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Single-cell RNA Sequencing of Human Esophageal Epithelium in Homeostasis and Allergic Inflammation

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Abstract

Inflammation of the esophageal epithelium is a hallmark of eosinophilic esophagitis (EoE), an emerging chronic allergic disease. Herein, we probed human esophageal epithelial cells at single-cell resolution during homeostasis and EoE. During allergic inflammation, the epithelial differentiation program was blocked, leading to loss of *KRT6^{high}* differentiated populations and expansion of *TOP2^{high}* proliferating and *DSP^{high}*, *SERPINB3^{high}* transitioning populations; however, there was stability of the stem cell-enriched *PDPN^{high}* basal epithelial compartment. This differentiation program blockade was associated with dysregulation of transcription factors, including nuclear receptor signalers, in the most differentiated epithelial cells and altered NOTCH-related cell-to-cell communication. Each epithelial population expressed genes with allergic disease risk variants, supporting their functional interplay. The esophageal epithelium differed notably between EoE in histologic remission and controls, indicating that remission is a transitory state poised to relapse. Collectively, our data uncover the dynamic nature of the inflamed human esophageal epithelium and provide a framework to better understand esophageal health and disease.

Introduction

The esophagus has been traditionally thought of as a relatively simple organ that primarily functions as a conduit for food passage from the oral cavity to the stomach. Yet, accumulating data are changing this view with the emergence of the esophagus as a complex mucosa with a multi-layered epithelium designed to maintain homeostasis in the setting of the constant onslaught of antigenic and biophysical stimuli (1, 2). To achieve this, the human esophagus is lined with a multilayered, squamous, non-keratinized epithelium that forms a protective barrier against extrinsic (e.g., bacteria and food antigens) and intrinsic (e.g., acid) stimuli.

The epithelial cells of the protective mucosal barrier of the human esophagus are primarily defined by their shape, proliferation status, and spatial localization. The layer of the human esophageal epithelium furthest from the lumen (the basal epithelium) consists of mostly quiescent cells and serves as a reservoir of the epithelial progenitors defined by COL17A1/KRT15^{high} expression (1, 3). Adjacent to the basal layer and closer to the lumen are a few layers of actively proliferating cells. As the epithelial cells move towards the luminal surface, they embark in the differentiation process and become progressively flattened, form a tighter barrier, and lose their nuclei. Differentiated epithelial cells are characterized by the high expression of KRT4, KRT13, and other esophagus-enriched proteins (4). The molecular properties and functional relationship between human epithelial subpopulations, developmental trajectory of the epithelium, and interepithelial communications under homeostasis and allergic inflammation are at an early stage of characterization (1).

Several diseases of the esophagus are characterized by profound epithelial responses, including gastroesophageal reflux disease (GERD), squamous cell carcinoma, and allergic eosinophilic esophagitis (EoE). In EoE, RNA sequencing (RNA-seq) performed on whole tissue specimens has identified numerous pathways involved in immunity and epithelial biology (5, 6), but it has not revealed the contribution of distinct epithelial subpopulations. Therefore, the detailed changes in the epithelial differentiation program and the origin of basal zone hyperplasia, seen in many esophageal inflammatory diseases, remain unexplored. At the molecular level, genes genetically linked to food allergy and specifically EoE are often expressed in the esophagus (7, 8); however, it remains to be determined which specific cell type(s), if any, is responsible for the disease susceptibility and pathology. To address these gaps in knowledge, we performed single-cell RNA-seq (scRNA-seq) of the esophageal biopsies from a spectrum of individuals, including healthy controls and individuals with active and inactive stages of EoE as identified by histologic criteria, and focused on the epithelial compartment of the esophageal tissue, defined herein as the esophageal epithelial unit (EEU). Collectively, our data highlight previously unappreciated heterogeneity of the homeostatic and inflamed esophageal epithelium and provide a framework to better understand esophageal health and disease.

Results

Esophageal tissue cellular composition in the homeostatic and inflamed esophagus

To systematically examine the cellular and transcriptional changes in the homeostatic and inflamed esophagus, we performed scRNA-seq of 40,297 cells derived from esophageal biopsies (n = 5 individuals with active EoE, n = 3 individuals with EoE in disease remission, n = 2 healthy controls) (Figure 1A). To define the major cellular repertoire that was comparable across all samples, we integrated all samples, while retaining sample and disease status information for each cell, and performed unbiased clustering and Uniform Manifold Approximation Projection (UMAP) (9) by Seurat (10). It revealed 6 major cell types, with epithelial cells being the most prevalent in all conditions (82% on average, Figure 1B,C). Representative markers of the major subpopulations included *CNFN* and *SPRRs* (epithelial cells), *CD3D* (lymphocytes), *HLA* (myeloid cells), *TPSAB1* and *CPA3* (mast cells), *AQP1* and *CLDN5* (endothelial cells), and *COL3A1* (fibroblasts). Marker genes representative for each cell type and gene ontology (GO) analysis confirmed the cell identities (Figure 1B, Supplemental Figure 1, and Supplemental Table 1). The percentages of lymphocytes, mast cells, endothelial cells, and fibroblasts were increased, whereas the percentage of epithelial cells was moderately decreased in active EoE compared to healthy controls (Figure 1C). Notably, the cellular composition in EoE remission displayed a higher percentage of mast cells, endothelial cells, and fibroblasts and a modestly decreased percentage of epithelial cells compared to that of healthy controls (Figure 1C). Analysis of the expression of the genes most highly dysregulated in the EoE transcriptome defined by sequencing bulk tissue RNA-seq (6) revealed the contribution of each cell type to the transcriptional response in the disease (Figure 1D). Notably, esophageal epithelial cells and fibroblasts upregulated several genes that are critical to EoE pathogenesis, including *CDH26*,

POSTN, *ANO1*, and *CCL26*; the latter two were shared between these cell types (Figure 1D, upregulated). In contrast, downregulated genes were primarily expressed in the epithelial component of the esophagus (Figure 1D, downregulated). These findings collectively signify a key role of epithelial responses and their unique cellular trajectory in the inflamed esophagus.

EEU in the homeostatic esophagus

We sought to explore the heterogeneity of the esophageal epithelium under homeostatic states. Unbiased clustering of the epithelial compartment from healthy individuals revealed 6 subpopulations of the EEU (representative markers are shown in parentheses): Quiescent (*DST*, *KRT15*), Proliferating (*HMGB2*, *TOP2A*), Transitioning 1 (Trans1) (*DSC2*, *DSP*), Transitioning 2 (Trans2) (*SERPINB3*), Differentiated^{low} (*PADI1*, *TGM3*), and Differentiated^{high} (*MT1G*, *RNASE7*, *KRT16*) (Figure 2A, B and Supplemental Table 2). Consistent with distinct transcriptional signatures, each epithelial subpopulation was characterized by unique biological processes reflecting functional diversity (Figure 2C, biological processes), substantiating that they are discrete subpopulations with a stable presence and defined function. Quiescent cells were highly enriched in genes related to membrane protein targeting and translation; proliferating cells were associated with the cell division genes; and transitioning and differentiated subpopulations were enriched in genes associated with epithelial differentiation, cell junctional complexes, adhesion, and cornification. Notably, the Trans2 subpopulation specifically expressed the esophagus-enriched serine protease inhibitor genes *SERPINB3* and *SERPINB4*, cystatin family genes *CSTA* and *CSTB*, and the peptidase inhibitor 3 gene (*PI3*) and was uniquely enriched in endopeptidase activity, suggesting that the Trans2 subpopulation functions as a primary regulator of the proteolytic activity germane to the protective properties of

the esophageal epithelium under homeostatic conditions (7). The Differentiated^{high} subpopulation was enriched in genes related to response to ions, including copper, zinc, and cadmium (metallothioneins), and had specific expression of the antimicrobial gene *RNASE7* (Figure 2B and Supplemental Figure 2). Immunostaining of the representative markers of each subpopulation revealed that basal cell markers (e.g., *KRT15*) were most strongly expressed in the basal layer of the esophagus, proliferating cell markers (e.g., *TOP2A*) were expressed in the layers adjacent to the basal layer but not the lamina propria, and the transitioning and differentiated cell markers (e.g., *DSP*, *SERPINB3*, *TGM3*, *RNASE7*) were primarily expressed in the suprabasal zone (Figure 2D). When comparing the number of detected genes and the read depth (number of UMI) across the distinct epithelial subpopulations, we observed that Trans2 and differentiated cells expressed a lower number of genes than did other epithelial subpopulations, suggesting that these cells were highly specialized in function (Figure 2E). These results demonstrate that the differentiation program of the esophageal epithelium mirrors epithelial stratification; less differentiated and proliferating cells reside closer to the lamina propria, and the most differentiated cells reside adjacent to the lumen.

Basal and suprabasal epithelial layer properties

To further delineate early events in the differentiation of the esophageal epithelium, we aimed to molecularly characterize the basal epithelial layer of the esophagus adjacent to the lamina propria. Accordingly, we sorted biopsy-derived epithelial cells by their expression of the basal layer marker podoplanin (PDPN) (11) and defined the gene signature of the basal (PDPN^{high}) and the suprabasal (PDPN^{low}) compartments by bulk RNA-seq (Figure 3A, Supplemental Tables 3 and 4). Differential expression analysis identified 151 genes specific to basal (PDPN^{high}) cells,

including *IGFBP3*, *COL17A1*, and *KRT15* (RPKM > 5, fold change [FC] > 2 vs. suprabasal [PDPN^{low}] cells, false discovery rate [FDR]-adjusted p < 0.05; Supplemental Table 3). A unique set of 248 genes was expressed in the suprabasal (PDPN^{low}) cells, including *KRT4* and *KRT13*, *SPINK5*, *SERPINB13*, and most of the esophagus-enriched genes (7) (green font in Supplemental Table 4). Immunostaining of the most highly expressed markers of each cell type showed clear morphologic separation of the epithelium into basal and suprabasal compartments (Figure 3B). Functional enrichment analysis revealed that genes expressed in the basal (PDPN^{high}) cells were associated with cell adhesion, migration, and extracellular matrix processes, whereas genes expressed in the suprabasal (PDPN^{low}) cells were linked to epithelial development, differentiation, and cornification (Supplemental Figure 3A).

We sought to explore the proliferating status of the basal and the suprabasal cells. To do this, we overlaid average gene expression signatures of the PDPN^{low} and PDPN^{high} cells with those of quiescent and proliferating populations and with the cell cycle genes. The PDPN^{high} signature overlaid with the quiescent and part of the proliferating population, whereas the PDPN^{low} signature was found exclusively in the proliferating population (Figure 3C). Cell cycle analysis using Seurat revealed the presence of genes from the full spectrum of the cell cycle: G1, S, and G2M. Most of the basal (PDPN^{high}) cells were in G1 or S stage, and a small portion of basal (PDPN^{high}) cells were in the G2M stage. Suprabasal (PDPN^{low}) cells were in S and G2M stage (Figure 3D). This finding suggests continuous transition from quiescent basal to proliferating basal to proliferating suprabasal cells in the epithelial compartment.

Basal (PDPN^{high}) cells expressed markers previously associated with epithelial progenitors, including *COL17A1*, *DST*, *KRT15* (1), and specifically those with antiproliferative properties, such as *ZFP36L2* (12) and *BTG2* (13) (Supplemental Figure 3B), collectively suggesting that the

basal cells are the source of the esophageal epithelial stem cells. Indeed, ex vivo colony formation revealed preferential growth of the stem cell–like colonies from the basal (PDPN^{high}) compared with suprabasal (PDPN^{low}) cells (Figure 3E, arrows); these colonies expressed the epithelial progenitor markers *ITGA6*, *KRT5*, and *SOX2* (Figure 3F). Collectively, these findings establish the hierarchical developmental trajectory of the EEU of the homeostatic esophagus, suggesting that the sequence of early events stems from the KRT15^{high}, quiescent basal progenitors that rarely divide and progress toward the KRT4^{high}/KRT13^{high}, suprabasal proliferating cells. This trajectory resembles the differentiation program of the epidermis (14). The colony-forming property of the basal (PDPN^{high}) cells revealed that these populations are the source of the esophageal epithelial progenitors.

EEU differentiation dynamics in allergic inflammation

We sought to compare the EEU in individuals with active EoE to the homeostatic conditions along the differentiation trajectory. First, we performed sample integration, UMAP, and clustering analysis by grouping samples by their disease status: normal (healthy control), remission (inactive EoE), and active EoE. To compare EEU differentiation by disease status, we performed pseudotime analysis using Slingshot (15) by combining all three groups to project them onto a common pseudotime axis and identified a linear differentiation trajectory (Supplemental Figure 4A). Accordingly, individual cells were assigned with a pseudotime value along the unified trajectory for all samples and color-coded in the UMAP of the corresponding groups (Figure 4A) generated by separate processing of the group and the number of detected genes and the read depth (number of UMI) across epithelial subpopulations (Supplemental Figure 4B). Despite the shared differentiation trajectory of the subepithelial units, there was

dramatic loss of the fully differentiated cells and an increase of the transitional and proliferating cells (Figure 4A and Supplemental Figure 4B). To further examine EoE-dependent perturbation of differentiation, we visualized cell density along the pseudotime axis and compared the relative proportion of cells at each differentiation stage (Figure 4B). Indeed, active EoE displayed significantly increased proliferating and Trans1 cells and a significant decrease of Differentiated^{low/high} subpopulations relative to normal controls (Figure 4C). The EoE in remission displayed a similar decrease of Differentiated^{low/high} cells, but the decrease was significantly less than that of active EoE (Figure 4C and Supplemental Figure 4B).

Focusing on the quiescent and proliferating subpopulations, we found that only proliferating suprabasal, but not basal cells were significantly increased and that the proportion of quiescent basal cells remained unchanged (Figure 4D). This finding suggests that basal zone hyperplasia, which is commonly observed in EoE and other types of esophagitis, is primarily driven by the proliferation of the suprabasal epithelial compartment, likely by the proliferating and Trans1 subpopulations. At the same time, EoE remission also displayed a significant increase in the proportion of proliferating suprabasal cells relative to normal but to a lesser extent than the increase of active EoE (Figure 4D). Accordingly, when comparing overall epithelial subpopulation composition by hierarchical clustering, EoE remission samples were more similar to active EoE samples than normal control samples (Figure 4E). These results demonstrate that the differentiation program of the EEU is dynamically regulated as a function of disease activity and that there is a profound disruption of this program in EoE as evidenced by an increased proportion of transitioning and proliferating epithelial cells and a loss of differentiated epithelial cells. In disease remission, despite histologic improvement, these changes persist at the single-cell level, albeit with less magnitude than that of active disease.

