective strategies for behavioural or environmental modification.

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The authors for this manuscript are: Christel M Middeldorp^{1,2,3}, Janine F Felix^{4,5,6}, Anubha Mahajan^{7,8}, Momoko Horikoshi^{7,8,9}, Neil R Robertson^{7,8}, Robin N Beaumont¹⁰, Jonathan P Bradfield^{11,12}, Mariona Bustamante^{13,14,15}, Diana L Cousminer^{16,17}, Felix R Day¹⁸, N Maneka De Silva¹⁹, Monica Guxens^{13,14,15}, Dennis O Mook-Kanamori^{20,21}, Beate St Pourcain^{22,23}, Nicole M Warrington²⁴, Linda S Adair²⁵, Emma Ahlqvist²⁶, Tarunveer S Ahluwalia^{27,28,29}, Peter Almgren²⁶, Wei Ang³⁰, Mustafa Atalay³¹, Juha Auvinen³², Meike Bartels^{3,33,34}, Jacques S Beckmann³⁵, Jose Ramon Bilbao^{36,37,38}, Tom Bond¹⁹, Judith

- B Borja^{39,40}, Alana Cavadino^{41,42}, Pimphen Charoen^{19,43}, Zhanghua Chen⁴⁴, Lachlan Coin⁴⁵, Cyrus Cooper⁴⁶, John A Curtin⁴⁷, Adnan Custovic⁴⁸, Shikta Das⁴², Gareth E Davies⁴⁹, George V Dedoussis⁵⁰, Liesbeth Duijts^{4,51,52}, Peter R Eastwood^{53,54}, Anders U Eliassen^{55,56}, Paul Elliott¹⁹, Johan G Eriksson^{57,58,59}, Xavier Estivill⁶⁰, João Fadista⁶¹, Iryna O Fedko^{3,33}, Timothy M Frayling¹⁰, Romy Gaillard⁵, W James Gauderman⁴⁴, Frank Geller⁶¹, Frank Gilliland⁴⁴, Vincente Gilsanz⁶², Raquel Granel⁶³, Niels Grarup²⁸, Leif Groop^{26,64}, Dexter Hadley⁶⁵, Hakon Hakonarson^{11,16,66}, Torben Hansen²⁸, Catharina A Hartman⁶⁷, Andrew T Hattersley^{10,68}, M Geoffrey Hayes⁶⁹, Johannes Hebebrand⁷⁰, Joachim Heinrich^{71,72}, Øyvind Helgeland^{73,74,75}, Anjali K Henders⁴⁵, John Henderson⁶⁵, Tine B Henriksen⁷⁶, Joel N Hirschhorn^{77,78,79}, Marie-France Hivert^{80,81,82}, Berthold Hocher^{83,84}, John W Holloway⁸⁵, Patrick Holt⁸⁶, Jouke-Jan Hottenga^{3,33,34}, Elina Hyppönen^{42,87,88}, Carmen Iniguez^{15,89,90}, Stefan Johansson^{73,91}, Astanand Jugessur^{92,93,94}, Mika Kähönen^{95,96}, Heidi J Kalkwarf⁹⁷, Jaakko Kaprio^{64,98}, Ville Karhunen⁹⁹, John P Kemp^{23,24,63}, Marjan Kerkhof¹⁰⁰, Gerard H Koppelman¹⁰¹, Antje Körner^{102,103}, Sailesh Kotecha¹⁰⁴, Eskil Kreiner-Møller^{27,105}, Benard Kulohoma⁷, Ashish Kumar^{106,107}, Zoltán Kutalik^{108,109}, Jari Lahti^{110,111}, Joan M Lappe¹¹², Henrik Larsson^{113,114}, Terho Lehtimäki^{115,116}, Alexandra M Lewin¹⁹, Jin Li¹¹, Paul Lichtenstein¹¹⁴, Cecilia M Lindgren^{7,117,118}, Virpi Lindi³¹, Allan Linneberg^{119,120}, Xueping Liu⁶¹, Jun Liu⁵, William L Lowe Jr⁶⁹, Sebastian Lundström^{121,122}, Leo-Pekka Lytykäinen^{115,116}, Ronald CW Ma^{123,124,125}, Aurélien Macé¹⁰⁸, Reedik Mägi¹²⁶, Per Magnus⁹³, Abdullah A Mamun¹²⁷, Minna Mannikko³², Nicholas G Martin¹²⁸, Hamdi Mbarek^{3,33,34,129}, Nina S McCarthy¹³⁰, Sarah E Medland¹²⁸, Mads Melbye^{61,131}, Erik Melén^{106,132}, Karen L Mohlke¹³³, Claire Monnereau^{4,5,6}, Camilla S Morgen¹³⁴, Andrew P Morris^{7,126,135}, Jeffrey C Murray¹³⁶, Ronny Myhre⁹², Jakob M Najman¹³⁷, Michel G Nivard^{3,33}, Ellen A Nohr¹³⁸, Ilja M Nolte¹³⁹, Ioanna Ntalla¹⁴⁰, Paul O'Reilly¹⁴¹, Sharon E Oberfield¹⁴², Emily Oken¹⁴³, Albertine J Oldehinkel⁶⁷, Katja Pakkala^{144,145}, Teemu Palviainen⁶⁴, Kalliope Panoutsopoulou¹⁴⁶, Oluf Pedersen²⁸, Craig E Pennell¹⁴⁷, Göran Pershagen^{106,148}, Niina Pitkänen¹⁴⁴, Robert Plomin¹⁴⁹, Christine Power⁴², Rashmi B Prasad²⁶, Inga Prokopenko^{7,150}, Lea Pulkkinen¹⁵¹, Katri Räikkönen¹¹¹, Olli T Raitakari^{144,152}, Rebecca M Reynolds¹⁵³, Rebecca C Richmond^{23,63}, Fernando Rivadeneira^{4,5,154}, Alina Rodriguez^{19,155}, Richard J Rose¹⁵⁶, Rany Salem^{78,157,158,159}, Loreto Santa-Marina^{15,160,161}, Seang-Mei Saw^{162,163}, Theresia M Schnurr²⁸, James G Scott^{137,164,165}, Saskia Selzam¹⁴⁹, John A Shepherd¹⁶⁶, Angela Simpson⁴⁷, Line Skotte⁶¹, Patrick MA Sleiman^{11,66}, Harold Snieder¹³⁹, Thorkild IA Sørensen^{23,28,134}, Marie Standl⁷¹, Eric AP Steegers¹⁶⁷, David P Strachan¹⁶⁸, Leon Straker¹⁶⁹, Timo Strandberg^{32,170,171}, Michelle Taylor^{23,63}, Yik-Ying Teo^{162,172,173}, Elisabeth Thiering^{71,174}, Maties Torrent^{15,175,176}, Jessica Tyrrell^{10,177}, André G Uitterlinden^{4,5,154}, Toos van Beijsterveldt^{3,33}, Peter J van der Most¹³⁹, Cornelia M van Duijn⁵, Jorma Viikari^{178,179}, Natalia Vilor-Tejedor^{180,181}, Suzanne Voegelezeang^{4,5,6}, Judith M Vonk^{139,182}, Tanja GM Vrijkotte¹⁸³, Eero Vuoksimaa⁶⁴, Carol A Wang¹⁴⁷, William J Watkins¹⁰⁴, H-Erich Wichmann^{71,184,185}, Gonneke Willemsen^{3,33,34}, Gail M Williams¹³⁷, James F Wilson^{186,187}, Naomi R Wray^{45,188}, Shujing Xu⁴⁴, Cheng-Jian Xu¹⁰¹, Hanieh Yaghooskar¹⁸⁹, Lu Yi¹¹⁴, Mohammad Hadi Zafarmand^{183,190}, Eleftheria Zeggini¹⁴⁶, Babette S Zemel¹⁹¹, Anke Hinney⁷⁰, Timo A Lakka^{31,192,193}, Andrew JO Whitehouse⁸⁶, Jordi Sunyer^{13,14,15,194}, Elisabeth E Widén⁶⁴, Bjarke Feenstra⁶¹, Sylvain Sebert^{19,32,195,196}, Bo Jacobsson^{75,197}, Pål R Njølstad^{73,74}, Camilla Stoltenberg¹⁹⁸, George Davey Smith^{23,63}, Debbie A Lawlor^{23,63,199}, Lavinia Paternoster^{23,63}, Nicholas J Timpson^{23,63}, Ken K Ong^{18,200}, Hans Bisgaard²⁷, Klaus Bønnelykke²⁷, Vincent WV Jaddoe^{4,5,6}, Henning Tiemeier^{201,202}, Marjo-Riitta Järvelin^{19,32,195,203,204}, David M Evans^{23,24,63}, John RB Perry¹⁸, Struan FA Grant^{11,16,17,66}, Dorret I Boomsma^{3,33,34,129}, Rachel M Freathy^{10,23}, Mark I McCarthy^{7,8,205}
1. Child Health Research Centre, University of Queensland, Brisbane, QLD, Australia.
 2. Child and Youth Mental Health Service, Children's Health Queensland Hospital and Health Service, Brisbane, QLD, Australia.
 3. Department of Biological Psychology, Vrije Universiteit Amsterdam, Amsterdam, 1081 BT, The Netherlands.
 4. The Generation R Study Group, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands.
 5. Department of Epidemiology, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands.
 6. Department of Pediatrics, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands.
 7. Wellcome Centre for Human Genetics, University of Oxford, Oxford, OX3 7BN, UK.
 8. Oxford Centre for Diabetes, Endocrinology and Metabolism, University of Oxford, Oxford, OX3 7LE, UK.
 9. RIKEN, Centre for Integrative Medical Sciences, Laboratory for Endocrinology, Metabolism and Kidney diseases, Yokohama, Kanagawa, 230-0045, Japan.
 10. Institute of Biomedical and Clinical Science, University of Exeter Medical School, University of Exeter, Royal Devon and Exeter Hospital, Exeter, EX2 5DW, UK.
 11. Center for Applied Genomics, The Children's Hospital of Philadelphia, Philadelphia, PA 19104, USA.
 12. Quantinuum Research LLC, San Diego, CA, 92101, USA.
 13. ISGlobal, Institute for Global Health, Barcelona, 08003, Spain.
 14. Universitat Pompeu Fabra (UPF), Barcelona, 08003, Spain.
 15. CIBER de Epidemiología y Salud Pública (CIBERESP), Madrid, 28029, Spain.
 16. Division of Human Genetics, The Children's Hospital of Philadelphia, Philadelphia, PA 19104, USA.
 17. Department of Genetics, Perelman School of Medicine, University of Pennsylvania, Philadelphia, 19104, USA.
 18. MRC Epidemiology Unit, University of Cambridge School of Clinical Medicine, Cambridge, CB2 0QQ, UK.
 19. Department of Epidemiology and Biostatistics, MRC-PHE Centre for Environment & Health, School of Public Health, Imperial College London, London, W2 1PG, UK.
 20. Department of Clinical Epidemiology, Leiden University Medical Center, Leiden, 2333 ZA, The Netherlands.
 21. Department of Public Health and Primary Care, Leiden University Medical Center, Leiden, 2333 ZA, The Netherlands.
 22. Max Planck Institute for Psycholinguistics, Nijmegen, 6525 XD, The Netherlands.
 23. Medical Research Council Integrative Epidemiology Unit at the University of Bristol, Bristol, BS8 2BN, UK.
 24. University of Queensland Diamantina Institute, Translational Research Institute, Brisbane, QLD, 4072, Australia.
 25. Department of Nutrition, University of North Carolina, Chapel Hill, NC 27599, USA.
 26. Department of Clinical Sciences, Diabetes and Endocrinology, Lund University Diabetes Centre, Malmö, SE-205 02, Sweden.
 27. COPSAC, Copenhagen Prospective Studies on Asthma in Childhood, Herlev and Gentofte Hospital, University of Copenhagen, Copenhagen, 2900 Hellerup, Denmark.
 28. Novo Nordisk Foundation Center for Basic Metabolic Research, Section of Metabolic Genetics, Faculty of Health and Medical Sciences, University of Copenhagen, Copenhagen, DK-2200, Denmark.
 29. Steno Diabetes Center Copenhagen, Gentofte, 2820, Denmark.
 30. Division of Obstetrics and Gynaecology, The University of Western Australia, Crawley, WA, 6009, Australia.
 31. Institute of Biomedicine, Physiology, University of Eastern Finland, Kuopio, 70211, Finland.
 32. Center for Life Course Health Research, Faculty of Medicine, University of Oulu, Oulu, FI-90014, Finland.
 33. Amsterdam Public Health, Amsterdam, The Netherlands.
 34. Netherlands Twin Register, Department of Biological Psychology, VU University, Amsterdam, 1081 HV, The Netherlands.
 35. University of Lausanne, Lausanne, CH-1015, Switzerland.
 36. University of the Basque Country (UPV/EHU), Spain.
 37. Biocruces Health Research Institute, Spain.
 38. CIBER Diabetes y Enfermedades Metabólicas (CIBERDEM), Spain.
 39. USC-Office of Population Studies Foundation, Inc., University of San Carlos, Cebu City, 6000, Philippines.
 40. Department of Nutrition and Dietetics, University of San Carlos, Cebu City, 6000, Philippines.
 41. Section of Epidemiology & Biostatistics, School of Population Health, University of Auckland, Auckland, New Zealand.
 42. Population, Policy and Practice, UCL Great Ormond Street Institute of Child Health, University College London, London, WC1N 1EH, UK.
 43. Department of Tropical Hygiene, Faculty of Tropical Medicine, Mahidol University, Bangkok, 10400, Thailand.
 44. Department of Preventive Medicine, Keck School of Medicine,