Altered EEU differentiation program in EoE

Given the observation of the near-complete loss of the Differentiated^{low/high} subpopulations and the increased proportion of the transitioning subpopulations, we hypothesized that the EEU of the inflamed esophagus has a disrupted capacity to differentiate. To test this hypothesis, we compared gene expression of the individual epithelial subpopulations stratified by the disease status. Given that our samples are from humans and the numbers are limited, it was important to take into account sample-to-sample variability when examining the changes in EoE. Therefore, bulk RNA-seq differential analysis was used to convert the subpopulation-stratified scRNA-seq data into pseudo-bulk RNA-seq data (16). Specifically, we converted summed UMI counts per gene for each epithelial subpopulation per sample, thereby generating a total of 50 samples (i.e., 10 samples $\times$ 5 cellular subpopulations [Differentiated^{low/high} subpopulations were merged]), and then performed DESeq2 differential analysis (17). This process is analogous to FACS cell purification followed by bulk RNA-seq for comparative analysis of homogeneous cell populations except that the cells are purified computationally. This analysis is independent of the increase or decrease of specific subpopulations because gene expression levels are normalized by the cell counts per sample; thus, it enables robust interrogation of transcriptomic changes in each subpopulation. First, principal component analysis (PCA) was performed to assess the similarity of the pseudo-bulk RNA-seq samples and to examine the trajectory of each cellular compartment as a function of cellular differentiation (Figure 5A). Unlike other epithelial subpopulations, differentiated cells were widely spread along the developmental trajectory in a manner dependent upon the disease status. Differentiated cells from active EoE esophagi were located closer to the transitioning subpopulations than differentiated cells from normal esophagi (Figure 5A),

suggesting blockade of transitioning to differentiated cells (Figure 5A, line). Using keratin expression as a surrogate marker for epithelial differentiation, we first identified subpopulation-specific keratin genes (Figure 5B) and then examined their changes in EoE (Figure 5C). We observed a significant loss of keratins preferentially expressed in the normal differentiated cells, including *KRT16*, *KRT17*, *KRT80*, *KRT78*, *KRT23*, and *KRT19* (compare average expression heatmap [Figure 5B] to transcriptional change [Figure 5C] in the differentiated subpopulation in active EoE). In EoE remission, expression of keratins in the differentiated subpopulations was largely normalized (Figure 5C) except for a few that remain dysregulated as much as in active EoE. Similarly, in the PCA analysis, differentiated cells from individuals with EoE in remission clustered closer to those from healthy controls (Figure 5A). This suggests that epithelial differentiation in EoE is blocked at the terminal stage and that this blockade is partially reversed during disease remission.

We further assessed the dysregulation of the epithelial differentiation program in EoE by comparing transcriptional profiles of individual subpopulations of the EEU between active EoE and normal controls (Figure 5D). Differential analysis (FDR-adjusted $p < 0.05$, $FC > 1.5$) revealed that the largest number of dysregulated genes was in the Differentiated^{low/high} subpopulations. Differentially expressed genes (DEGs) in the differentiated cells were evenly divided between upregulated and downregulated genes (2078 genes upregulated; 2156 genes downregulated) compared to controls, suggesting that these subpopulations remain highly transcriptionally active despite their major loss in EoE. In contrast, the Trans2 subpopulation had the smallest contribution to the transcriptional response in EoE (66 genes upregulated, 76 genes downregulated). Gene ontology (GO) analysis revealed enrichment in epithelial differentiation and keratinization that were shared between quiescent, Trans2, and differentiated subpopulations

for the downregulated genes. In the proliferating and Trans2 cells, downregulated genes were enriched in responses to metal ions, whereas in the differentiated cells, downregulated genes were associated with small GTPase-mediated signal transduction (Supplemental Figure 5A, downregulated). Similar analysis of the upregulated genes revealed enrichment in endopeptidase activity and type I interferon signaling that was shared between the epithelial subpopulations and enrichment in mRNA metabolism and splicing that was specific to the differentiated subpopulations (Supplemental Figure 5A, upregulated). In EEU in EoE remission, approximately 100 genes remained dysregulated, and these were primarily in the differentiated subpopulations (Supplemental Figure 5B).

To better dissect the gene transcriptional changes in EEU differentiation programs, we performed unbiased hierarchical clustering focusing on the differential gene expression between quiescent and differentiated subpopulations (Figure 5E). We observed two large groups of genes that were either induced or repressed upon differentiation in the normal esophagus. Interestingly, each group of genes, induced or repressed, displayed three types of changes in EoE. Type 1 genes were severely dysregulated and Type 2 genes were moderately dysregulated by disease status, and Type 3 genes were normally expressed/repressed irrespective of disease status. Although some genes were normally expressed in active EoE (Type 3, compare normal and active EoE [Active]), the majority of the genes were dysregulated (Types 1 and 2), including severely dysregulated genes that failed to be either induced or repressed during differentiation compared to the normal esophagus (Type 1). Focusing on the genes normally induced in differentiation, dysregulated genes (Types 1 and 2) were enriched for genes linked to endosomal transport, small GTPase signaling, and response to zinc ions. Notably, genes that were upregulated during differentiation independently of the disease status (Type 3) were functionally

enriched for keratinocyte and epidermal differentiation, suggesting that these cells are actually differentiated but are functionally defective in the inflamed esophagus. In EoE remission, several clusters of genes in the differentiated cells remained dysregulated (Figure 5E, asterisks; compare EoE remission [Remiss] and normal in Differentiated cells), collectively suggesting that the cellular composition and transcriptional signature of the EEU in EoE remission represents a transition state between the healthy and inflamed esophagus that likely poises the epithelium to relapse.

Transcription factor signature of altered epithelial differentiation

To explore the molecular basis of the altered differentiation program, we analyzed the expression of transcription factors (TFs) in EEU. First, we identified subpopulation-specific TFs in normal EEU (Figure 6A and Supplemental Figure 6A) and then compared their changes in EoE (Figure 6B and Supplemental Figure 6B). We found that TFs of the Differentiated^{high} population were significantly downregulated and that TFs of less differentiated populations were upregulated in active EoE compared to controls (compare average expression heatmap [Figure 6A] to transcriptional change [Figure 6B]). This dichotomic relationship persisted for extended 134 TFs that were expressed in a differentiation-dependent manner (Supplemental Figure 6A). Expression of most TFs was not statistically different in remission compared to control, with the exception of *ZNF430*, *BHLHE40* and *XBP1*; the latter remained upregulated in the Differentiated population in active EoE and remission (Supplemental Figure 6A, asterisks). Focusing on the TFs downregulated in the Differentiated^{high} cells, we generated a high confidence interactome (confidence 0.9) using the Search Tool for the Retrieval of Interacting Genes/Proteins (STRING) database (18). We found that this interactome included several genes related to nuclear hormone

receptor signaling, such as the members of the NR1 subfamily of nuclear hormone receptors *RORA* and *NR1D1*, the retinoic acid receptor *RXRA*, and the transcriptional coactivators for nuclear hormone receptors *NCOA2* and *A3* (Supplemental Figure 6B). Indeed, nuclear receptor signaling genes were significantly enriched in the TFs dysregulated in the most differentiated subpopulation in EoE (chi-square test, $p < 0.0001$). In contrast, the interactome of genes that were upregulated in the differentiated cells were enriched for *HIF1A*, which has been previously implicated in EoE pathogenesis (19); *STAT1*; and *TP53* (Supplemental Figure 6C).

We also found that the expression of the NOTCH pathway–related genes were dysregulated in active EoE in several epithelial subpopulations. For example, the NOTCH ligand *JAG1*, coactivator *MAML2*, and major transcriptional effector *RBPJ* were significantly increased in the differentiated cells, whereas the ligand *DLL1* and receptor *NOTCH4* were downregulated in the proliferating population (Figure 6C, D). Indeed, compared to the untreated cells, cells treated with the NOTCH inhibitors DAPT and Compound E had decreased esophageal epithelial differentiation, including transesophageal electrical resistance (TEER) (Figure 6E, graph). Histologically, IL-13 caused thickening of the epithelium, likely due to increased proliferation, whereas NOTCH inhibitors impaired stratification (Figure 6E, insets). Altered differentiation was accompanied by decreased expression of involucrin (Figure 6F). These results are consistent with prior findings that the NOTCH signaling pathway is a critical regulator of the esophageal epithelium (20). Collectively, these findings suggest that dysregulated expression of TFs specific to the differentiated cells and altered cell-to-cell communications, especially involving the NOTCH family, inhibit the differentiation program of transition-stage epithelial cells in the EEU during allergic inflammation.

Genetic etiology of food allergy/EoE at the single-cell level

To assess the contribution of esophageal cell types to the genetic etiology of EoE, we examined the expression of genes previously associated with a broad spectrum of food allergic diseases, including EoE, by genome-wide association study (GWAS), Mendelian association, or candidate gene approaches in cell types identified in the biopsies (7, 8, 21). Remarkably, those genes were expressed in each esophageal cell type, indicating that each cellular subpopulation was likely manifesting part of the genetic risk (Supplemental Figure 7A). Epithelial cells were enriched in susceptibility genes that included the proteases and protease inhibitors *SPINK5*, *SERPINB2*, *SERPINB10*, and *CAPN14*; the junctional proteins *DSG1* and *DSP*; *TSLP*; and the eosinophilic chemoattractant *CCL26*. *TSLP* and *CCL26* were also expressed in fibroblasts. Fibroblasts showed specific expression of the phosphatase *PTEN* and shared expression of the transcriptional repressor *C11ORF30* (*EMSY*) with lymphocytes. *IL33* and *TGFBR2* were preferentially expressed in the endothelial cells, and expression of the leucine-rich membrane protein *LRRC32* was shared between endothelial cells and fibroblasts. The pro-allergic cytokines *IL5* and *IL13* were enriched in lymphocytes and mast cells.

Focusing on the EEU, we stratified the expression of the genes genetically linked to EoE within the epithelial subpopulations: 34 genes were robustly detected in at least one epithelial subpopulation in the biopsies from healthy controls (Figure 7A), displaying subpopulation-specific expression patterns. Differential analysis by pseudo-bulk RNA-seq revealed that genes enriched in the Differentiated^{low/high} subpopulations (e.g., *FLG*, *SPINK5*) were decreased, whereas genes enriched in less differentiated populations (e.g., *TGFBR1*, *STAT6*) were increased in active EoE (Figure 7B). Notably, expression of *CAPN14*, the protein product of the main EoE susceptibility locus (2p23), and expression of *CCL26*, the critical driver of the eosinophilic

infiltration in EoE, paralleled each other, suggesting common regulation in response to IL-13, and were significantly upregulated throughout the EEU. Focusing on the genes significantly dysregulated in the epithelium of patients with active EoE compared to control individuals (Figure 7B, marked by #), we assessed their expression in the larger cohort of the patients with EoE by bulk RNA-seq (Supplemental Figure 7B). The majority of the genes showed a similar pattern of transcriptional change, suggesting that the epithelium is a major regulator of their expression. Most active EoE genes had normalized expression in EoE remission with the notable exceptions of *CAPN14* and *IFFO2* (encoding Intermediate Filament Family Orphan 2). These two genes remaining significantly upregulated in the Differentiated^{low/high} cells suggests a fixed defect. Notably, the EoE risk variant rs28530674 (risk allele frequency 0.04, $P = 3 \times 10^{-7}$, odds ratio 1.83) is located within *IFFO2* gene (22). Collectively, these findings demonstrate dynamic disease-dependent expression of genes genetically associated with food allergy/EoE, signify the interplay of the identified heterogeneous esophageal cell types, and delineate the full trajectory of the EEU to allergic inflammatory responses in the esophagus.

Discussion

Overall, our study provides a global view of cellular and molecular machinery of the esophageal epithelium during homeostasis and an allergically inflamed state at the single-cell level. We report high-resolution transcriptional mapping of the human EEU under homeostatic and inflamed conditions, going beyond classical morphologic analysis of the epithelium. By applying bulk RNA and scRNA sequencing analyses and pseudotime analysis, we identify the molecular and functional properties and map the spatial localization of 6 major epithelial subpopulations that varied in a disease-dependent manner. We define the developmental trajectory of the human EEU as the following progression: *KRT15^{high}* quiescent cells → *TOP2A*-positive proliferating cells → 2 transitioning cell subpopulations defined by expression of *DSP* and *SERPINB3* → 2 *KRT6^{high}* differentiated cell subpopulations that expressed metallothioneins and antimicrobial proteins (e.g., *RNASE7*). By assessing cellular and transcriptional properties of the EEU in the esophageal tissue of individuals with allergic inflammation, we define the dynamic interplay of these epithelial subpopulations as a function of disease state and activity. We determine that allergic inflammation, as assessed in human EoE, is associated with a blockade of the last step of the differentiation program. This differentiation blockade leads to the loss of terminally differentiated cells and hyperproliferation of less mature epithelial subpopulations yet stability of the quiescent, stem cell-enriched basal epithelial compartment. This blockade is associated with and likely driven by a failed transcriptional mechanism involving nuclear receptors in the most differentiated epithelial cells and altered cell-to-cell communication involving the NOTCH signaling pathway. Notably, despite histologic remission of allergic inflammation in inactive EoE, the cellular composition and gene expression signatures of the epithelial subpopulations of EoE remission were distinguishable from those of healthy controls, indicating that remission is a

transitory state between the homeostatic and inflamed esophagus and is poised to relapse. We present evidence that susceptibility genes for a range of allergic diseases (e.g., food allergy) are expressed by all 6 epithelial compartments, indicating the importance of each cell subpopulation in different aspects of disease pathogenesis and supporting cooperative pathogenesis at the single-cell level. Collectively, our data highlight the previously unappreciated heterogeneity of the homeostatic and inflamed esophageal epithelium and provide a framework to better understand esophageal health and disease. The collective findings highlight the need for more extensive analysis of various parts of the esophagus in a larger group of patients in order to better understand the contribution of genetics, sex, comorbidities, and intensity of eosinophilic infiltration and to develop clinically relevant molecular diagnostic standards for the disease.

A fundamental property of the EEU that differs between humans and mice is the presence of the quiescent basal layer cells. These human cells have unique morphologic characteristics (e.g., cylindrical cells in contact with lamina propria) and are characterized by the gene expression of structural components (e.g., *KRT15*), TGF β signaling proteins, HSP70 family chaperones, and epigenome modifiers (*MECP2*, linker histone H1.0 and polycomb repressor complex genes) (3, 23). Under homeostatic conditions, only 2–5% of the esophageal basal cells are actively dividing (1, 24), consistent with the basal layer being a prime source of the epithelial stem cells. In individuals who undergo chemotherapy and radiation therapy for cancer treatment, approximately 20% of the basal cells of the squamous epithelium of the oral cavity become actively proliferating (25). Remarkably, in the allergic inflamed esophagus, the proportion of basal cell proliferation remains unchanged; most of these cells remain quiescent despite the major increase in the proliferating compartment consistent with the histologically defined basal

zone hyperplasia (Figure 4 and (26)). These findings suggest the existence of a cell-to-cell communication program that simultaneously increases the proliferation of the upper epithelial layers and preserves the quiescent status of the basal cells. Several signaling pathways have been previously implicated in the regulation of the esophageal epithelial proliferation and differentiation under homeostatic and allergically inflamed conditions, including NOTCH, WNT, and BMP (27-29). Though many of the NOTCH pathway–related genes were dysregulated in EoE, their expression was not limited to the quiescent basal subpopulation. In contrast, insulin-like growth factor binding protein 3 (*IGFBP3*) was increased in EoE and was the most differentially expressed gene in the epithelial basal layer compared to the suprabasal cells. IGFBP proteins are critical regulators of the insulin-like growth factor (IGF) signaling pathway that modulates cell survival, proliferation, and differentiation (30). IGFBPs bind with high affinity to IGF, thereby precluding it from binding to the receptor. Under physiologic and pathologic conditions (e.g., asthma), IGFBPs are subjected to proteolytic degradation by various serine and metalloproteases, thus facilitating IGF binding to the receptor (30). In the homeostatic esophagus, the Trans2 subpopulation is enriched in genes associated with proteolytic activity, whereas in the inflamed esophagus, dysregulated expression of proteases and protease inhibitors occurs throughout the EEU. For example, the cysteine protease *CAPN14* that is normally expressed in the differentiated cells is upregulated in all epithelial subpopulations. The serine peptidase inhibitors *SPINK5* and *SPINK7* are also enriched in the differentiated epithelium in the homeostatic esophagus but are depleted in the inflamed esophagus (31). However, *SERPINS*, whose expression is confined to the Trans2 subpopulation in control biopsies, are highly upregulated in other epithelial subpopulations in active EoE, suggesting that compartmentalization of the proteolytic activity is an integral part of the EoE-altered innate anti-

inflammatory properties of the esophagus. Whether epithelial proteases of the homeostatic and inflamed esophagus regulate IGFBP processing and subsequent IGF signaling and the functional consequences of these events require further investigation. IGFBP3 also exerts an IGF-independent effect on cell proliferation by regulating NF κ B signaling in a caspase-dependent manner (32); this pathway recently has been implicated in the maturation and release of the critical pro-allergic alarmin IL-33 that is uniquely expressed in the quiescent basal layer cells in active EoE as part of an allergen-sensing pathway (26, 33). Our results collectively highlight the potentially critical role of the basal layer cells in propagating allergic inflammatory responses in EoE via multiple mechanisms that do not require proliferation.