- University of Southern California, Los Angeles, California, USA. 45. Institute for Molecular Bioscience, University of Queensland, QLD, Australia. 46. Medical Research Council Lifecourse Epidemiology Unit, University of Southampton, Southampton, SO17 1BJ, UK. 47. Division of Infection Immunity and Respiratory Medicine, School of Biological Sciences, The University of Manchester, Manchester Academic Health Science Centre, and Manchester University NHS Foundation Trust, Manchester, M13 9NT, UK. 48. Department of Paediatrics, Imperial College London, London, SW7 2AZ, UK. 49. Avera Institute for Human Genetics, Sioux Falls, South Dakota, USA. 50. Department of Nutrition and Dietetics, School of Health Science and Education, Harokopio University, Athens, 17671, Greece. 51. Department of Pediatrics, Division of Respiratory Medicine, Erasmus MC, University Medical Center Rotterdam, Rotterdam, The Netherlands. 52. Department of Pediatrics, Division of Neonatology, Erasmus MC, University Medical Center Rotterdam, Rotterdam, The Netherlands. 53. School of Human Sciences, The University of Western Australia, WA, Australia. 54. West Australian Sleep Disorders Research Institute, Department of Pulmonary Physiology & Sleep Medicine, Sir Charles Gairdner Hospital, WA, Australia. 55. Copenhagen Prospective Studies on Asthma in Childhood, Herlev and Gentofte Hospital, University of Copenhagen, Denmark. 56. Department of Bio and Health Informatics, Technical University of Denmark, Denmark. 57. National Institute for Health and Welfare, Helsinki, 00271, Finland. 58. Department of General Practice and Primary Health Care, University of Helsinki and Helsinki University Hospital, Helsinki, 00014, Finland. 59. Folkhälsan Research Center, Helsinki, 00250, Finland. 60. Sidra Medicine Research Center, Sidra Medicine, Doha, Qatar. 61. Department of Epidemiology Research, Statens Serum Institute, Copenhagen, DK-2300, Denmark. 62. Department of Radiology, Children's Hospital Los Angeles, Los Angeles, CA 90027, USA. 63. Population Health Sciences, Bristol Medical School, University of Bristol, Bristol, BS8 2BN, UK. 64. Institute for Molecular Medicine Finland FIMM, University of Helsinki, Helsinki, Finland. 65. Department of Pediatrics, University of California San Francisco School of Medicine, San Francisco, CA 94143, USA. 66. Department of Pediatrics, Perelman School of Medicine, University of Pennsylvania, Philadelphia, PA 19104, USA. 67. Department of Psychiatry, University of Groningen, University Medical Center Groningen, Groningen, The Netherlands. 68. NIHR Exeter Clinical Research Facility, University of Exeter Medical School and Royal Devon and Exeter NHS Foundation Trust, Exeter, EX2 5DW, UK. 69. Department of Medicine, Division of Endocrinology, Metabolism, and Molecular Medicine, Feinberg School of Medicine, Northwestern University, Chicago, IL 60611, USA. 70. Department of Child and Adolescent Psychiatry, Psychosomatics and Psychotherapy, University Hospital Essen, University of Duisburg-Essen, Essen, 45141, Germany. 71. Institute of Epidemiology, Helmholtz Zentrum München - German Research Center for Environmental Health, Neuherberg, Germany. 72. Institute and Outpatient Clinic for Occupational, Social and Environmental Medicine, University Hospital of Ludwig Maximilians University, Munich, Germany. 73. KG Jebsen Center for Diabetes Research, Department of Clinical Science, University of Bergen, Bergen, N-5020, Norway. 74. Department of Pediatrics, Haukeland University Hospital, Bergen, 5021, Norway. 75. Department of Genetics and Bioinformatics, Domain of Health Data and Digitalisation, Norwegian Institute of Public Health, Oslo, N-0473, Norway. 76. Department of Paediatrics and Adolescent Medicine, Aarhus University Hospital, Aarhus N, DK-8200, Denmark. 77. Programs in Metabolism and Medical & Population Genetics, Broad Institute of Harvard and MIT, Cambridge, MA 02142, USA. 78. Department of Genetics, Harvard Medical School, Boston, MA 02115, USA. 79. Division of Endocrinology and Center for Basic and Translational Obesity Research, Boston Children's Hospital, Boston, MA, 02115, USA. 80. Department of Population Medicine, Harvard Pilgrim Health Care Institute, Harvard Medical School, Boston, MA 02215, USA. 81. Diabetes Center, Massachusetts General Hospital, Boston, MA 02114, USA. 82. Department of Medicine, Universite de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada. 83. Institute of Nutritional Science, University of Potsdam, Nuthetal, 14558, Germany. 84. The First Affiliated Hospital of Jinan University, Guangzhou, 510630, China. 85. Human Development & Health, Faculty of Medicine, University of Southampton, Southampton, SO17 1BJ, UK. 86. Telethon Kids Institute (TKI), The University of Western Australia, WA, Australia. 87. Australian Centre for Precision Health, University of South Australia Cancer Research Institute, Adelaide, SA, 5001, Australia. 88. South Australian Health and Medical Research Institute, Adelaide, SA, 5001, Australia. 89. Department of Statistics and Computational Research, Universitat de València, Spain. 90. Epidemiology and Environmental Health Joint Research Unit, FISABIO-Universitat Jaume I-Universitat de València, Spain. 91. Department of Medical Genetics, Haukeland University Hospital, Bergen, Norway. 92. Department of Genetics and Bioinformatics, Norwegian Institute of Public Health, Oslo, N-0403, Norway. 93. Centre for Fertility and Health, Norwegian Institute of Public Health, Oslo, N-0403, Norway. 94. Department of Global Public Health and Primary Care, University of Bergen, Norway. 95. Department of Clinical Physiology, Tampere University Hospital, Tampere, Finland. 96. Department of Clinical Physiology, Finnish Cardiovascular Research Center - Tampere, Faculty of Medicine and Life Sciences, University of Tampere, Tampere, Finland. 97. Division of Gastroenterology, Hepatology and Nutrition, Cincinnati Children's Hospital Medical Center, Cincinnati, OH 45229, USA. 98. Department of Public Health, University of Helsinki, Helsinki, Finland. 99. Department of Epidemiology and Biostatistics, School of Public Health, Imperial College London, London, UK. 100. Observational & Pragmatic Research Institute Pte Ltd, Singapore, Singapore. 101. University of Groningen, University Medical Center Groningen, Department of Pediatric Pulmonology and Pediatric Allergology, Beatrix Children's Hospital, GRIAC Research Institute Groningen, Groningen, The Netherlands. 102. Pediatric Research Center, Department of Women's & Child Health, University of Leipzig, Leipzig, 04109, Germany. 103. IFB Adiposity Diseases, University of Leipzig, Leipzig, 04109, Germany. 104. Department of Child Health, School of Medicine, Cardiff University, Cardiff, CF10 3AT, UK. 105. Danish Pediatric Asthma Center, Copenhagen University Hospital, Gentofte, DK-2100, Denmark. 106. Institute of Environmental Medicine, Karolinska Institutet, Sweden. 107. Department of Public Health Epidemiology, Unit of Chronic Disease Epidemiology, Swiss Tropical and Public Health Institute, Basel, University of Basel, Switzerland. 108. Institute of Social and Preventive Medicine, Lausanne University Hospital (CHUV), Lausanne, 1011, Switzerland. 109. Swiss Institute of Bioinformatics, Lausanne, 1015, Switzerland. 110. Helsinki Collegium for Advanced Studies, University of Helsinki, Helsinki, Finland. 111. Department of Psychology and Logopedics, Faculty of Medicine, University of Helsinki, Helsinki, Finland. 112. Division of Endocrinology, Department of Medicine, Creighton University, Omaha, NE 68178, USA. 113. School of Medicine Sciences, Örebro University, Sweden. 114. Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Sweden. 115. Department of Clinical Chemistry, Fimlab Laboratories, Tampere University Hospital, Tampere, Finland. 116. Department of Clinical Chemistry, Finnish Cardiovascular Research Center - Tampere, Faculty of Medicine and Life Sciences, University of Tampere, Tampere, 33520, Finland. 117. Li Ka Shing Centre for Health Information and Discovery, The Big Data Institute, University of Oxford, Oxford, OX3 7LF, UK. 118. The Broad Institute of Harvard and MIT, Cambridge, USA. 119. Center for Clinical Research and Prevention, Bispebjerg and Frederiksberg Hospital, The Capital Region, Frederiksberg, 2000, Denmark. 120. Department of Clinical Medicine, Faculty of Health and Medical Sciences, University of Copenhagen, Copenhagen, Denmark. 121. Centre for Ethics, Law and Mental Health, University of Gothenburg, Sweden. 122. Gillberg Neuropsychiatry Centre, University of Gothenburg, Sweden. 123. Department of Medicine and Therapeutics, The Chinese University of Hong Kong, Hong Kong, China. 124. Li Ka Shing Institute of Health

- Sciences, The Chinese University of Hong Kong, Hong Kong, China. 125. Hong Kong Institute of Diabetes and Obesity, The Chinese University of Hong Kong, Hong Kong, China. 126. Estonian Genome Center, University of Tartu, Tartu, 50090, Estonia. 127. Institute for Social Science Research, University of Queensland, QLD, Australia. 128. QIMR Berghofer Medical Research Institute, QLD, Australia. 129. Amsterdam Reproduction and Development, Amsterdam, The Netherlands. 130. Centre for Genetic Origins of Health and Disease (GOHAD), The University of Western Australia, Crawley, WA, 6000, Australia. 131. Department of Medicine, Stanford School of Medicine, Stanford, CA 94305, USA. 132. Sachs' Children's Hospital, Sweden. 133. Department of Genetics, University of North Carolina, Chapel Hill, NC 27599, USA. 134. Department of Public Health, Section of Epidemiology, Faculty of Health and Medical Sciences, University of Copenhagen, Copenhagen, DK-1014, Denmark. 135. Department of Biostatistics, University of Liverpool, Liverpool, L69 3GL, UK. 136. Department of Pediatrics, University of Iowa, Iowa City, IA 52242, USA. 137. School of Public Health, The University of Queensland, QLD, Australia. 138. Research Unit for Gynaecology and Obstetrics, Institute of Clinical Research, University of Southern Denmark, Odense, DK-5000, Denmark. 139. Department of Epidemiology, University of Groningen, University Medical Center Groningen, Groningen, The Netherlands. 140. William Harvey Research Institute, Barts and the London School of Medicine and Dentistry, Queen Mary University of London, London, EC1M 6BQ, UK. 141. Medical Research Council (MRC), Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology & Neuroscience, King's College London, London, SE5 8AF, UK. 142. Division of Pediatric Endocrinology, Diabetes, and Metabolism, Department of Pediatrics, Columbia University Medical Center, New York, NY 10032, USA. 143. Obesity Prevention Program, Department of Population Medicine, Harvard Medical School and Harvard Pilgrim Health Care Institute, Boston, MA 02215, USA. 144. Research Centre of Applied and Preventive Cardiovascular Medicine, University of Turku, Turku, 20014, Finland. 145. Paavo Nurmi Centre, Sports and Exercise Medicine Unit, Department of Physical Activity and Health, University of Turku, Turku, Finland. 146. Wellcome Sanger Institute, Hinxton, Cambridgeshire, CB10 1HH, UK. 147. School of Medicine and Public Health, Faculty of Medicine and Health, The University of Newcastle, Callaghan, NSW, 2308, Australia. 148. Centre for Occupational and Environmental Medicine, Stockholm County Council, Sweden. 149. MRC Social, Genetic and Developmental Psychiatry Centre, King's College London, London, UK. 150. Section of Genomics of Common Disease, Department of Medicine, Imperial College London, London, SW7 2AZ, UK. 151. Department of Psychology, University of Jyväskylä, Jyväskylä, Finland. 152. Department of Clinical Physiology and Nuclear Medicine, Turku University Hospital, Turku, 20520, Finland. 153. BHF Centre for Cardiovascular Science, University of Edinburgh, Queen's Medical Research Institute, Edinburgh, EH16 4TJ, UK. 154. Department of Internal Medicine, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 155. Department of Psychology, Mid Sweden University, Östersund, SE-831 25, Sweden. 156. Department of Psychological and Brain Sciences, Indiana University, Bloomington, Indiana, USA. 157. Department of Medicine, Division of Endocrinology, Boston Children's Hospital, Boston, MA 02115, USA. 158. Program in Medical and Population Genetics, Broad Institute of Harvard and MIT, Cambridge, MA 02142, USA. 159. Center for Basic and Translational Obesity Research, Boston Children's Hospital, Boston, MA 02115, USA. 160. Subdirección de Salud Pública y Adicciones de Gipuzkoa, San Sebastián, Spain. 161. Instituto de Investigación Sanitaria Biodonostia, San Sebastián, Spain. 162. Saw Swee Hock School of Public Health, National University of Singapore, National University Health System, Singapore, 119077, Singapore. 163. Singapore Eye Research Institute, Singapore, 168751, Singapore. 164. Metro North Mental Health Service, QLD, Australia. 165. Queensland Centre for Mental Health Research, QLD, Australia. 166. Department of Epidemiology, Cancer Center, University of Hawaii (Manoa), Honolulu, Hawaii, 96813, USA. 167. Department of Obstetrics and Gynecology, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 168. Population Health Research Institute, St George's University of London, London, SW17 0RE, UK. 169. School of Physiotherapy and Exercise Science, Faculty of Health Sciences, Curtin University, Perth, WA, Australia. 170. Helsinki University Central Hospital, University of Helsinki, Helsinki, Finland. 171. Clinicum, University of Helsinki, Helsinki, Finland. 172. Department of Statistics and Applied Probability, National University of Singapore, Singapore, 117546, Singapore. 173. Life Sciences Institute, National University of Singapore, Singapore, 117456, Singapore. 174. Division of Metabolic and Nutritional Medicine, Dr. von Hauner Children's Hospital, University of Munich Medical Center, Munich, 80337, Germany. 175. ib-salut, Area de Salut de Menorca, Spain. 176. Fundació Institut d'Investigació Sanitària Illes Balears – IdISBa, Spain. 177. European Centre for Environment and Human Health, University of Exeter, Truro, TR1 3HD, UK. 178. Department of Medicine, University of Turku, Turku, Finland. 179. Division of Medicine, Turku University Hospital, Turku, Finland. 180. Center for Genomic Regulation (CRG), Barcelona Institute of Science and Technology, Spain. 181. Barcelonabeta Brain Research Center (BBRC), Pasqual Maragall Foundation, Barcelona, Spain. 182. Groningen Research Institute for Asthma and COPD (GRIAC), University of Groningen, University Medical Center Groningen, Groningen, 9700 RB, The Netherlands. 183. Department of Public Health, Amsterdam Public Health Research Institute, Academic Medical Center (AMC), University of Amsterdam, Amsterdam, 1105 AZ, The Netherlands. 184. Institute of Medical Statistics and Epidemiology, Technical University Munich, Munich, D-80333, Germany. 185. Institute of Medical Informatics, Biometry and Epidemiology, Ludwig Maximilians University, Munich, 81377, Germany. 186. Usher Institute for Population Health Sciences and Informatics, University of Edinburgh, Edinburgh, EH8 9AG, UK. 187. MRC Human Genetics Unit, Institute of Genetics and Molecular Medicine, University of Edinburgh, Edinburgh, EH4 2XU, UK. 188. Queensland Brain Institute, University of Queensland, QLD, Australia. 189. Genetics of Complex Traits, University of Exeter Medical School, Royal Devon & Exeter Hospital, Exeter, EX2 5DW, UK. 190. Department of Clinical Epidemiology and Biostatistics, Amsterdam Public Health Research Institute, Academic Medical Center, University of Amsterdam, Amsterdam, The Netherlands, 1105 AZ, The Netherlands. 191. Division of Gastroenterology, Hepatology and Nutrition, The Children's Hospital of Philadelphia, Philadelphia, PA 19104, USA. 192. Department of Clinical Physiology and Nuclear Medicine, Kuopio University Hospital, Kuopio, 70210, Finland. 193. Kuopio Research Institute of Exercise Medicine, Kuopio, 70100, Finland. 194. IMIM (Hospital del Mar Medical Research Institute), Barcelona, 08003, Spain. 195. Biocenter Oulu, University of Oulu, Oulu, 90220, Finland. 196. Department of Genomics of Complex Diseases, Imperial College, London, UK. 197. Department of Obstetrics and Gynecology, Sahlgrenska Academy, University of Gothenburg, Diagnosvägen 15, SE-416 85 Gothenburg, Sweden. 198. Norwegian Institute of Public Health, Norway. 199. Bristol NIHR Biomedical Research Centre, Bristol, UK. 200. Department of Paediatrics, University of Cambridge, Cambridge, CB2 0QQ, UK. 201. Child and Adolescent Psychiatry, Erasmus Medical Center, Rotterdam, The Netherlands. 202. Social and Behavioral Sciences, Harvard TH Chan School of Public Health, Harvard University, Boston, USA. 203. Unit of Primary Care, Oulu University Hospital, Oulu, 90220, Finland. 204. Department of Life Sciences, College of Health and Life Sciences, Brunel University London, Middlesex, UB8 3PH, UK. 205. Oxford National Institute for Health Research (NIHR) Biomedical Research Centre, Churchill Hospital, Oxford, OX3 7LE, UK.