Functional characteristics of the differentiated epithelial subpopulations are consistent with their primary role in protecting the underlying tissue against environmental insults. Accordingly, the transcriptional signature of the differentiated cells is enriched in genes that regulate keratinization, cornification, cell-cell junction organization, and antibacterial responses. The Differentiated^{high} subpopulation specifically expresses ribonuclease A family member 7 (*RNASE7*), a protein that has a broad-spectrum antimicrobial activity against bacteria and fungi. Loss of *RNASE7* expression may be related to the dysbiosis observed in individuals with active EoE (34, 35). Moreover, differentiated cells express peptidyl arginine deiminase (*PADI*) and transglutaminase (*TGM*) genes that drive calcium-dependent protein deamination (citrullination) and structural protein crosslinking. Although these processes have been primarily implicated in keratinization of the skin epithelium and hair development, (36, 37) esophagus-specific expression of *PADI1*, *PADI3*, and *TGM3* in the differentiated cells in the EEU and their loss in active EoE underscore that overlapping molecular mechanisms are involved in the formation of

the esophageal epithelial barrier. This notion is further supported by a damaging mutation in *PADI3* being associated with uncombable hair syndrome, central centrifugal cicatricial alopecia, and active EoE (38, 39).

Another mechanism of the barrier formation by the differentiated esophageal epithelium may involve nuclear receptors, such as retinoid acid receptor RXRA and a member of the NR1 subfamily RORA. These are ligand-regulated TFs that have been implicated in epithelial differentiation and skin homeostasis (40, 41). Notably, TFs that were downregulated in the most differentiated epithelial cells in active EoE compared to control biopsies were highly enriched in the nuclear hormone receptors. Moreover, *RORA* recently has been identified as a genetic susceptibility risk locus in EoE by a GWAS (42), collectively signifying the potential role of this pathway in the protective function of the homeostatic esophageal epithelium.

Differentiated^{high} epithelial cells are characterized by specific expression of cysteine-rich metal-binding proteins, called metallothioneins, that sequester zinc, copper, and heavy metal ions (43). These proteins emerge as modulators of innate and adaptive immunologic responses, primarily as regulators of zinc metabolism and protection of cells against oxidative stress (44). Increased production of reactive oxygen species has been linked to the imbalance between self-renewal and differentiation of the esophageal epithelial cells caused by altered BMP signaling in EoE (28). Metallothionein expression is dramatically decreased in active EoE, likely due to loss of the Differentiated^{low/high} subpopulations, and is induced by proton pump inhibitors, which are widely used for treating EoE (45). These findings suggest involvement of zinc- and copper-mediated

processes in EoE pathogenesis and warrant further investigation of the immunomodulatory properties of metallothioneins in the esophageal epithelium.

Chronicity is a leading feature of EoE as clinical and histologic features of esophageal inflammation persist over time in most individuals (46). Despite initial improvement in symptoms, endoscopic characteristics, and histology of the esophageal biopsies in response to pharmacologic and dietary interventions, most individuals quickly relapse after cessation of medications, consistent with a fraction of the EoE transcriptome being refractory to treatment (47-49). The disease remission is primarily defined by the histologic assessment of the eosinophil density in the esophageal biopsies, which is not always sufficient to explain the symptoms. For example, pain is not well correlated with eosinophil counts (50). Our analysis reveals that the cellular composition of the esophageal biopsies in disease remission is marked by the decreased proportion of the differentiated compartment and increased proportion of the proliferating and transitioning compartments compared to those of healthy controls. Despite largely normalized gene expression and histologic remission in inactive disease, the single-cell epithelial differentiation program blocked at the differentiation stage in active EoE is only partially reversed in inactive disease, indicating that remission is a transitory state between the homeostatic and inflamed esophagus and is poised to relapse. It is tempting to speculate that esophageal epithelial cells maintain epithelial inflammatory memory similar to their skin counterparts (51, 52) and thus contribute to disease relapses. In the homeostatic esophageal epithelium, expression of *CAPN14*, the critical driver of allergic inflammation and genetically linked in EoE, is confined to the Differentiated^{low/high} subpopulations. In contrast, in active EoE *CAPN14* expression is detected in the transitioning and quiescent cells, where it remains highly

expressed even in EoE remission. Notably, CAPN14-mediated cleavage of DSG1, PPL, and DSP can trigger the loss of epithelial barrier integrity (53, 54). As TSLP release is highly responsive to the loss of epithelial barrier integrity (55) and the quiescent subpopulation specifically expresses *TSLP* (Figure 2B), these findings provide a plausible mechanism for disease relapse and underscore the necessity for improved diagnostic criteria for disease remission based on a molecular, single-cell profiling platform.

Methods

Subject inclusion criteria and biopsy sample acquisition. Biopsies and blood samples were acquired systemically from individuals who were having an endoscopy for EoE or related symptoms at Cincinnati Children's Hospital Medical Center (CCHMC). EoE was defined by a histologic finding of ≥ 15 esophageal eosinophils per microscopic high-power field with clinical symptoms. EoE remission (inactive EoE control) was defined by a history of EoE and an esophageal tissue eosinophil count of < 2 eosinophils/HPF at the time of biopsy. Healthy controls were defined by no history of EoE and a negative endoscopy with 0 eosinophils/HPF at the time of biopsy. Individuals' clinical and demographic information was obtained from the electronic medical record and research questionnaires.

Endoscopic biopsy processing. For each sample, three biopsies from the distal esophagus of a donor were collected into RPMI medium with 10% FBS, kept on ice, and transported to the research laboratory within 30 minutes. The biopsies were then transferred into EDTA buffer (5 mM EDTA, 10% FBS, 1 mM HEPES in PBS) for 15 minutes in a 37°C water bath, washed once with PBS, minced, and then subjected to collagenase A digestion (Roche, 10103578001, derived from *Clostridium histolyticum*, 2 mg/mL) in 10% FBS-RPMI at 37°C for 30 minutes. The resulting suspension was diluted with 10 mL ice-cold PBS, passed through a 19-gauge needle 5 times, filtered through 2 layers of gauze, washed twice with ice-cold PBS (10 mL each), and then centrifuged at 450 *g* for 5 minutes, resulting in a visible, clear-edged, translucent pellet. Isolated cells were subjected to 10X Genomics sequencing in the CCHMC Gene Expression Core according to the manufacturer instructions.

FACS sorting. Single-cell suspensions were generated from biopsies, and FACS was performed on ice for 30 minutes with the following antibodies: Invitrogen Live/Dead Yellow, human podoplanin PE (337003), human CD45 APC-Cy7 (304014), Human E-Cadherin (E-cad) APC (324108, all purchased from BioLegend Inc.). The 2 populations of interest were sorted by MoFlo machine under 2-way sorting settings with representative sorting chart shown (Figure 3A). Live singlet events were pre-selected by a Live/Dead+ FSC-A/FSC-H diagonal gate. The PDPN^{high} population was defined and sorted as live CD45-PDPN^{high}E-cadherin^{high} events, whereas the PDPN^{low} population was defined as live CD45-PDPN^{low}E-cadherin^{high} events. Sorting typically lasted around 30-45 minutes, with frequent agitation to collect the droplets attaching to the collection tube wall. Three biopsies collected from the distal esophagus typically yielded ~2,500–10,000 epithelial cells in each subpopulation, which were subsequently collected into RPMI-1640 media supplemented with 10% FBS and pelleted/centrifuged for immediate RNA isolation procedures using RNeasy Micro Kit (Qiagen).

Bulk RNA-sequencing of FACS-sorted cells. Total RNA was amplified using the Ovation RNA-Seq System v2 assay (Tecan Genomics) according to the manufacturer's protocol. The libraries were prepared with the Nextera XT DNA Sample Preparation kit (Illumina Technologies). One ng of cDNA was resuspended in Tagment DNA Buffer, and tagmentation (fragmentation and tagging with the adaptors) was performed with the Nextera enzyme (Amplicon Tagment Mix), incubating at 55°C for 10 min. NT Buffer was then added to neutralize the samples. Libraries were prepared by PCR with the random primer Nextera PCR Master Mix and 2 Nextera Indexes (N7XX and N5XX) according to the following program: 1

cycle of 72°C for 3 min; 1 cycle of 98°C for 30 s; 12 cycles of 95°C for 10 s, 55°C for 30 s, and 72°C for 1 min; and 1 cycle of 72°C for 5 min. The size of the libraries for each sample was measured using the Agilent HS DNA chip (Agilent Technologies). The samples were placed in a pool. The concentration of the pool was optimized to acquire at least 25-30 million reads per sample. Libraries were sequenced on the Illumina HiSeq2500 following the manufacturer's protocol using Paired-End Reads with a read length of 75 bps. RNA sequencing analysis was performed by BioWardrobe, as previously described (56).

Colony-forming ex vivo assay and immunofluorescence of the colonies. PDPN^{high} and PDPN^{low} cells were sorted in 200 mL of the SCM-68 medium, counted, and seeded in a 96-well plate together with 30,000 irradiated mouse fibroblasts NIH 3T3 that served as a feeder layer. SCM-68 medium contained freshly prepared cFAD medium and supplements. cFAD medium components were DMEM + Ham's F12 ratio 3:1 v/v; FBS (2% final) (Atlanta biologicals S10295); Human insulin (5 mg/mL) (Sigma 91077C); Adenine (24.3 mg/mL) (Sigma A2786); 3,3,5- triiodo-L-thyronine (T3) (2×10^{-9} M) (Sigma T6397); Hydrocortisone (0.4 mg/mL) (Sigma H0888); Cholera toxin (1×10^{-10} M), (Millipore 227036); and antibiotic-antimycotic solution (Fisher 15-240-096). Supplements included Recombinant Human R-Spondin 1 Protein, CF (125 ng/mL) (R&D, 4645-RS/CF); Jagged-1 (1 mM) (AnaSpec AS-61298); human Noggin (100 ng/mL) (Peprotech 120-10C); Rock-inhibitor (2.5 mM) (InSolution™ Y-27632); SB431542 (2 mM) (Cayman Chemicals SB-431542); and Nicotinamide (10 mM) (Sigma N0636). Colonies were typically counted 3–5 days after seeding. For immunofluorescence, primary epithelial cells were isolated by FACS sorting as above and seeded at 20,000–50,000 cells with 30,000 feeder layer fibroblasts per well on the 8-well ibiTreat chambers (Ibidi, 80826) for 3 days before

staining and imaging following a standard protocol. Antibodies used for staining were ITGA6 (BD Pharmingen 551129), E-cadherin (R&D AF648), SOX2 (Cell Signaling 3579), and cytokeratin 5 (Abcam ab24647), all at a 1/200 dilution in 2% donkey serum. Affinity-purified polyclonal secondary antibodies from the donkey serum were purchased from Jackson laboratories (017-000-121). DNA was stained with Hoechst 33342 Solution (Thermo Fisher). Imaging was performed with a Nikon A1 inverted confocal microscope.

Air-liquid interphase cultures. Cells from the esophageal epithelial TERT-immortalized cell line EPC2 (a gift from Anil Rustgi, University of Pennsylvania, Philadelphia, Pennsylvania, USA) were differentiated following an ALI protocol on 0.4- μ m pore-sized polyester permeable supports (Corning Incorporated, Corning, NY) in keratinocyte serum-free media (KSFM) (Life Technologies) essentially as previously described (45). Cultures were treated with the NOTCH inhibitors DAPT (final concentration 20 μ M) and Compound E (final concentration 1 μ M) and with IL-13 (final concentration 100 ng/mL) starting at day 1 of the exposure to air. Transepithelial electrical resistance (TEER) was measured using an EVOM (World Precision Instruments).

scRNA-seq library preparation

Single-cell suspensions were prepared from biopsies as described above. Bulk population cells were directly subjected to the 10X mass genomics chip (10X Genomics, Inc.), targeting 10,000 simultaneously captured live events. Each cell was uniquely barcoded during the cDNA library

generation by Single Cell 3' Reagent Kits v2 per the manufacturer instructions and subsequently sequenced on an Illumina HiSeq 2500 at the CCHMC DNA Sequencing and Genotyping Core.

scRNA-seq data analysis. All scRNA-seq data were processed using Cell Ranger version 3.0.2 and the hg19 reference. The UMI count matrix was imported to Seurat (10) for post processing and downstream analysis. For each sample, first, doublets were filtered out using Scrublet (57). Then, cells either with high mitochondrial reads, a low number of detected genes, or excess UMI counts were discarded. The UMI count matrix was normalized and scaled following the standard Seurat pipeline by adjusting for mitochondrial read counts and UMI counts. After the post processing, samples were integrated in two different ways: 1) by the disease status (i.e., healthy control, EoE remission, and active EoE) and 2) by all 10 samples using Seurat to compare the cellular population repertoire in an unbiased manner. Preliminary clustering was performed using the top 20 principal components to detect major cell types first, including epithelial cells and others, which were projected onto UMAP (58). Also, marker genes were called for cell type confirmation, detecting genes exclusively expressed in distinct populations. To do so, we performed a series of pairwise differential expression analyses against each of all the other cell clusters using the “FindMarkers” function in Seurat with the parameters $\log_2 \text{FC} > 0.25$ and $\text{min.pct} > 0.1$ and selected genes that were commonly highly expressed in each cluster. Epithelial cells were selected for the second-round clustering to identify subpopulations, and marker gene identification was performed the same way. This process was repeated for all 10-sample integrations and for each group-wise integration independently to confirm the similar cellular repertoire of epithelial subpopulations. The proportion of each cell type was measured for each sample and was compared between the different disease statuses using Student's t-test to

examine the change by the disease status. Detailed maps of quiescent and proliferating cells were also examined by combining PDPN^{low} or PDPN^{high} marker gene expression patterns and cell cycle mapping by Seurat in a UMAP. Pseudotime analysis was performed using Slingshot for all 10-sample integrations to map each cell from different groups onto a common pseudotime axis, which corresponded to the human esophageal epithelial differential trajectory. Cell densities along the epithelial differentiation pseudotime were visualized and compared across the different EoE statuses using a density plot, and a Student's t-test was performed to test the significance. Likewise, the same t-test was performed to compare cell density changes in quiescent basal, proliferating basal, and proliferating suprabasal cells. Overall sample-to-sample similarity in the epithelial cellular repertoire was visualized by hierarchical clustering based on the epithelial subpopulation proportion vector using a Pearson correlation coefficient as a similarity measure under Ward's criteria (59).