EGG Membership *Members as of July 2018 are listed in alphabetical order.*

Linda S Adair¹, Emma Ahlqvist², Tarunveer S Ahluwalia^{3,4,5}, Peter Almgren², Wei Ang⁶, Mustafa Atalay⁷, Robin N Beaumont⁸, Jacques S Beckmann⁹, Hans Bisgaard³, Tom Bond¹⁰, Klaus Bønnelykke³, Dorret I Boomsma^{11,12,13,14}, Judith B Borja^{15,16}, Jonathan P Bradfield^{17,18}, Mariona Bustamante^{19,20,21}, Alana Cavadino^{22,23}, Pimphen Charoen^{10,24}, Lachlan Coin²⁵, Cyrus Cooper²⁶, Diana L Cousminer^{27,28}, John A Curtin²⁹, Adnan Custovic³⁰, Shikta Das³¹, Felix R Day³¹, N Maneka De Silva¹⁰, George V Dedoussis³², Paul Elliott¹⁰, Johan G Eriksson^{33,34,35}, David M Evans^{36,37,38}, João Fadista³⁹, Bjarke Feenstra³⁹, Janine F Felix^{40,41,42}, Timothy M Frayling⁸, Rachel M Freathy^{8,36}, Romy Gaillard⁴¹, Frank Geller³⁹, Vincente Gilsanz⁴³, Struan FA Grant^{17,27,28,44}, Niels Grunup⁴, Leif Groop^{2,45}, Monica Guxens^{19,20,21}, Dexter Hadley⁴⁶, Hakon Hakonarson^{17,27,44}, Torben Hansen⁴, Andrew T Hattersley^{8,47}, M Geoffrey Hayes⁴⁸, Johannes Hebebrand⁴⁹, Joachim Heinrich^{50,51}, Øyvind Helgeland^{52,53,54}, Tine B Henriksen⁵⁵, Anke Hinney⁴⁹, Joel N Hirschhorn^{56,57,58}, Marie-France Hivert^{59,60,61}, Berthold Hocher^{62,63}, John W Holloway⁶⁴, Momoko Horikoshi^{65,66,67}, Jouke-Jan Hottenga^{11,12,14}, Elina Hyppönen^{23,68,69}, Bo Jacobsson^{54,70}, Vincent WV Jaddoe^{40,41,42}, Marjo-Riitta Järvelin^{10,71,72,73,74}, Stefan Johansson^{52,75}, Heidi J Kalkwarf⁷⁶, Marjan Kerkhof⁷⁷, Antje Körner^{78,79}, Sailesh Kotecha⁸⁰, Eskil Kreiner-Møller^{3,81}, Benard Kulohoma⁶⁵, Zoltán Kutalik^{82,83}, Timo A Lakka^{7,84,85}, Joan M Lappe⁸⁶, Debbie A Lawlor^{36,37,87}, Terho Lehtimäki^{88,89}, Alexandra M Lewin¹⁰, Cecilia M Lindgren^{65,90,91}, Virpi Lindi⁷, Allan Linneberg^{92,93}, Xueping Liu³⁹, Jun Liu⁴¹, William L Lowe Jr⁴⁸, Ronald CW Ma^{94,95,96}, Aurélien Macé⁸², Reedik Mägi⁹⁷, Per Magnus⁹⁸, Anubha Mahajan^{65,66}, Nina S McCarthy⁹⁹, Mark I McCarthy^{65,66,100}, Mads Melbye^{39,101}, Karen L Mohlke¹⁰², Claire Monnereau^{40,41,42}, Dennis O Mook-Kanamori^{103,104}, Camilla S Morgen¹⁰⁵, Andrew P Morris^{65,97,106}, Jeffrey C Murray¹⁰⁷, Ronny Myhre¹⁰⁸, Pål R Njølstad^{52,53}, Ellen A Nohr¹⁰⁹, Ioanna Ntalla¹¹⁰, Paul O'Reilly¹¹¹, Sharon E Oberfield¹¹², Emily Oken¹¹³, Ken K Ong^{31,114}, Kalliope Panoutsopoulou¹¹⁵, Oluf Pedersen⁴, Craig E Pennell¹¹⁶, John RB Perry³¹, Niina Pitkänen¹¹⁷, Beate St Pourcain^{36,118}, Christine Power²³, Rashmi B Prasad², Inga Prokopenko^{65,119}, Olli T Raitakari^{117,120}, Rebecca M Reynolds¹²¹, Rebecca C Richmond^{36,37}, Alina Rodriguez^{10,122}, Rany Salem^{57,123,124,125}, Seang-Mei Saw^{126,127}, Theresia M Schnurr⁴, Sylvain Sebert^{10,71,73,128}, John A Shepherd¹²⁹, Angela Simpson²⁹, Line Skotte³⁹, Thorkild IA Sørensen^{4,36,105}, Marie Standl⁵⁰, Eric AP Steegers¹³⁰, David P Strachan¹³¹, Jordi Sunyer^{19,20,21,132}, Michelle Taylor^{36,37}, Yik-Ying Teo^{126,133,134}, Elisabeth Thiering^{50,135}, Nicholas J Timpson^{36,37}, Jessica Tyrrell^{8,136}, André G Uitterlinden^{40,41,137}, Cornelia M van Duijn⁴¹, Suzanne Voegelzang^{40,41,42}, Tanja GM Vrijkotte¹³⁸, Carol A Wang¹¹⁶, Nicole M Warrington³⁸, William J Watkins⁸⁰, H-Erich Wichmann^{50,139,140}, Elisabeth E Widén⁴⁵, Gonneke Willemsen^{11,12,14}, James F Wilson^{141,142}, Hanieh Yaghootkar¹⁴³, Mohammad Hadi Zafarmand^{138,144}, Eleftheria Zeggini¹¹⁵, Babette S Zemel¹⁴⁵