When comparing the expression profile of epithelial subpopulations between different EoE statuses, we sought to detect robust changes by utilizing the statistical power of the biological replicates. Therefore, rather than simply pooling all cells from biological replicates into single subpopulation clusters, we converted the UMI matrix into pseudo-bulk RNA-seq data by summing UMI counts per gene for each sample per epithelial subpopulation, using a total of 50 pseudo-bulk RNA-seq data (10 samples x 5 clusters). We subsequently performed differential gene expression analysis using DESeq2 (17) comparing healthy control vs. EoE remission and healthy control vs. active EoE. Thus, we were able to detect robust sets of EoE-dysregulated genes not biased to a specific sample. Genes with a FC > 1.5 and FDR-adjusted p < 0.05 were selected as differential genes. Gene ontology analysis was performed using Enrichr (60). We noticed that many of the EoE differentiation genes were dysregulated, especially in the

differentiated cells. Thus, we performed another differential analysis comparing the extreme two ends of cell clusters, quiescent cells and differentiated cells, for each of the disease status (healthy control, EoE remission, active EoE) samples. Genes differentially expressed as a function of epithelial differentiation and by EoE status for each epithelial subpopulation were pooled and subjected to hierarchical clustering to examine the EoE-dependent dysregulation of gene expression required for epithelial differentiation. We identified three types of patterns: 1) Type 1 - severely dysregulated (induce or repressed) in active EoE vs. healthy control; 2) Type 2 - moderately dysregulated (induced or repressed) in active EoE vs. healthy control; 3) Type 3 - normally expressed, i.e. similar level of expression as that of healthy control. Gene ontology analysis was performed for these groups of genes using Enrichr (60). The list of all human TFs was obtained from Lambert *et al.* (61) for the visualization of their expression level in epithelial subpopulations and their changes by disease status. TF expression was visualized in two ways, a short list and an extended list. The short list of TFs was prepared by identifying exclusively expressed TFs in each subpopulation, and the extended list was prepared by identifying TFs that display altered expression between any subpopulations.

Statistics

Statistical results were performed with GraphPad Prism, version 9, software. Data are reported as mean $\pm$ SD. For comparison of 2 groups, statistical significance was determined by unpaired, 2-tailed Student's t-tests. For comparison of more than 2 groups, 1-way ANOVA was used. $P < 0.05$ was considered significant.

Data availability

Next-generation sequencing data have been uploaded to GEO under the accession numbers GSE201154 (bulk RNAseq) and GSE201154 (scRNAseq).

Study approval

Samples were obtained following informed consent under the auspices of the Institutional Review Board (IRB) of CCHMC (#2008-0090).

Author Contributions

T.W. and M.E.R. designed the study; T.W. and M.R. performed experiments; M.K., P.J.B., N.B.-B.M., and H.-W.L. analyzed the data; M.R., J.C., H.-W.L., and M.E.R. wrote the manuscript; M.E.R. supervised the study. All authors reviewed and edited the manuscript.

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Declaration of Interests

Conflict of interest: M.E.R. is a consultant for Pulm One, Spoon Guru, ClostraBio, Serpin Pharm, Allakos, Celgene, Astra Zeneca, Arena Pharmaceuticals, Ellodi Pharma, GlaxoSmithKline, Regeneron/Sanofi, Revolo Biotherapeutics, and Guidepoint and has an equity interest in the first five listed and royalties from reslizumab (Teva Pharmaceuticals), PEESV2 (Mapi Research Trust), and UpToDate. M.E.R. is an inventor of patents owned by Cincinnati Children's Hospital Medical Center. The other authors have no potential conflicts to disclose.

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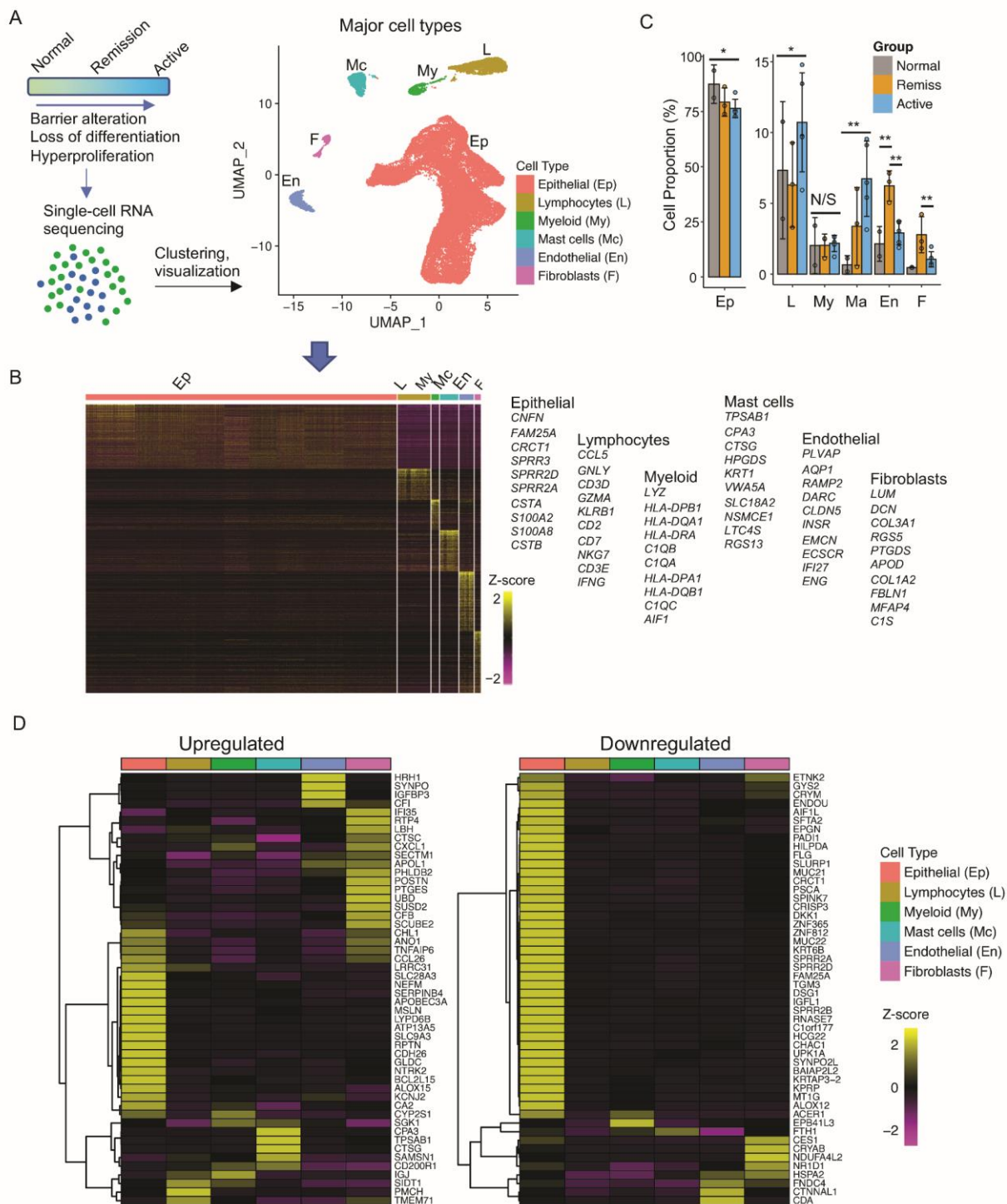


Figure 1. Single-cell analysis of human esophageal biopsies delineating major esophageal cell types. A, schematic representation of the experimental design and the uniform manifold approximation and projection (UMAP) of all samples depicting major cell types from the esophageal biopsies. $n = 2$, healthy controls (normal); $n = 3$, EoE in remission (remission); $n = 5$, active EoE inflammation (active). B, marker gene expression heatmap of major cell types and top 10 representative genes per cell type. Each column represents a single cell, and each row represents an individual gene. C, quantification of the cell types and comparison of their proportion by disease status (* $p = 0.06$; ** $p < 0.05$; N/S, not significant, Student's t-test. Error bar: standard error). D, heatmap of average expression of all 10 samples for top 50 upregulated and downregulated genes from the bulk RNA-seq EoE transcriptome (6) stratified by the cell type.

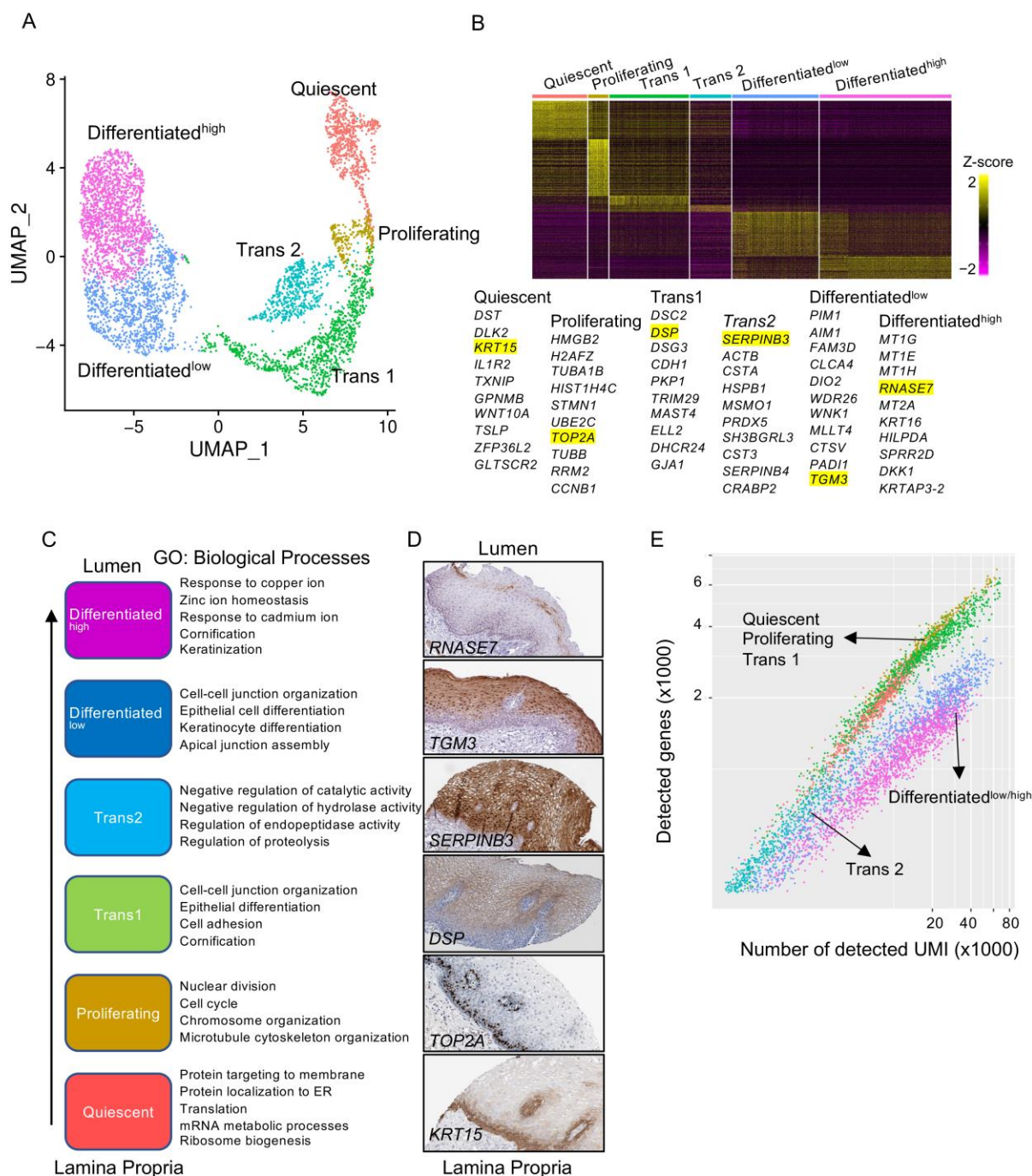


Figure 2. Single-cell RNA sequencing analysis of homeostatic (normal) esophageal epithelium. A, UMAP projection depicting 6 esophageal epithelial subpopulations. B, marker gene expression heatmap and top 10 representative genes of epithelial subpopulations. Each column represents a single cell, and each row represents an individual gene. Genes highlighted in yellow are accompanied by immunohistochemical images in D. C, the spatial organization of the epithelial subpopulations in the esophageal epithelium. Arrow indicates the direction of the putative differentiation program from the basal cells adjacent to the lamina propria toward the lumen. Most significant biological process GO terms are shown for each subpopulation. D, immunohistochemical images of the representative markers (yellow background in B) from the Human Protein Atlas (HPA) for each subpopulation. E, scatter plot of UMI counts versus number of detected genes per cell showing relatively smaller number of expressed genes in the differentiated subpopulations. Color coding same as in A.