1. Department of Nutrition, University of North Carolina, Chapel Hill, NC 27599, USA. 2. Department of Clinical Sciences, Diabetes and Endocrinology, Lund University Diabetes Centre, Malmö, SE-205 02, Sweden. 3. COPSAC, Copenhagen Prospective Studies on Asthma in Childhood, Herlev and Gentofte Hospital, University of Copenhagen, Copenhagen, 2900 Hellerup, Denmark. 4. Novo Nordisk Foundation Center for Basic Metabolic Research, Section of Metabolic Genetics, Faculty of Health and Medical Sciences, University of Copenhagen, Copenhagen, DK-2200, Denmark. 5. Steno Diabetes Center Copenhagen, Gentofte, 2820, Denmark. 6. Division of Obstetrics and Gynaecology, The University of Western Australia, Crawley, WA, 6009, Australia. 7. Institute of Biomedicine, Physiology, University of Eastern Finland, Kuopio, 70211, Finland. 8. Institute of Biomedical and Clinical Science, University of Exeter Medical School, University of Exeter, Royal Devon and Exeter Hospital, Exeter, EX2 5DW, UK. 9. University of Lausanne, Lausanne, CH-1015, Switzerland. 10. Department of Epidemiology and Biostatistics, MRC-PHE Centre for Environment &

Health, School of Public Health, Imperial College London, London, W2 1PG, UK. 11. Department of Biological Psychology, Vrije Universiteit Amsterdam, Amsterdam, 1081 BT, The Netherlands. 12. Amsterdam Public Health, Amsterdam, The Netherlands. 13. Amsterdam Reproduction and Development, Amsterdam, The Netherlands. 14. Netherlands Twin Register, Department of Biological Psychology, VU University, Amsterdam, 1081 HV, The Netherlands. 15. USC-Office of Population Studies Foundation, Inc., University of San Carlos, Cebu City, 6000, Philippines. 16. Department of Nutrition and Dietetics, University of San Carlos, Cebu City, 6000, Philippines. 17. Center for Applied Genomics, The Children's Hospital of Philadelphia, Philadelphia, PA 19104, USA. 18. Quantinuum Research LLC, San Diego, CA, 92101, USA. 19. ISGlobal, Institute for Global Health, Barcelona, 08003, Spain. 20. Universitat Pompeu Fabra (UPF), Barcelona, 08003, Spain. 21. CIBER de Epidemiología y Salud Pública (CIBERESP), Madrid, 28029, Spain. 22. Section of Epidemiology & Biostatistics, School of Population Health, University of Auckland, Auckland, New Zealand. 23. Population, Policy and Practice, UCL Great Ormond Street Institute of Child Health, University College London, London, WC1N 1EH, UK. 24. Department of Tropical Hygiene, Faculty of Tropical Medicine, Mahidol University, Bangkok, 10400, Thailand. 25. Institute for Molecular Bioscience, University of Queensland, QLD, Australia. 26. Medical Research Council Lifecourse Epidemiology Unit, University of Southampton, Southampton, SO17 1BJ, UK. 27. Division of Human Genetics, The Children's Hospital of Philadelphia, Philadelphia, PA 19104, USA. 28. Department of Genetics, Perelman School of Medicine, University of Pennsylvania, Philadelphia, 19104, USA. 29. Division of Infection Immunity and Respiratory Medicine, School of Biological Sciences, The University of Manchester, Manchester Academic Health Science Centre, and Manchester University NHS Foundation Trust, Manchester, M13 9NT, UK. 30. Department of Paediatrics, Imperial College London, London, SW7 2AZ, UK. 31. MRC Epidemiology Unit, University of Cambridge School of Clinical Medicine, Cambridge, CB2 0QQ, UK. 32. Department of Nutrition and Dietetics, School of Health Science and Education, Harokopio University, Athens, 17671, Greece. 33. National Institute for Health and Welfare, Helsinki, 00271, Finland. 34. Department of General Practice and Primary Health Care, University of Helsinki and Helsinki University Hospital, Helsinki, 00014, Finland. 35. Folkhälsan Research Center, Helsinki, 00250, Finland. 36. Medical Research Council Integrative Epidemiology Unit at the University of Bristol, Bristol, BS8 2BN, UK. 37. Population Health Sciences, Bristol Medical School, University of Bristol, Bristol, BS8 2BN, UK. 38. University of Queensland Diamantina Institute, Translational Research Institute, Brisbane, QLD, 4072, Australia. 39. Department of Epidemiology Research, Statens Serum Institute, Copenhagen, DK-2300, Denmark. 40. The Generation R Study Group, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 41. Department of Epidemiology, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 42. Department of Pediatrics, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 43. Department of Radiology, Children's Hospital Los Angeles, Los Angeles, CA 90027, USA. 44. Department of Pediatrics, Perelman School of Medicine, University of Pennsylvania, Philadelphia, PA 19104, USA. 45. Institute for Molecular Medicine Finland FIMM, University of Helsinki, Helsinki, Finland. 46. Department of Pediatrics, University of California San Francisco School of Medicine, San Francisco, CA 94143, USA. 47. NIHR Exeter Clinical Research Facility, University of Exeter Medical School and Royal Devon and Exeter NHS Foundation Trust, Exeter, EX2 5DW, UK. 48. Department of Medicine, Division of Endocrinology, Metabolism, and Molecular Medicine, Feinberg School of Medicine, Northwestern University, Chicago, IL 60611, USA. 49. Department of Child and Adolescent Psychiatry, Psychosomatics and Psychotherapy, University Hospital Essen, University of Duisburg-Essen, Essen, 45141, Germany. 50. Institute of Epidemiology, Helmholtz Zentrum München - German Research Center for

- Environmental Health, Neuherberg, Germany. 51. Institute and Outpatient Clinic for Occupational, Social and Environmental Medicine, University Hospital of Ludwig Maximilians University, Munich, Germany. 52. KG Jebsen Center for Diabetes Research, Department of Clinical Science, University of Bergen, Bergen, N-5020, Norway. 53. Department of Pediatrics, Haukeland University Hospital, Bergen, 5021, Norway. 54. Department of Genetics and Bioinformatics, Domain of Health Data and Digitalisation, Norwegian Institute of Public Health, Oslo, N-0473, Norway. 55. Department of Paediatrics and Adolescent Medicine, Aarhus University Hospital, Aarhus N, DK-8200, Denmark. 56. Programs in Metabolism and Medical & Population Genetics, Broad Institute of Harvard and MIT, Cambridge, MA 02142, USA. 57. Department of Genetics, Harvard Medical School, Boston, MA 02115, USA. 58. Division of Endocrinology and Center for Basic and Translational Obesity Research, Boston Children's Hospital, Boston, MA, 02115, USA. 59. Department of Population Medicine, Harvard Pilgrim Health Care Institute, Harvard Medical School, Boston, MA 02215, USA. 60. Diabetes Center, Massachusetts General Hospital, Boston, MA 02114, USA. 61. Department of Medicine, Universite de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada. 62. Institute of Nutritional Science, University of Potsdam, Nuthetal, 14558, Germany. 63. The First Affiliated Hospital of Jinan University, Guangzhou, 510630, China. 64. Human Development & Health, Faculty of Medicine, University of Southampton, Southampton, SO17 1BJ, UK. 65. Wellcome Centre for Human Genetics, University of Oxford, Oxford, OX3 7BN, UK. 66. Oxford Centre for Diabetes, Endocrinology and Metabolism, University of Oxford, Oxford, OX3 7LE, UK. 67. RIKEN, Centre for Integrative Medical Sciences, Laboratory for Endocrinology, Metabolism and Kidney diseases, Yokohama, Kanagawa, 230-0045, Japan. 68. Australian Centre for Precision Health, University of South Australia Cancer Research Institute, Adelaide, SA, 5001, Australia. 69. South Australian Health and Medical Research Institute, Adelaide, SA, 5001, Australia. 70. Department of Obstetrics and Gynecology, Sahlgrenska Academy, University of Gothenburg, Diagnosvägen 15, SE-416 85 Gothenburg, Sweden. 71. Biocenter Oulu, University of Oulu, Oulu, 90220, Finland. 72. Unit of Primary Care, Oulu University Hospital, Oulu, 90220, Finland. 73. Center for Life Course Health Research, Faculty of Medicine, University of Oulu, Oulu, FI-90014, Finland. 74. Department of Life Sciences, College of Health and Life Sciences, Brunel University London, Middlesex, UB8 3PH, UK. 75. Department of Medical Genetics, Haukeland University Hospital, Bergen, Norway. 76. Division of Gastroenterology, Hepatology and Nutrition, Cincinnati Children's Hospital Medical Center, Cincinnati, OH 45229, USA. 77. Observational & Pragmatic Research Institute Pte Ltd, Singapore, Singapore. 78. Pediatric Research Center, Department of Women's & Child Health, University of Leipzig, Leipzig, 04109, Germany. 79. IFB Adiposity Diseases, University of Leipzig, Leipzig, 04109, Germany. 80. Department of Child Health, School of Medicine, Cardiff University, Cardiff, CF10 3AT, UK. 81. Danish Pediatric Asthma Center, Copenhagen University Hospital, Gentofte, DK-2100, Denmark. 82. Institute of Social and Preventive Medicine, Lausanne University Hospital (CHUV), Lausanne, 1011, Switzerland. 83. Swiss Institute of Bioinformatics, Lausanne, 1015, Switzerland. 84. Department of Clinical Physiology and Nuclear Medicine, Kuopio University Hospital, Kuopio, 70210, Finland. 85. Kuopio Research Institute of Exercise Medicine, Kuopio, 70100, Finland. 86. Division of Endocrinology, Department of Medicine, Creighton University, Omaha, NE 68178, USA. 87. Bristol NIHR Biomedical Research Centre, Bristol, UK. 88. Department of Clinical Chemistry, Fimlab Laboratories, Tampere University Hospital, Tampere, Finland. 89. Department of Clinical Chemistry, Finnish Cardiovascular Research Center - Tampere, Faculty of Medicine and Life Sciences, University of Tampere, Tampere, 33520, Finland. 90. Li Ka Shing Centre for Health Information and Discovery, The Big Data Institute, University of Oxford, Oxford, OX3 7LF, UK. 91. The Broad Institute of Harvard and MIT, Cambridge, USA. 92. Center for Clinical Research and Prevention, Bispebjerg and Frederiksberg Hospital, The Capital Region, Frederiksberg, 2000, Denmark. 93. Department of Clinical Medicine, Faculty of Health and Medical Sciences, University of Copenhagen, Copenhagen, Denmark. 94. Department of Medicine and Therapeutics, The Chinese University of Hong Kong, Hong Kong, China. 95. Li Ka Shing Institute of Health Sciences, The Chinese University of Hong Kong, Hong Kong, China. 96. Hong Kong Institute of Diabetes and Obesity, The Chinese University of Hong Kong, Hong Kong, China. 97. Estonian Genome Center, University of Tartu, Tartu, 50090, Estonia. 98. Centre for Fertility and Health, Norwegian Institute of Public Health, Oslo, N-0403, Norway. 99. Centre for Genetic Origins of Health and Disease (GOHaD), The University of Western Australia, Crawley, WA, 6000, Australia. 100. Oxford National Institute for Health Research (NIHR) Biomedical Research Centre, Churchill Hospital, Oxford, OX3 7LE, UK. 101. Department of Medicine, Stanford School of Medicine, Stanford, CA 94305, USA. 102. Department of Genetics, University of North Carolina, Chapel Hill, NC 27599, USA. 103. Department of Clinical Epidemiology, Leiden University Medical Center, Leiden, 2333 ZA, The Netherlands. 104. Department of Public Health and Primary Care, Leiden University Medical Center, Leiden, 2333 ZA, The Netherlands. 105. Department of Public Health, Section of Epidemiology, Faculty of Health and Medical Sciences, University of Copenhagen, Copenhagen, Copenhagen, DK-1014, Denmark. 106. Department of Biostatistics, University of Liverpool, Liverpool, L69 3GL, UK. 107. Department of Pediatrics, University of Iowa, Iowa City, IA 52242, USA. 108. Department of Genetics and Bioinformatics, Norwegian Institute of Public Health, Oslo, N-0403, Norway. 109. Research Unit for Gynaecology and Obstetrics, Institute of Clinical Research, University of Southern Denmark, Odense, DK-5000, Denmark. 110. William Harvey Research Institute, Barts and the London School of Medicine and Dentistry, Queen Mary University of London, London, EC1M 6BQ, UK. 111. Medical Research Council (MRC), Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology & Neuroscience, King's College London, London, SE5 8AF, UK. 112. Division of Pediatric Endocrinology, Diabetes, and Metabolism, Department of Pediatrics, Columbia University Medical Center, New York, NY 10032, USA. 113. Obesity Prevention Program, Department of Population Medicine, Harvard Medical School and Harvard Pilgrim Health Care Institute, Boston, MA 02215, USA. 114. Department of Paediatrics, University of Cambridge, Cambridge, CB2 0QQ, UK. 115. Wellcome Sanger Institute, Hinxton, Cambridgeshire, CB10 1HH, UK. 116. School of Medicine and Public Health, Faculty of Medicine and Health, The University of Newcastle, Callaghan, NSW, 2308, Australia. 117. Research Centre of Applied and Preventive Cardiovascular Medicine, University of Turku, Turku, 20014, Finland. 118. Max Planck Institute for Psycholinguistics, Nijmegen, 6525 XD, The Netherlands. 119. Section of Genomics of Common Disease, Department of Medicine, Imperial College London, London, SW7 2AZ, UK. 120. Department of Clinical Physiology and Nuclear Medicine, Turku University Hospital, Turku, 20520, Finland. 121. BHF Centre for Cardiovascular Science, University of Edinburgh, Queen's Medical Research Institute, Edinburgh, EH16 4TJ, UK. 122. Department of Psychology, Mid Sweden University, Östersund, SE-831 25, Sweden. 123. Department of Medicine, Division of Endocrinology, Boston Children's Hospital, Boston, MA 02115, USA. 124. Program in Medical and Population Genetics, Broad Institute of Harvard and MIT, Cambridge, MA 02142, USA. 125. Center for Basic and Translational Obesity Research, Boston Children's Hospital, Boston, MA 02115, USA. 126. Saw Swee Hock School of Public Health, National University of Singapore, National University Health System, Singapore, 119077, Singapore. 127. Singapore Eye Research Institute, Singapore, 168751, Singapore. 128. Department of Genomics of Complex Diseases, Imperial College, London, UK. 129. Department of Epidemiology, Cancer Center, University of Hawaii (Manoa), Honolulu, Hawaii, 96813, USA. 130. Department of Obstetrics and Gynecology, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 131.