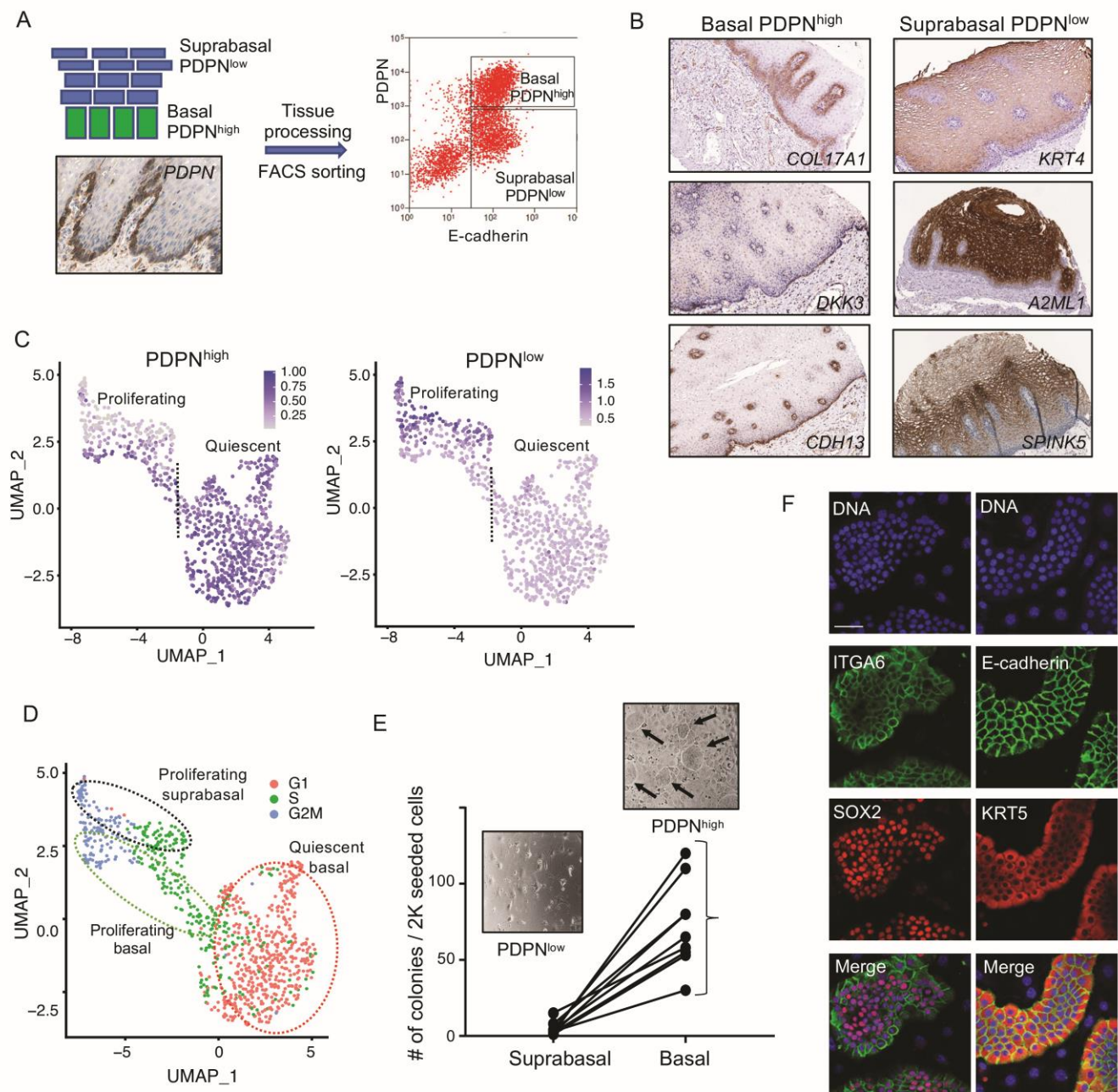


Figure 3. Functional and molecular properties of the human esophageal basal layer cells in homeostasis. A, schematic representation of the experimental design to purify and characterize basal layer cells (upper left). Podoplanin (PDPN) staining depicting basal layer localization from the Human Protein Atlas (HPA) (lower left). A representative FACS plot shows the gating strategy to purify PDPN^{high} for basal cells and PDPN^{low} for suprabasal cells (right). B, immunohistochemical images from HPA of the representative markers for basal and suprabasal cells identified by differential analysis of bulk RNA-seq data comparing PDPN^{high} and PDPN^{low} cells. C, average expression of top 20 PDPN^{high} and PDPN^{low} marker genes projected onto UMAP of quiescent and proliferating cells from healthy controls distinguishing basal and suprabasal cells; dotted line separates quiescent and proliferating cells. D, cell cycle status of cells inferred by Seurat projected onto UMAP of quiescent and proliferating cells. E, ex vivo colony-forming assay for sorted basal and suprabasal cells. Each line represents cells from a biopsy obtained from a distinct individual. A total number of colonies per 2000 seeded cells are plotted. Representative images of the high-power microscopic field show colony growth of basal PDPN^{high} cells (arrows; upper image, x10 magnification). Cells in the PDPN^{low} image are mitotically inactivated murine fibroblasts that served as feeder layer cells for colony growth. F, Immunofluorescence images of the colonies grown from the PDPN^{high} cells. Scale bar is 50 μ m for all images.

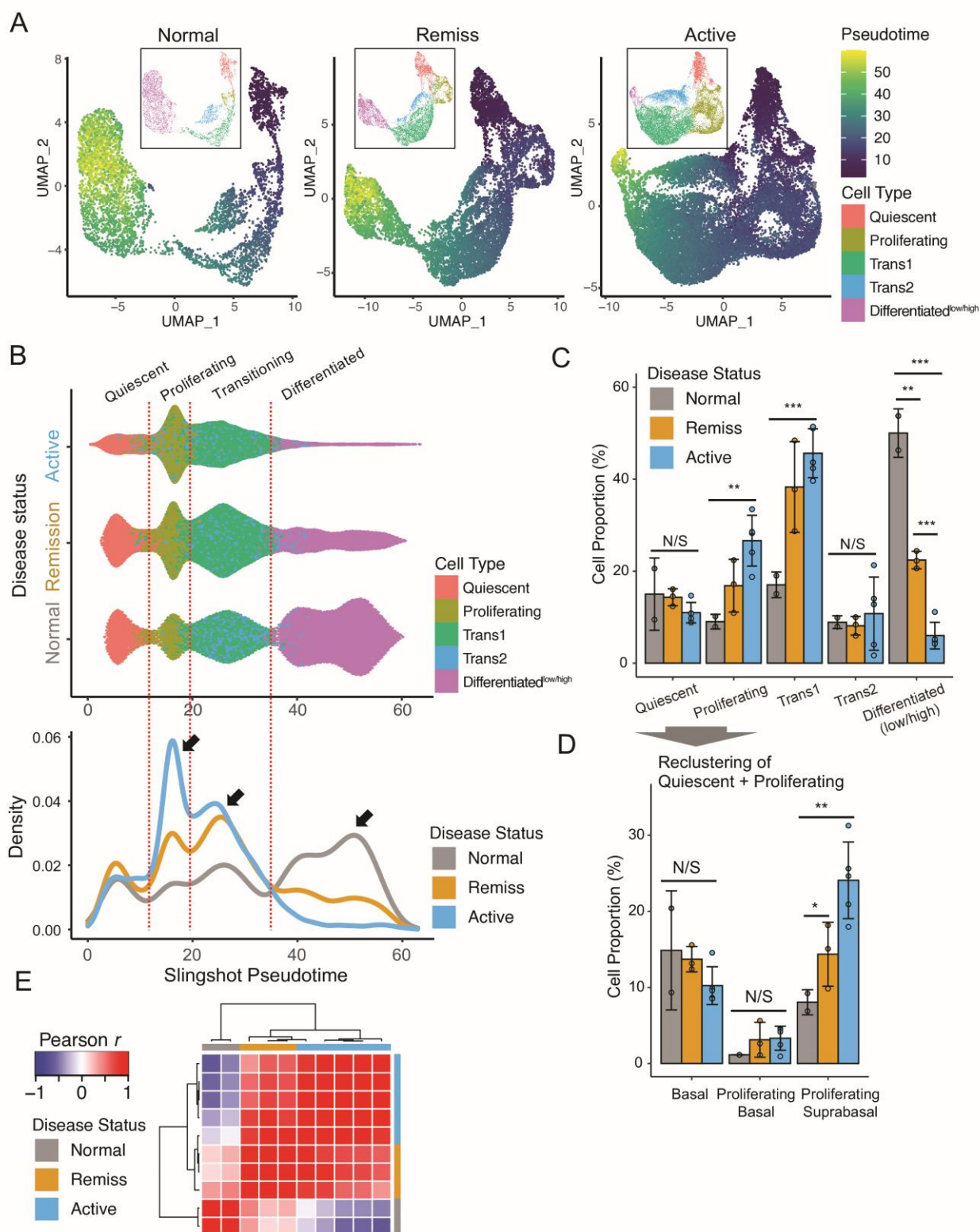


Figure 4. Human esophageal epithelial responses in allergic inflammation. A, slingshot pseudotime of esophageal epithelium differentiation projected onto UMAP in color scale for healthy controls (Normal), EoE remission (Remiss), and active EoE (Active). Insets show the epithelial subpopulations identified by unbiased clustering. B, swarm and density plots showing cell densities along the pseudotime. C, D, statistical comparison of the epithelial subpopulation composition among the disease states (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; N/S, not significant, Student's t-test. Error bar: standard error). E, hierarchical clustering of all 10 samples comparing the epithelial subpopulation composition by disease status using Pearson correlation coefficient as a similarity measure (healthy controls [Normal], EoE remission [Remiss], and active EoE [Active]). Each column represents an individual sample.

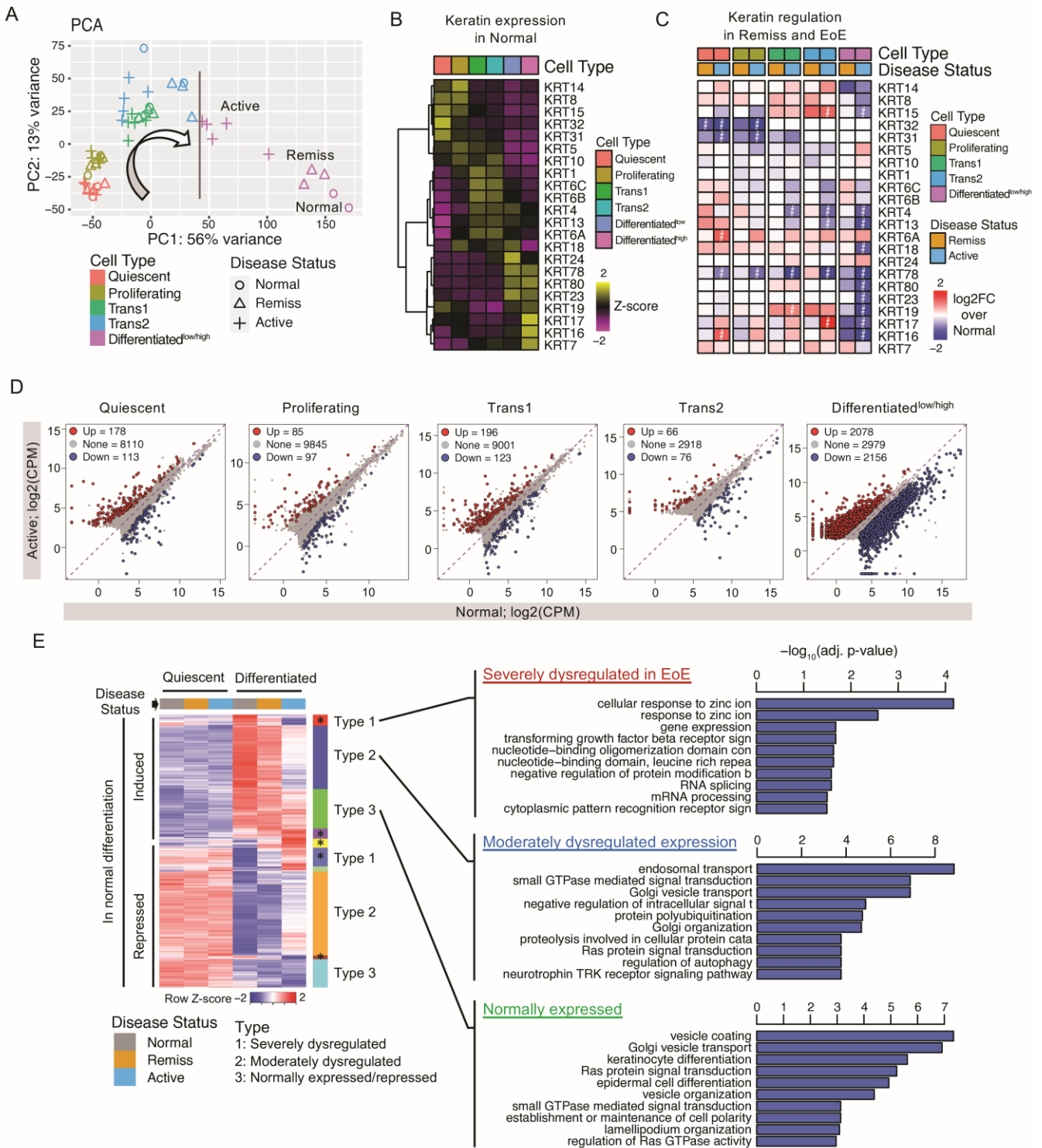


Figure 5. Pseudo-bulk RNA-seq analysis to compare gene expression dysregulation and epithelial cell fate of human esophageal epithelial subpopulations by disease status. A, principal component analysis (PCA) of the pseudo-bulk RNA-seq samples derived from scRNA-seq by summing UMI counts per gene per epithelial subpopulation per biopsy. The arrow shows developmental trajectory; the vertical line represents developmental blockage in active EoE. B, hierarchical clustering heatmap of keratin gene expression in the healthy control epithelium (Normal). C, log2 fold change (log2FC) of keratin gene expression in active EoE (Active) and EoE remission (Remiss) samples compared to normal by the differential expression analysis of the pseudo-bulk RNA-seq (# FDR-adjusted $p < 0.05$). Genes are ordered the same as in B. Note that the Differentiated^{high} and Differentiated^{low} cell subpopulations are represented by one unified cell population. D, scatter plots show differentially expressed genes in epithelial subpopulations of active EoE (EoE) compared to healthy controls (NL) ($FC > 1.5$ and FDR-adjusted $p < 0.05$). E, hierarchical clustering heatmap of differentially expressed genes between Differentiated and Quiescent epithelial subpopulations in the normal and diseased esophagus. Two groups of genes are observed that are either induced or repressed upon normal differentiation. In each group, induced or repressed, three types of patterns are observed: Type 1, severely dysregulated; Type 2, moderately dysregulated; and Type 3, normally expressed (induced or repressed). Top significantly enriched biological process GO terms are presented for the differentiation-induced genes.

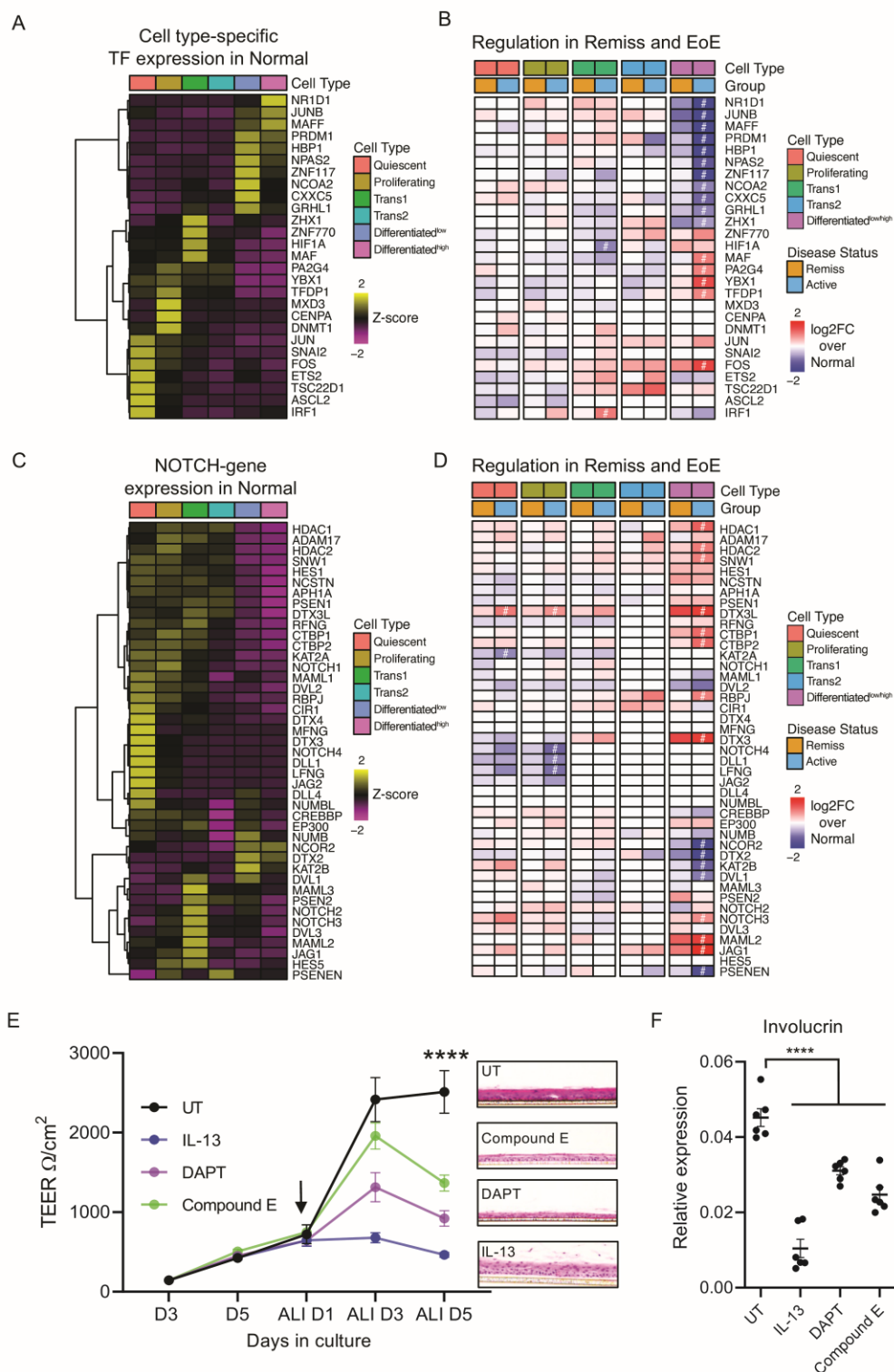


Figure 6. Expression of transcription factors and NOTCH-related genes in human esophageal epithelial cells. A, gene expression heatmap of subpopulation-specific transcription factors (TF) in the healthy control esophagus (Normal). B, log₂FC of the subpopulation-specific TFs in the active EoE (Active) and remission EoE (Remiss) esophagus compared to the normal esophagus by pseudo-bulk RNA-seq differential analysis (# FDR-adjusted $p < 0.05$). Genes are ordered the same as in B. C, gene expression heatmap of the NOTCH signaling pathway genes (KEGG) in the normal epithelial subpopulations. D, log₂FC of the NOTCH gene expression in the active EoE (Active) and remission EoE (Remiss) esophagus compared to the normal esophagus by pseudo-bulk RNA-seq differential analysis (# FDR-adjusted $p < 0.05$). Genes are ordered the same as in C. For B and D, Differentiated^{high} and Differentiated^{low} cell subpopulations are represented by one unified cell population. E, Transepithelial electrical resistance (TEER) was measured in the EPC2 cells grown at the air-liquid interface (ALI) and treated as indicated. Data are from 3–5 independent experiments performed in triplicate (mean $\pm$ SEM); **** $p < 0.0001$ for ALI Day 5 (D5) compared to untreated (UT), ANOVA. Insets show representative hematoxylin & eosin staining of the ALI cultures (x10 magnification). F, relative expression of involucrin in the EPC2 cells grown at the ALI for 5 days (ALI D5). Expression was normalized to GAPDH. Combined data for 3 independent cultures performed in duplicates is shown (mean $\pm$ SEM); **** $p < 0.0001$ compared to UT, ANOVA.

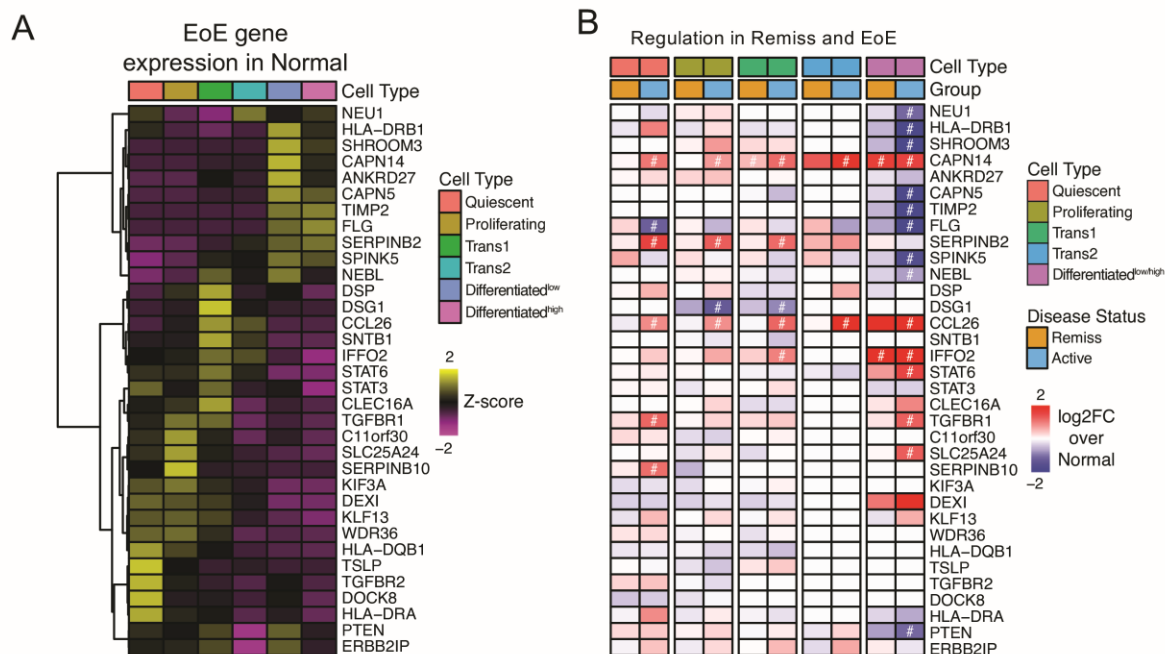


Figure 7. Expression of the epithelial genes genetically linked to EoE and food allergy. A, gene expression heatmap of 34 genes genetically linked to EoE and food allergy by genome-wide association (GWAS), Mendelian association, or candidate gene approaches delineated by the epithelial subpopulations in the healthy control esophagus (Normal). B, log₂FC of the genetically linked genes in the active EoE (Active) and EoE remission (Remiss) esophagus compared to healthy control obtained by pseudo-bulk RNA-seq differential analysis (# FDR-adjusted $p < 0.05$). Genes are ordered the same as in A. Note that the Differentiated^{high} and Differentiated^{low} cell subpopulations are represented by one unified cell population.

Supplemental Table 1. Markers of cell types defined in human esophageal biopsies

gene	logfc_min	adjp_max	cell type
FAM25A	2.52	2.63711E-25	Epithelial
CRCT1	2.48	3.48371E-10	Epithelial
SPRR3	2.44	5.86954E-25	Epithelial
SPRR2D	2.41	6.91323E-24	Epithelial
SPRR2A	2.40	1.17387E-43	Epithelial
CSTA	2.37	1.91E-286	Epithelial
S100A2	2.35	0	Epithelial
S100A8	2.35	3.2851E-110	Epithelial
CSTB	2.28	2.0581E-170	Epithelial
KRT15	2.27	1.6021E-158	Epithelial
S100A14	2.27	0	Epithelial
S100A9	2.25	4.77E-134	Epithelial
MAL	2.23	1.80918E-53	Epithelial
KRT13	2.22	1.1053E-240	Epithelial
KRT4	2.22	5.5932E-111	Epithelial
CRNN	2.21	7.57608E-50	Epithelial
SPINK5	2.14	2.6257E-171	Epithelial
KRT19	2.12	3.2511E-237	Epithelial
SPRR1B	2.09	2.3192E-93	Epithelial
LY6D	2.04	3.3703E-206	Epithelial
RHCG	2.04	4.5585E-191	Epithelial
KRT5	1.99	4.0849E-187	Epithelial
SPRR1A	1.99	1.71331E-75	Epithelial
KRT78	1.97	2.75045E-29	Epithelial
SERPINB3	1.95	1.4186E-177	Epithelial
AQP3	1.93	1.1087E-245	Epithelial
MIR205HG	1.89	1.2417E-189	Epithelial
TMPRSS11B	1.87	1.82401E-24	Epithelial
SFN	1.85	3.3424E-245	Epithelial
KRT6A	1.82	1.532E-210	Epithelial
PERP	1.80	1.0708E-290	Epithelial
FXYD3	1.71	1.0602E-245	Epithelial
LYPD2	1.70	6.31601E-21	Epithelial
FABP5	1.70	3.2951E-121	Epithelial
EMP1	1.68	5.81865E-35	Epithelial
S100P	1.68	4.51351E-34	Epithelial
TGM3	1.66	2.25588E-52	Epithelial
SPRR2E	1.65	7.25342E-32	Epithelial
DSP	1.59	1.2432E-251	Epithelial

CRABP2	1.58	1.2519E-139	Epithelial
TXN	1.57	3.2772E-200	Epithelial
FLG	1.57	1.61785E-08	Epithelial
MT1G	1.54	7.39294E-17	Epithelial
SERPINB4	1.54	1.0903E-99	Epithelial
PI3	1.54	3.51393E-54	Epithelial
CALML3	1.52	2.4917E-174	Epithelial
KRT14	1.51	1.56334E-30	Epithelial
IL1RN	1.50	3.8333E-125	Epithelial
PPL	1.48	1.0465E-131	Epithelial
C19orf33	1.44	1.4077E-246	Epithelial
SPINK7	1.44	1.9309E-16	Epithelial
LYPD3	1.43	1.0904E-177	Epithelial
ERO1L	1.39	1.58565E-40	Epithelial
LCN2	1.39	4.88444E-63	Epithelial
SCEL	1.38	4.7283E-126	Epithelial
SLPI	1.37	2.4053E-123	Epithelial
MT1X	1.37	1.40819E-88	Epithelial
HSPB1	1.36	1.512E-193	Epithelial
TACSTD2	1.33	4.1431E-233	Epithelial
KRT16	1.32	2.11151E-78	Epithelial
PSCA	1.32	2.02122E-18	Epithelial
MUC21	1.31	1.04406E-28	Epithelial
ALDH3A1	1.27	9.5824E-172	Epithelial
PRSS27	1.26	7.45898E-35	Epithelial
GSTP1	1.20	1.5141E-184	Epithelial
C9orf169	1.20	1.51186E-67	Epithelial
GBP6	1.20	6.9692E-144	Epithelial
KRT6B	1.20	1.39208E-98	Epithelial
LYNX1	1.20	4.81483E-56	Epithelial
DAPL1	1.19	4.6895E-142	Epithelial
ECM1	1.18	1	Epithelial
SBSN	1.18	7.36337E-63	Epithelial
KLF5	1.14	1.6785E-197	Epithelial
DSG3	1.13	6.5922E-151	Epithelial
NCCRP1	1.11	8.7252E-52	Epithelial
A2ML1	1.11	2.84241E-92	Epithelial
MAL2	1.09	1.693E-163	Epithelial
CLDN7	1.08	5.7239E-184	Epithelial
LGALS7B	1.05	9.6335E-113	Epithelial
KLK11	1.04	3.547E-166	Epithelial
RAB25	1.04	1.4692E-170	Epithelial
CRISP3	1.03	1.64062E-17	Epithelial

TMEM40	1.01	3.8975E-136	Epithelial
S100A16	1.01	2.1839E-273	Epithelial
CAPN14	1.01	1.31681E-85	Epithelial
GJB2	1.00	8.1541E-108	Epithelial
PDZK1IP1	1.00	6.4428E-136	Epithelial
DSC3	0.99	2.5571E-150	Epithelial
FAM129B	0.98	4.5393E-102	Epithelial
EPS8L1	0.98	2.83361E-22	Epithelial
SDC1	0.98	1.5049E-164	Epithelial
PITX1	0.97	7.2247E-139	Epithelial
ELF3	0.96	7.4642E-102	Epithelial
SERPINB13	0.96	7.2959E-129	Epithelial
PKP3	0.96	8.7595E-149	Epithelial
DSC2	0.96	7.5028E-122	Epithelial
TMPRSS11E	0.96	3.17959E-41	Epithelial
TXNDC17	0.96	1.4899E-188	Epithelial
S100A11	0.94	1.3353E-204	Epithelial
CLCA4	0.94	9.49745E-73	Epithelial
TRIM29	0.94	6.9995E-160	Epithelial
MGST1	0.93	7.5246E-125	Epithelial
MUC1	0.93	2.73329E-30	Epithelial
SERPINB2	0.92	2.25276E-96	Epithelial
JUP	0.92	2.1293E-170	Epithelial
FGFBP1	0.92	3.171E-87	Epithelial
SERPINB5	0.91	7.2069E-133	Epithelial
ANXA1	0.91	6.505E-166	Epithelial
ADH7	0.89	2.6564E-137	Epithelial
SLURP1	0.89	4.19654E-34	Epithelial
LMO7	0.88	1.03798E-66	Epithelial
RHOV	0.87	9.2743E-121	Epithelial
PKP1	0.86	8.1012E-132	Epithelial
CLDN4	0.86	2.2897E-99	Epithelial
HILPDA	0.85	3.33448E-20	Epithelial
MXD1	0.83	1.16923E-07	Epithelial
CEACAM6	0.83	5.51263E-56	Epithelial
LGALS7	0.80	1.60954E-73	Epithelial
PGD	0.79	8.3469E-147	Epithelial
C6orf132	0.78	2.8189E-93	Epithelial
CLCA2	0.78	1.9951E-114	Epithelial
KRT6C	0.76	1.14486E-58	Epithelial
LAD1	0.76	2.024E-146	Epithelial
CAPNS2	0.75	4.0669E-113	Epithelial
C2orf54	0.75	1.50455E-97	Epithelial