Population Health Research Institute, St George's University of London, London, SW17 0RE, UK. 132. IMIM (Hospital del Mar Medical Research Institute), Barcelona, 08003, Spain. 133. Department of Statistics and Applied Probability, National University of Singapore, Singapore, 117546, Singapore. 134. Life Sciences Institute, National University of Singapore, Singapore, 117456, Singapore. 135. Division of Metabolic and Nutritional Medicine, Dr. von Hauner Children's Hospital, University of Munich Medical Center, Munich, 80337, Germany. 136. European Centre for Environment and Human Health, University of Exeter, Truro, TR1 3HD, UK. 137. Department of Internal Medicine, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 138. Department of Public Health, Amsterdam Public Health Research Institute, Academic Medical Center (AMC), University of Amsterdam, Amsterdam, 1105 AZ, The Netherlands. 139. Institute of Medical Statistics and Epidemiology, Technical University Munich, Munich, D-80333, Germany. 140. Institute of Medical Informatics, Biometry and Epidemiology, Ludwig Maximilians University, Munich, 81377, Germany. 141. Usher Institute for Population Health Sciences and Informatics, University of Edinburgh, Edinburgh, EH8 9AG, UK. 142. MRC Human Genetics Unit, Institute of Genetics and Molecular Medicine, University of Edinburgh, Edinburgh, EH4 2XU, UK. 143. Genetics of Complex Traits, University of Exeter Medical School, Royal Devon & Exeter Hospital, Exeter, EX2 5DW, UK. 144. Department of Clinical Epidemiology and Biostatistics, Amsterdam Public Health Research Institute, Academic Medical Center, University of Amsterdam, Amsterdam, The Netherlands, 1105 AZ, The Netherlands. 145. Division of Gastroenterology, Hepatology and Nutrition, The Children's Hospital of Philadelphia, Philadelphia, PA 19104, USA.

EAGLE Membership *Members as of July 2018 are listed in alphabetical order.*

Tarunveer S Ahluwalia^{1,3}, Juha Auvinen⁴, Meike Bartels^{5,6,7}, Jose Ramon Bilbao^{8,9,10}, Hans Bisgaard¹, Klaus Bønnelykke¹, Dorret I Boomsma^{5,6,7,11}, Jonathan P Bradfield^{12,13}, Mariona Bustamante^{14,15,16}, Zhanghua Chen¹⁷, John A Curtin¹⁸, Adnan Custovic¹⁹, George Davey Smith^{20,21}, Gareth E Davies²², Liesbeth Duijts^{23,24,25}, Peter R Eastwood^{26,27}, Anders U Eliassen^{28,29}, Xavier Estivill³⁰, David M Evans^{20,21,31}, Iryna O Fedko^{5,6}, Janine F Felix^{23,32,33}, W James Gauderman¹⁷, Frank Gilliland¹⁷, Raquel Granell²¹, Struan FA Grant^{12,34,35,36}, Monica Guxens^{14,15,16}, Hakon Hakonarson^{12,34,35}, Catharina A Hartman³⁷, Joachim Heinrich^{38,39}, Anjali K Henders⁴⁰, John Henderson²¹, Patrick Holt⁴¹, Jouke-Jan Hottenga^{5,6,7}, Elina Hypönen^{42,43,44}, Carmen Iniguez^{16,45,46}, Bo Jacobsson^{47,48}, Vincent WV Jaddoe^{23,32,33}, Marjo-Riitta Järvelin^{4,49,50,51,52}, Astanand Jugessur^{53,54,55}, Mika Kähönen^{56,57}, Jaakko Kaprio^{58,59}, Ville Karhunen⁶⁰, John P Kemp^{20,21,31}, Gerard H Koppelman⁶¹, Ashish Kumar^{62,63}, Jari Lahti^{64,65}, Henrik Larsson^{66,67}, Debbie A Lawlor^{20,21,68}, Terho Lehtimäki^{69,70}, Jin Li¹², Paul Lichtenstein⁶⁷, Sebastian Lundström^{71,72}, Leo-Pekka Lyytikäinen^{69,70}, Per Magnus⁵⁴, Abdullah A Mamun⁷³, Minna Mannikko⁴, Nicholas G Martin⁷⁴, Hamdi Mbarek^{5,6,7,11}, Sarah E Medland⁷⁴, Erik Melén^{62,75}, Christel M Middeldorp^{6,76,77}, Jacob M Najman⁷⁸, Michel G Nivard^{5,6}, Ilja M Nolte⁷⁹, Albertine J Oldehinkel³⁷, Katja Pahkala^{80,81}, Teemu Palviainen⁵⁸, Lavinia Paternoster^{20,21}, Craig E Pennell⁸², Göran Pershagen^{62,83}, Niina Pitkänen⁸⁰, Robert Plomin⁸⁴, Beate St Pourcain^{20,85}, Christine Power⁴⁴, Lea Pulkkinen⁸⁶, Katri Räikkönen⁶⁵, Olli T Raitakari^{80,87}, Rebecca C Richmond^{20,21}, Fernando Rivadeneira^{23,32,88}, Richard J Rose⁸⁹, Loreto Santa-Marina^{16,90,91}, James G Scott^{78,92,93}, Sylvain Sebert^{4,49,50,94}, Saskia Selzam⁸⁴, Angela Simpson¹⁸, Patrick MA Sleiman^{12,35}, Harold Snieder⁷⁹, Marie Standl³⁸, Camilla Stoltenberg⁹⁵, David P Strachan⁹⁶, Leon Straker⁹⁷, Timo Strandberg^{4,98,99}, Jordi Sunyer^{14,15,16,100}, Elisabeth Thiering^{38,101}, Henning Tiemeier^{102,103}, Nicholas J Timpson^{20,21}, Maties Torrent^{16,104,105}, André G Uitterlinden^{23,32,88}, Toos van Beijsterveldt^{5,6}, Peter J van der Most⁷⁹, Cornelia M van Duijn³², Jorma Viikari^{106,107}, Natalia

Vilor-Tejedor^{108,109}, Judith M Vonk^{79,110}, Tanja GM Vrijkotte¹¹¹, Eero Vuoksimaa⁵⁸, Carol A Wang⁸², Andrew JO Whitehouse⁴¹, Gonneke Willemsen^{5,6,7}, Gail M Williams⁷⁸, Naomi R Wray^{40,112}, Shujing Xu¹⁷, Cheng-Jian Xu⁶¹, Lu Yi⁶⁷, Mohammad Hadi Zafarmand^{111,113}

1. COPSAC, Copenhagen Prospective Studies on Asthma in Childhood, Herlev and Gentofte Hospital, University of Copenhagen, Copenhagen, 2900 Hellerup, Denmark. 2. Novo Nordisk Foundation Center for Basic Metabolic Research, Section of Metabolic Genetics, Faculty of Health and Medical Sciences, University of Copenhagen, Copenhagen, DK-2200, Denmark. 3. Steno Diabetes Center Copenhagen, Gentofte, 2820, Denmark. 4. Center for Life Course Health Research, Faculty of Medicine, University of Oulu, Oulu, FI-90014, Finland. 5. Amsterdam Public Health, Amsterdam, The Netherlands. 6. Department of Biological Psychology, Vrije Universiteit Amsterdam, Amsterdam, 1081 BT, The Netherlands. 7. Netherlands Twin Register, Department of Biological Psychology, VU University, Amsterdam, 1081 HV, The Netherlands. 8. University of the Basque Country (UPV/EHU), Spain. 9. Biocruces Health Research Institute, Spain. 10. CIBER Diabetes y Enfermedades Metabólicas (CIBERDEM), Spain. 11. Amsterdam Reproduction and Development, Amsterdam, The Netherlands. 12. Center for Applied Genomics, The Children's Hospital of Philadelphia, Philadelphia, PA 19104, USA. 13. Quantinuum Research LLC, San Diego, CA, 92101, USA. 14. ISGlobal, Institute for Global Health, Barcelona, 08003, Spain. 15. Universitat Pompeu Fabra (UPF), Barcelona, 08003, Spain. 16. CIBER de Epidemiología y Salud Pública (CIBERESP), Madrid, 28029, Spain. 17. Department of Preventive Medicine, Keck School of Medicine, University of Southern California, Los Angeles, California, USA. 18. Division of Infection Immunity and Respiratory Medicine, School of Biological Sciences, The University of Manchester, Manchester Academic Health Science Centre, and Manchester University NHS Foundation Trust, Manchester, M13 9NT, UK. 19. Department of Paediatrics, Imperial College London, London, SW7 2AZ, UK. 20. Medical Research Council Integrative Epidemiology Unit at the University of Bristol, Bristol, BS8 2BN, UK. 21. Population Health Sciences, Bristol Medical School, University of Bristol, Bristol, BS8 2BN, UK. 22. Avera Institute for Human Genetics, Sioux Falls, South Dakota, USA. 23. The Generation R Study Group, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 24. Department of Pediatrics, Division of Respiratory Medicine, Erasmus MC, University Medical Center Rotterdam, Rotterdam, The Netherlands. 25. Department of Pediatrics, Division of Neonatology, Erasmus MC, University Medical Center Rotterdam, Rotterdam, The Netherlands. 26. School of Human Sciences, The University of Western Australia, WA, Australia. 27. West Australian Sleep Disorders Research Institute, Department of Pulmonary Physiology & Sleep Medicine, Sir Charles Gairdner Hospital, WA, Australia. 28. Copenhagen Prospective Studies on Asthma in Childhood, Herlev and Gentofte Hospital, University of Copenhagen, Denmark. 29. Department of Bio and Health Informatics, Technical University of Denmark, Denmark. 30. Sidra Medicine Research Center, Sidra Medicine, Doha, Qatar. 31. University of Queensland Diamantina Institute, Translational Research Institute, Brisbane, QLD, 4072, Australia. 32. Department of Epidemiology, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 33. Department of Pediatrics, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 34. Division of Human Genetics, The Children's Hospital of Philadelphia, Philadelphia, PA 19104, USA. 35. Department of Pediatrics, Perelman School of Medicine, University of Pennsylvania, Philadelphia, PA 19104, USA. 36. Department of Genetics, Perelman School of Medicine, University of Pennsylvania, Philadelphia, 19104, USA. 37. Department of Psychiatry, University of Groningen, University Medical Center Groningen, Groningen, The Netherlands. 38. Institute of Epidemiology, Helmholtz Zentrum München - German Research Center for Environmental Health, Neuherberg, Germany. 39. Institute and Outpatient Clinic for Occupational, Social and Environmental Medicine, University Hospital of Ludwig

Maximilians University, Munich, Germany. 40. Institute for Molecular Bioscience, University of Queensland, QLD, Australia. 41. Telethon Kids Institute (TKI), The University of Western Australia, WA, Australia. 42. Australian Centre for Precision Health, University of South Australia Cancer Research Institute, Adelaide, SA, 5001, Australia. 43. South Australian Health and Medical Research Institute, Adelaide, SA, 5001, Australia. 44. Population, Policy and Practice, UCL Great Ormond Street Institute of Child Health, University College London, London, WC1N 1EH, UK. 45. Department of Statistics and Computational Research, Universitat de València, Spain. 46. Epidemiology and Environmental Health Joint Research Unit, FISABIO-Universitat Jaume I-Universitat de València, Spain. 47. Department of Obstetrics and Gynecology, Sahlgrenska Academy, University of Gothenburg, Diagnosvägen 15, SE-416 85 Gothenburg, Sweden. 48. Department of Genetics and Bioinformatics, Domain of Health Data and Digitalisation, Norwegian Institute of Public Health, Oslo, N-0473, Norway. 49. Department of Epidemiology and Biostatistics, MRC-PHE Centre for Environment & Health, School of Public Health, Imperial College London, London, W2 1PG, UK. 50. Biocenter Oulu, University of Oulu, Oulu, 90220, Finland. 51. Unit of Primary Care, Oulu University Hospital, Oulu, 90220, Finland. 52. Department of Life Sciences, College of Health and Life Sciences, Brunel University London, Middlesex, UB8 3PH, UK. 53. Department of Genetics and Bioinformatics, Norwegian Institute of Public Health, Oslo, N-0403, Norway. 54. Centre for Fertility and Health, Norwegian Institute of Public Health, Oslo, N-0403, Norway. 55. Department of Global Public Health and Primary Care, University of Bergen, Norway. 56. Department of Clinical Physiology, Tampere University Hospital, Tampere, Finland. 57. Department of Clinical Physiology, Finnish Cardiovascular Research Center - Tampere, Faculty of Medicine and Life Sciences, University of Tampere, Tampere, Finland. 58. Institute for Molecular Medicine Finland FIMM, University of Helsinki, Helsinki, Finland. 59. Department of Public Health, University of Helsinki, Helsinki, Finland. 60. Department of Epidemiology and Biostatistics, School of Public Health, Imperial College London, London, UK. 61. University of Groningen, University Medical Center Groningen, Department of Pediatric Pulmonology and Pediatric Allergology, Beatrix Children's Hospital, GRIAC Research Institute Groningen, Groningen, The Netherlands. 62. Institute of Environmental Medicine, Karolinska Institutet, Sweden. 63. Department of Public Health Epidemiology, Unit of Chronic Disease Epidemiology, Swiss Tropical and Public Health Institute, Basel, University of Basel, Switzerland. 64. Helsinki Collegium for Advanced Studies, University of Helsinki, Helsinki, Finland. 65. Department of Psychology and Logopedics, Faculty of Medicine, University of Helsinki, Helsinki, Finland. 66. School of Medicine Sciences, Örebro University, Sweden. 67. Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Sweden. 68. Bristol NIHR Biomedical Research Centre, Bristol, UK. 69. Department of Clinical Chemistry, Fimlab Laboratories, Tampere University Hospital, Tampere, Finland. 70. Department of Clinical Chemistry, Finnish Cardiovascular Research Center - Tampere, Faculty of Medicine and Life Sciences, University of Tampere, Tampere, 33520, Finland. 71. Centre for Ethics, Law and Mental Health, University of Gothenburg, Sweden. 72. Gillberg Neuropsychiatry Centre, University of Gothenburg, Sweden. 73. Institute for Social Science Research, University of Queensland, QLD, Australia. 74. QIMR Berghofer Medical Research Institute, QLD, Australia. 75. Sachs' Children's Hospital, Sweden. 76. Child Health Research Centre, University of Queensland, Brisbane, QLD, Australia. 77. Child and Youth Mental Health Service, Children's Health Queensland Hospital and Health Service, Brisbane, QLD, Australia. 78. School of Public Health, The University of Queensland, QLD, Australia. 79. Department of Epidemiology, University of Groningen, University Medical Center Groningen, Groningen, The Netherlands. 80. Research Centre of Applied and Preventive Cardiovascular Medicine, University of Turku, Turku, 20014, Finland. 81. Paavo Nurmi Centre, Sports and Exercise Medicine Unit, Department of Physical Activity and Health, University

of Turku, Turku, Finland. 82. School of Medicine and Public Health, Faculty of Medicine and Health, The University of Newcastle, Callaghan, NSW, 2308, Australia. 83. Centre for Occupational and Environmental Medicine, Stockholm County Council, Sweden. 84. MRC Social, Genetic and Developmental Psychiatry Centre, King's College London, London, UK. 85. Max Planck Institute for Psycholinguistics, Nijmegen, 6525 XD, The Netherlands. 86. Department of Psychology, University of Jyväskylä, Jyväskylä, Finland. 87. Department of Clinical Physiology and Nuclear Medicine, Turku University Hospital, Turku, 20520, Finland. 88. Department of Internal Medicine, Erasmus MC, University Medical Center Rotterdam, Rotterdam, 3015 CE, The Netherlands. 89. Department of Psychological and Brain Sciences, Indiana University, Bloomington, Indiana, USA. 90. Subdirección de Salud Pública y Adicciones de Gipuzkoa, San Sebastián, Spain. 91. Instituto de Investigación Sanitaria Biodonostia, San Sebastián, Spain. 92. Metro North Mental Health Service, QLD, Australia. 93. Queensland Centre for Mental Health Research, QLD, Australia. 94. Department of Genomics of Complex Diseases, Imperial College, London, UK. 95. Norwegian Institute of Public Health, Norway. 96. Population Health Research Institute, St George's University of London, London, SW17 0RE, UK. 97. School of Physiotherapy and Exercise Science, Faculty of Health Sciences, Curtin University, Perth, WA, Australia. 98. Helsinki University Central Hospital, University of Helsinki, Helsinki, Finland. 99. Clinicum, University of Helsinki, Helsinki, Finland. 100. IMIM (Hospital del Mar Medical Research Institute), Barcelona, 08003, Spain. 101. Division of Metabolic and Nutritional Medicine, Dr. von Hauner Children's Hospital, University of Munich Medical Center, Munich, 80337, Germany. 102. Child and Adolescent Psychiatry, Erasmus Medical Center, Rotterdam, The Netherlands. 103. Social and Behavioral Sciences, Harvard TH Chan School of Public Health, Harvard University, Boston, USA. 104. ib-salut, Area de Salut de Menorca, Spain. 105. Fundació Institut d'Investigació Sanitària Illes Balears – IdISBa, Spain. 106. Department of Medicine, University of Turku, Turku, Finland. 107. Division of Medicine, Turku University Hospital, Turku, Finland. 108. Center for Genomic Regulation (CRG), Barcelona Institute of Science and Technology, Spain. 109. Barcelonabeta Brain Research Center (BBRC), Pasqual Maragall Foundation, Barcelona, Spain. 110. Groningen Research Institute for Asthma and COPD (GRIAC), University of Groningen, University Medical Center Groningen, Groningen, 9700 RB, The Netherlands. 111. Department of Public Health, Amsterdam Public Health Research Institute, Academic Medical Center (AMC), University of Amsterdam, Amsterdam, 1105 AZ, The Netherlands. 112. Queensland Brain Institute, University of Queensland, QLD, Australia. 113. Department of Clinical Epidemiology and Biostatistics, Amsterdam Public Health Research Institute, Academic Medical Center, University of Amsterdam, Amsterdam, The Netherlands, 1105 AZ, The Netherlands.

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