CLIC3	0.74	2.17986E-81	Epithelial
PRDX1	0.73	1.8279E-99	Epithelial
GLTP	0.73	1.2013E-133	Epithelial
CLTB	0.73	1.3281E-108	Epithelial
EVPL	0.73	2.52113E-94	Epithelial
AIF1L	0.73	7.18316E-25	Epithelial
DEFB1	0.72	2.73636E-96	Epithelial
PRSS22	0.72	1.47446E-42	Epithelial
KLK10	0.72	1.55837E-86	Epithelial
NMU	0.71	1.8419E-107	Epithelial
SPINT1	0.71	3.1754E-107	Epithelial
ALDH3A2	0.70	4.1233E-134	Epithelial
BLVRB	0.70	3.7513E-105	Epithelial
VSNL1	0.70	2.045E-104	Epithelial
TSPO	0.69	2.2916E-175	Epithelial
CXCL17	0.68	9.5985E-100	Epithelial
DMKN	0.65	7.1744E-90	Epithelial
TMPRSS11D	0.65	4.7658E-59	Epithelial
PADI1	0.64	9.71455E-24	Epithelial
ATP5G3	0.64	6.92278E-77	Epithelial
SH3BGRL2	0.64	3.92781E-49	Epithelial
CES2	0.62	2.66635E-95	Epithelial
MPZL2	0.61	3.6748E-161	Epithelial
SCIN	0.61	1.56562E-68	Epithelial
EHF	0.60	3.2361E-116	Epithelial
BARX2	0.60	4.29629E-84	Epithelial
GABRP	0.59	3.85975E-63	Epithelial
TTC9	0.59	8.77226E-51	Epithelial
CAPN1	0.59	1.5098E-115	Epithelial
ATP1B1	0.59	7.85701E-83	Epithelial
PAX9	0.58	4.11143E-96	Epithelial
FAM3B	0.58	2.2519E-67	Epithelial
FAM3D	0.58	2.25723E-33	Epithelial
DUSP5	0.57	0.034264846	Epithelial
PRSS3	0.56	2.82533E-31	Epithelial
DHCR24	0.56	1.582E-103	Epithelial
GRPEL2	0.56	2.5807E-22	Epithelial
CKMT1B	0.55	1.21511E-89	Epithelial
CKMT1A	0.55	1.03803E-96	Epithelial
SDCBP2	0.55	1.28928E-64	Epithelial
PVRL4	0.54	4.85655E-91	Epithelial
TMPRSS11BNL	0.54	8.81017E-69	Epithelial
HMGA1	0.54	5.8604E-108	Epithelial

SULT2B1	0.53	1.61253E-73	Epithelial
SDR16C5	0.53	2.06034E-82	Epithelial
SOX2	0.53	3.12276E-86	Epithelial
SERPINB1	0.53	8.27267E-57	Epithelial
TMPRSS11A	0.53	1.72022E-74	Epithelial
GIPC1	0.53	6.08328E-89	Epithelial
PRSS8	0.52	1.23184E-75	Epithelial
PTPRF	0.52	4.9313E-91	Epithelial
LTA4H	0.52	3.0217E-100	Epithelial
IRF6	0.52	1.48348E-94	Epithelial
COMTD1	0.51	3.8983E-104	Epithelial
S100A7	0.51	1.76755E-14	Epithelial
CTC-276P9.1	0.50	2.60437E-54	Epithelial
PPDPF	0.50	2.44388E-14	Epithelial
STAP2	0.49	6.40612E-97	Epithelial
PTTG1	0.49	1.30204E-82	Epithelial
KLK13	0.49	9.92419E-61	Epithelial
IVL	0.49	2.0799E-56	Epithelial
CXADR	0.49	8.6985E-106	Epithelial
ENO1	0.48	3.47564E-60	Epithelial
TUBB4B	0.48	1.65647E-76	Epithelial
HEBP2	0.48	4.36933E-83	Epithelial
CTNNBIP1	0.48	3.86964E-82	Epithelial
MUC4	0.47	2.3325E-20	Epithelial
ERBB3	0.47	4.1641E-78	Epithelial
TUBA1C	0.47	3.69071E-66	Epithelial
PRRG4	0.47	1.44902E-98	Epithelial
GPT2	0.47	3.37411E-60	Epithelial
GRHL1	0.47	9.08442E-71	Epithelial
SDC4	0.46	2.22209E-79	Epithelial
S100A10	0.46	2.78966E-59	Epithelial
PLIN3	0.46	1.04603E-70	Epithelial
IL20RB	0.46	2.81222E-84	Epithelial
ESRP1	0.46	2.85536E-90	Epithelial
C1orf116	0.45	2.89469E-55	Epithelial
GCHFR	0.45	4.51447E-56	Epithelial
ABLM1	0.45	3.14915E-79	Epithelial
RAB10	0.45	5.45993E-77	Epithelial
EIF5A	0.45	3.02206E-59	Epithelial
IL18	0.44	7.33146E-23	Epithelial
NAA20	0.44	6.27842E-91	Epithelial
COX6A1	0.44	3.07731E-54	Epithelial
DTX2	0.44	3.25699E-45	Epithelial

TKT	0.44	2.01265E-57	Epithelial
PRDX5	0.44	3.82396E-52	Epithelial
MDH2	0.43	5.50604E-68	Epithelial
C4orf3	0.43	6.75029E-06	Epithelial
DUOX1	0.43	5.28824E-65	Epithelial
EPS8L2	0.43	1.43692E-92	Epithelial
TALDO1	0.43	4.19509E-82	Epithelial
AKR1B10	0.43	8.64207E-40	Epithelial
GJB6	0.43	3.30349E-51	Epithelial
COA3	0.43	1.95261E-64	Epithelial
EPHA2	0.42	4.98956E-40	Epithelial
CDH1	0.42	3.62433E-69	Epithelial
CCDC64B	0.42	7.09568E-57	Epithelial
TGM1	0.42	1.20736E-34	Epithelial
RIOK3	0.42	2.08932E-79	Epithelial
USMG5	0.41	3.49715E-72	Epithelial
NTRK2	0.41	2.89432E-49	Epithelial
SH3YL1	0.41	4.03931E-83	Epithelial
TECR	0.41	7.0349E-67	Epithelial
YOD1	0.41	1.46686E-19	Epithelial
MRPL12	0.40	9.31834E-67	Epithelial
NTS	0.40	8.0887E-06	Epithelial
AHNAK	0.40	1.7839E-56	Epithelial
GGH	0.40	8.29197E-62	Epithelial
TMPRSS4	0.40	3.24495E-71	Epithelial
CAST	0.40	5.06739E-74	Epithelial
ATP5I	0.40	3.93654E-37	Epithelial
EIF6	0.40	4.31606E-65	Epithelial
COX7A2	0.39	4.9387E-66	Epithelial
ANXA2	0.39	2.48132E-80	Epithelial
KRT8	0.39	7.94497E-58	Epithelial
TP63	0.39	7.69886E-60	Epithelial
SLC7A1	0.39	1.39917E-59	Epithelial
PVRL1	0.39	2.06306E-67	Epithelial
ALDH9A1	0.39	5.21256E-65	Epithelial
ANXA3	0.38	1.13992E-51	Epithelial
SPINT2	0.38	1.73225E-80	Epithelial
CEACAM5	0.38	1.72037E-26	Epithelial
H2AFJ	0.38	1.32049E-40	Epithelial
NEAT1	0.38	1.65541E-09	Epithelial
ALDOA	0.37	1.22137E-41	Epithelial
DUOXA1	0.37	1.19147E-64	Epithelial
FUT3	0.37	4.62307E-36	Epithelial

VDAC2	0.37	2.68489E-64	Epithelial
AHCY	0.37	9.0698E-79	Epithelial
SCGB1A1	0.37	1.8286E-15	Epithelial
PTGR1	0.37	3.99418E-63	Epithelial
MPP7	0.37	5.86862E-65	Epithelial
MALL	0.37	1.61811E-18	Epithelial
RIPK4	0.36	3.04332E-55	Epithelial
TRNP1	0.36	3.08307E-32	Epithelial
KRT17	0.36	4.80502E-25	Epithelial
COX8A	0.36	1.2028E-63	Epithelial
KRT7	0.36	2.55241E-26	Epithelial
TMOD3	0.36	1.91431E-48	Epithelial
CD9	0.36	5.54401E-51	Epithelial
RP11-532F12.5	0.36	1.58331E-58	Epithelial
CDH26	0.36	3.03633E-20	Epithelial
TMEM79	0.35	2.52982E-57	Epithelial
RNF141	0.35	1.54573E-73	Epithelial
GPR110	0.35	1.0826E-23	Epithelial
UQCRQ	0.35	1.21689E-39	Epithelial
CBR1	0.35	6.15372E-58	Epithelial
ERBB2	0.35	6.72186E-58	Epithelial
KLK12	0.35	5.80852E-23	Epithelial
STK24	0.35	2.00465E-65	Epithelial
CYC1	0.34	1.55481E-49	Epithelial
VSIG10L	0.34	1.13841E-30	Epithelial
RHOD	0.34	9.77392E-59	Epithelial
CERS3	0.34	4.74216E-56	Epithelial
ZNF750	0.34	3.07612E-54	Epithelial
ATP5A1	0.34	6.13173E-39	Epithelial
ATP5B	0.34	7.73682E-47	Epithelial
SERINC2	0.34	6.11394E-56	Epithelial
GPR87	0.34	1.9587E-70	Epithelial
ALDH3B2	0.34	4.41042E-48	Epithelial
NUDT8	0.34	2.15426E-52	Epithelial
TMEM45B	0.34	2.44792E-39	Epithelial
DDR1	0.34	8.72232E-66	Epithelial
ASPG	0.33	1.65877E-45	Epithelial
IMPA2	0.33	2.23093E-67	Epithelial
CCNB1	0.33	1.98955E-19	Epithelial
CRNDE	0.33	2.88394E-68	Epithelial
COX5B	0.33	7.10409E-35	Epithelial
SLC25A3	0.33	5.03668E-41	Epithelial
TIMM13	0.33	1.40522E-47	Epithelial

PROM2	0.33	8.597E-55	Epithelial
RAPGEFL1	0.32	8.50597E-56	Epithelial
FGFR3	0.32	2.27205E-50	Epithelial
ETFB	0.32	6.80464E-59	Epithelial
SCNN1B	0.32	1.35029E-47	Epithelial
CCL26	0.32	1.02143E-14	Epithelial
ATP5H	0.32	1.39136E-55	Epithelial
DENND2C	0.32	2.18232E-45	Epithelial
ZNF812	0.32	2.64296E-17	Epithelial
MT-CO3	0.31	2.65291E-18	Epithelial
NAPRT1	0.31	1.69927E-70	Epithelial
TMEM54	0.31	7.27151E-63	Epithelial
FAM162A	0.31	3.1757E-50	Epithelial
TRIM16	0.31	2.51343E-64	Epithelial
DBI	0.31	6.0897E-52	Epithelial
FAM83D	0.31	1.50212E-51	Epithelial
SYTL1	0.31	2.3129E-112	Epithelial
MUC15	0.31	3.46274E-44	Epithelial
GJB5	0.31	1.38923E-61	Epithelial
EMP2	0.31	4.86952E-54	Epithelial
UQCRC1	0.31	3.87377E-52	Epithelial
MAPK13	0.31	6.83813E-67	Epithelial
PPIA	0.31	5.33517E-40	Epithelial
AP1M2	0.31	1.09025E-60	Epithelial
TMPRSS2	0.31	7.33634E-17	Epithelial
BNIP1L	0.31	3.18451E-47	Epithelial
CYP4B1	0.30	9.68088E-47	Epithelial
TP53AIP1	0.30	4.23912E-39	Epithelial
TIMM8B	0.30	1.27938E-61	Epithelial
C10orf99	0.30	3.52411E-40	Epithelial
P4HB	0.30	6.28671E-40	Epithelial
KCTD1	0.30	9.75514E-60	Epithelial
MYH14	0.30	5.28876E-43	Epithelial
RRM2	0.29	6.26751E-21	Epithelial
LINC01133	0.29	1.88675E-48	Epithelial
HSBP1L1	0.29	5.23911E-66	Epithelial
TRIP10	0.29	5.85632E-30	Epithelial
TMEM184A	0.29	3.08854E-39	Epithelial
CENPW	0.29	1.38696E-31	Epithelial
TPD52L1	0.29	4.28897E-98	Epithelial
TMEM134	0.29	2.95676E-79	Epithelial
RALA	0.29	4.57894E-74	Epithelial
GJB3	0.29	5.52061E-53	Epithelial

SRD5A1	0.29	7.44365E-59	Epithelial
CRB3	0.29	3.26726E-44	Epithelial
EPHX3	0.29	2.81656E-51	Epithelial
ANXA9	0.28	1.50186E-14	Epithelial
COX6B1	0.28	1.37665E-41	Epithelial
SOWAHC	0.28	2.67438E-54	Epithelial
C1QBP	0.28	3.89326E-41	Epithelial
C18orf25	0.28	1.90849E-24	Epithelial
ATP5G1	0.28	4.438E-49	Epithelial
SH3RF2	0.28	1.44596E-45	Epithelial
IDH1	0.28	1.86672E-66	Epithelial
ATP5J2	0.28	1.28399E-48	Epithelial
SPNS2	0.28	1	Epithelial
MTCH2	0.28	3.80111E-55	Epithelial
KRTCAP3	0.28	1.03475E-46	Epithelial
SCNN1A	0.28	3.54433E-42	Epithelial
SMIM5	0.27	9.2811E-39	Epithelial
LAMB3	0.27	1.31939E-27	Epithelial
TTC22	0.27	1.49636E-40	Epithelial
PPP1R14B	0.27	1.72707E-56	Epithelial
GID8	0.27	6.16067E-69	Epithelial
C14orf2	0.27	2.73616E-30	Epithelial
F12	0.27	1.90635E-45	Epithelial
AC004562.1	0.27	6.25298E-20	Epithelial
AKR1C2	0.27	5.46611E-25	Epithelial
TPRG1	0.27	3.76813E-30	Epithelial
C20orf24	0.27	1.18168E-51	Epithelial
NDUFB9	0.26	1.79476E-30	Epithelial
HK1	0.26	1.69298E-59	Epithelial
FAM83H	0.26	1.92744E-48	Epithelial
RAN	0.26	2.88174E-23	Epithelial
COL17A1	0.26	3.13479E-16	Epithelial
GPX2	0.26	7.47746E-36	Epithelial
ARHGAP32	0.26	3.52553E-44	Epithelial
CA2	0.26	1.15407E-15	Epithelial
RHBDL2	0.26	3.16029E-49	Epithelial
SFTA2	0.25	5.64525E-12	Epithelial
KCNK7	0.25	1.73109E-35	Epithelial
SCD	0.25	2.60286E-41	Epithelial
RPLP0	0.25	1.60126E-43	Epithelial
YWHAZ	0.25	2.60411E-95	Epithelial
VPS4B	0.25	1.43143E-58	Epithelial
ATP6V1D	0.25	1.68676E-60	Epithelial

CCDC34	0.25	1.47383E-36	Epithelial
PHLDA3	0.25	7.03691E-47	Epithelial
ATP5O	0.25	3.32445E-29	Epithelial
CCL5	3.39	9.9358E-186	Lymphocyte
GNLY	2.62	5.5608E-43	Lymphocyte
CD3D	2.60	2.063E-195	Lymphocyte
GZMA	2.57	2.1884E-119	Lymphocyte
KLRB1	2.55	1.21724E-88	Lymphocyte
CD2	2.48	3.8599E-180	Lymphocyte
CD7	2.45	3.7341E-168	Lymphocyte
NKG7	1.99	1.7497E-108	Lymphocyte
CD3E	1.98	2.529E-131	Lymphocyte
IFNG	1.88	1.02765E-40	Lymphocyte
IL32	1.78	2.8085E-165	Lymphocyte
CD3G	1.74	1.49312E-84	Lymphocyte
GZMB	1.69	6.71542E-65	Lymphocyte
PTPRCAP	1.64	1.4877E-157	Lymphocyte
LCK	1.51	1.98955E-75	Lymphocyte
CD8A	1.51	4.95003E-57	Lymphocyte
XCL2	1.50	9.54459E-36	Lymphocyte
KLRC1	1.41	7.34028E-31	Lymphocyte
AC092580.4	1.41	2.73124E-49	Lymphocyte
GZMH	1.37	4.29311E-38	Lymphocyte
ZFP36L2	1.36	3.6036E-132	Lymphocyte
XCL1	1.35	2.11838E-23	Lymphocyte
GZMK	1.31	2.43914E-21	Lymphocyte
ZNF683	1.29	5.656E-37	Lymphocyte
CD8B	1.28	5.06444E-41	Lymphocyte
CXCR4	1.16	6.8608E-110	Lymphocyte
KLRD1	1.12	9.75733E-32	Lymphocyte
STK17A	1.11	9.06398E-38	Lymphocyte
BTG1	1.10	1.5919E-209	Lymphocyte
CD96	1.09	1.68993E-40	Lymphocyte
CD247	1.09	2.22506E-37	Lymphocyte
CCL4	1.08	9.04321E-50	Lymphocyte
PPP2R5C	1.08	9.72995E-38	Lymphocyte
GZMM	1.04	1.85929E-34	Lymphocyte
GPR171	1.04	2.86669E-33	Lymphocyte
CD27	1.03	4.53677E-36	Lymphocyte
PRF1	0.99	1.24289E-28	Lymphocyte
SIT1	0.98	1.2641E-33	Lymphocyte
RORA	0.98	3.02349E-24	Lymphocyte
ACAP1	0.96	6.90086E-34	Lymphocyte

PTPRC	0.95	1.44811E-57	Lymphocyte
CXCR6	0.94	8.84389E-28	Lymphocyte
EVL	0.93	1.37017E-69	Lymphocyte
LAG3	0.91	3.27568E-24	Lymphocyte
CITED2	0.89	3.45554E-21	Lymphocyte
TIGIT	0.89	1.16993E-21	Lymphocyte
CST7	0.89	1.90103E-27	Lymphocyte
IL2RB	0.84	3.47656E-23	Lymphocyte
TBC1D10C	0.83	1.11059E-29	Lymphocyte
RGL4	0.83	9.89889E-23	Lymphocyte
APOBEC3G	0.82	1.63403E-19	Lymphocyte
SEPT1	0.82	1.95826E-23	Lymphocyte
ICOS	0.81	7.15584E-20	Lymphocyte
ISG20	0.80	2.65733E-17	Lymphocyte
CLEC2D	0.80	1.57213E-18	Lymphocyte
PYHIN1	0.80	1.91717E-19	Lymphocyte
CD6	0.80	3.42244E-22	Lymphocyte
GATA3	0.79	2.4379E-19	Lymphocyte
RP11-138A9.2	0.75	1.7247E-08	Lymphocyte
PTGER4	0.75	2.14235E-09	Lymphocyte
RARRES3	0.70	1.67323E-14	Lymphocyte
CYTIP	0.68	2.0246E-13	Lymphocyte
BCL11B	0.68	1.25894E-07	Lymphocyte
KIAA1551	0.66	3.54538E-10	Lymphocyte
ZAP70	0.64	2.03094E-14	Lymphocyte
STK17B	0.63	1.83607E-32	Lymphocyte
DUSP2	0.63	2.52134E-23	Lymphocyte
FYB	0.61	1.04236E-10	Lymphocyte
TOB1	0.61	1	Lymphocyte
DUSP4	0.60	3.74268E-09	Lymphocyte
RP11-51J9.5	0.59	2.50021E-11	Lymphocyte
B2M	0.59	6.0142E-150	Lymphocyte
RAB27A	0.58	4.57636E-09	Lymphocyte
LINC00152	0.57	0.000801003	Lymphocyte
STK4	0.57	8.182E-12	Lymphocyte
FAM46C	0.57	2.19956E-12	Lymphocyte
EML4	0.56	0.000100225	Lymphocyte
CCDC107	0.54	0.000211593	Lymphocyte
RP11-138A9.1	0.54	0.000447314	Lymphocyte
FKBP11	0.54	0.044919722	Lymphocyte
SPOCK2	0.53	3.64875E-09	Lymphocyte
CORO1A	0.53	1.62392E-21	Lymphocyte
TTC39C	0.53	1	Lymphocyte

TAGAP	0.53	0.025030844	Lymphocyte
CD48	0.52	4.81873E-06	Lymphocyte
PTPN22	0.52	6.53217E-09	Lymphocyte
PIK3IP1	0.52	4.832E-07	Lymphocyte
RASGRP1	0.51	0.001250313	Lymphocyte
PTPN4	0.51	3.17195E-07	Lymphocyte
CDC42SE2	0.50	0.572892456	Lymphocyte
ANKRD32	0.50	2.74369E-05	Lymphocyte
FNBP1	0.50	0.313900344	Lymphocyte
GNG2	0.50	7.17797E-07	Lymphocyte
PPP1R2	0.49	1	Lymphocyte
RNF213	0.49	1	Lymphocyte
IL7R	0.49	5.0678E-13	Lymphocyte
LEPROTL1	0.49	6.31464E-15	Lymphocyte
RP11-94L15.2	0.47	7.67105E-15	Lymphocyte
SLA	0.47	1	Lymphocyte
SEPT9	0.45	1	Lymphocyte
GYPC	0.45	0.075105013	Lymphocyte
RHOF	0.45	1	Lymphocyte
EMB	0.45	0.765178946	Lymphocyte
LYAR	0.44	1	Lymphocyte
PFKFB3	0.44	1	Lymphocyte
RP11-640M9.1	0.44	0.001269711	Lymphocyte
ICAM3	0.44	0.464183929	Lymphocyte
PARP8	0.43	0.001650707	Lymphocyte
BIN2	0.43	1	Lymphocyte
LTB	0.43	1	Lymphocyte
SRSF7	0.43	1	Lymphocyte
AAK1	0.43	0.006472225	Lymphocyte
BIN1	0.42	0.135826236	Lymphocyte
GABARAPL1	0.42	1	Lymphocyte
PNRC1	0.42	2.64488E-08	Lymphocyte
TNFRSF18	0.42	1	Lymphocyte
BATF	0.41	0.002228536	Lymphocyte
TRAF3IP3	0.41	2.66459E-08	Lymphocyte
ARL4C	0.40	1	Lymphocyte
BUB3	0.40	1	Lymphocyte
LDLRAD4	0.40	1	Lymphocyte
CLDND1	0.39	1	Lymphocyte
SH2D2A	0.39	1.03784E-07	Lymphocyte
PPP1R18	0.39	1	Lymphocyte
PCSK7	0.38	1	Lymphocyte
SMCHD1	0.38	1	Lymphocyte

SUN2	0.37	1	Lymphocyte
TSC22D4	0.37	0.000556946	Lymphocyte
PRDM1	0.37	1	Lymphocyte
ANKRD12	0.37	1	Lymphocyte
DOK2	0.36	1	Lymphocyte
ARHGEF1	0.36	1	Lymphocyte
DENND2D	0.36	2.24656E-07	Lymphocyte
CTSW	0.36	1	Lymphocyte
ZC3HAV1	0.35	1	Lymphocyte
SYTL3	0.35	0.042742159	Lymphocyte
CDKN1B	0.34	1	Lymphocyte
RASAL3	0.34	0.131464571	Lymphocyte
LIMD2	0.34	1	Lymphocyte
AKNA	0.34	1	Lymphocyte
DEF6	0.34	1	Lymphocyte
C9orf78	0.33	1	Lymphocyte
TUBA4A	0.33	2.23596E-12	Lymphocyte
RNF167	0.33	1	Lymphocyte
FAM177A1	0.33	1	Lymphocyte
ARHGAP9	0.33	1	Lymphocyte
RPS29	0.33	4.13705E-30	Lymphocyte
WIPF1	0.32	1	Lymphocyte
TERF2IP	0.32	1	Lymphocyte
PIP4K2A	0.32	0.075687788	Lymphocyte
PRPF38B	0.32	1	Lymphocyte
TBCC	0.31	1	Lymphocyte
TAPSAR1	0.31	1	Lymphocyte
RPS27	0.31	4.23486E-58	Lymphocyte
LNPEP	0.31	1	Lymphocyte
TNFRSF1B	0.31	1	Lymphocyte
PPP1CA	0.31	1	Lymphocyte
MALAT1	0.30	3.1909E-85	Lymphocyte
ID2	0.30	8.1697E-13	Lymphocyte
PIK3R1	0.30	1	Lymphocyte
RBL2	0.30	1	Lymphocyte
APBB1IP	0.30	1	Lymphocyte
FGFR1OP2	0.29	1	Lymphocyte
FAM107B	0.29	1	Lymphocyte
HMHA1	0.29	1	Lymphocyte
TMC6	0.29	1	Lymphocyte
PBXIP1	0.28	1	Lymphocyte
TAPBP	0.28	1	Lymphocyte
ARHGAP30	0.28	1	Lymphocyte

CCDC167	0.27	1	Lymphocyte
ARF6	0.27	7.82932E-06	Lymphocyte
TLK1	0.27	1	Lymphocyte
APOBEC3C	0.27	1	Lymphocyte
SPN	0.27	1	Lymphocyte
IKZF1	0.26	1	Lymphocyte
G3BP2	0.26	1	Lymphocyte
CRIP1	0.26	1	Lymphocyte
MGAT4A	0.26	1	Lymphocyte
MBNL1	0.26	1	Lymphocyte
RP11-349A22.5	0.26	1	Lymphocyte
CCND3	0.25	1	Lymphocyte
IL16	0.25	1	Lymphocyte
CD52	0.25	1.9874E-20	Lymphocyte
HMOX2	0.25	1	Lymphocyte
PRRC2C	0.25	1	Lymphocyte
GMFG	0.25	1	Lymphocyte
LYZ	3.58	1.0398E-122	Monocyte
HLA-DPB1	3.36	1.9344E-226	Monocyte
HLA-DQA1	3.15	6.1355E-200	Monocyte
HLA-DRA	3.14	1.2143E-242	Monocyte
C1QB	2.81	4.26943E-83	Monocyte
C1QA	2.81	8.61835E-88	Monocyte
HLA-DPA1	2.75	1.083E-225	Monocyte
HLA-DQB1	2.62	4.6946E-194	Monocyte
C1QC	2.61	6.31682E-82	Monocyte
AIF1	2.40	1.7821E-152	Monocyte
MS4A6A	2.27	1.3725E-121	Monocyte
IL1B	2.26	8.56476E-69	Monocyte
CD74	2.09	7.1812E-237	Monocyte
HLA-DRB1	2.09	3.0129E-228	Monocyte
S100B	2.01	1.50211E-66	Monocyte
HLA-DRB5	1.87	8.13328E-53	Monocyte
IL8	1.83	6.03691E-40	Monocyte
LST1	1.81	2.5373E-128	Monocyte
CD1E	1.65	1.1789E-63	Monocyte
CLEC10A	1.63	4.22237E-71	Monocyte
RNASE6	1.52	3.11742E-80	Monocyte
HLA-DQA2	1.50	4.31776E-50	Monocyte
HLA-DQB2	1.47	8.65273E-42	Monocyte
FCGBP	1.44	1.05906E-28	Monocyte
HLA-DMA	1.42	1.3708E-139	Monocyte
CD1A	1.38	5.31579E-38	Monocyte

HLA-DMB	1.34	2.5702E-101	Monocyte
CTSS	1.32	1.29544E-73	Monocyte
MNDA	1.32	1.06182E-57	Monocyte
LGALS2	1.32	6.26563E-45	Monocyte
CST3	1.24	1.8339E-43	Monocyte
FGL2	1.24	7.60248E-77	Monocyte
G0S2	1.21	2.00494E-17	Monocyte
CPVL	1.20	2.75012E-56	Monocyte
CD14	1.17	3.61395E-31	Monocyte
DNASE1L3	1.16	4.10837E-24	Monocyte
NPC2	1.10	1.36518E-38	Monocyte
IGSF6	1.10	3.07892E-52	Monocyte
CCL3	1.07	3.88758E-21	Monocyte
LY86	1.06	8.81352E-55	Monocyte
MS4A7	1.06	2.91301E-40	Monocyte
CD86	1.05	2.21221E-51	Monocyte
CSF1R	1.02	1.27301E-49	Monocyte
CTSZ	1.02	7.88123E-43	Monocyte
YWHAH	1.01	6.57919E-37	Monocyte
CD1C	1.00	2.16445E-39	Monocyte
CLEC7A	0.94	1.2095E-46	Monocyte
SERPINA1	0.94	3.25614E-35	Monocyte
MARCH1	0.90	3.88809E-47	Monocyte
FCGR2A	0.88	2.66298E-41	Monocyte
SPI1	0.83	1.05033E-52	Monocyte
FCGR2B	0.83	4.91077E-36	Monocyte
FAM26F	0.83	4.31416E-48	Monocyte
PKIB	0.83	2.65203E-45	Monocyte
CD207	0.82	4.39704E-15	Monocyte
HERPUD1	0.82	4.7212E-47	Monocyte
IER5	0.81	1.56625E-05	Monocyte
HCK	0.80	2.03629E-45	Monocyte
IER3	0.80	1	Monocyte
FCER1A	0.80	0.000125777	Monocyte
MPEG1	0.79	4.5766E-34	Monocyte
ATF3	0.79	7.16543E-30	Monocyte
CLEC4A	0.78	1.94311E-35	Monocyte
FCGR3A	0.77	3.32632E-19	Monocyte
GPX1	0.75	2.1094E-50	Monocyte
CTSB	0.74	1	Monocyte
HLA-DOA	0.70	2.70148E-34	Monocyte
PLEK	0.70	3.95641E-51	Monocyte
IFI30	0.68	1.57391E-31	Monocyte

RB1	0.67	4.99006E-25	Monocyte
OLR1	0.64	7.84272E-20	Monocyte
TUBA1B	0.63	3.72133E-29	Monocyte
IRF8	0.63	5.41712E-19	Monocyte
VMO1	0.63	4.00705E-14	Monocyte
LITAF	0.61	3.39981E-16	Monocyte
TYROBP	0.60	8.54171E-35	Monocyte
ADAM28	0.59	4.15841E-29	Monocyte
CD68	0.58	7.71902E-25	Monocyte
STAB1	0.58	2.97201E-10	Monocyte
ITGB2	0.58	7.61215E-61	Monocyte
FTL	0.57	1.08164E-06	Monocyte
GDI2	0.57	8.85885E-13	Monocyte
PPT1	0.57	6.17944E-17	Monocyte
SPP1	0.57	4.33408E-11	Monocyte
FPR3	0.56	5.37749E-19	Monocyte
CD4	0.56	3.38593E-24	Monocyte
COTL1	0.56	3.60902E-38	Monocyte
CLEC5A	0.55	2.9837E-20	Monocyte
THEMIS2	0.54	5.87876E-22	Monocyte
PHACTR1	0.53	1.4783E-31	Monocyte
ARPC3	0.53	6.05353E-41	Monocyte
RNASET2	0.52	7.22009E-35	Monocyte
FAM49B	0.52	1.56998E-46	Monocyte
SAMHD1	0.52	7.01873E-23	Monocyte
FGD2	0.51	1.66572E-17	Monocyte
TYMP	0.51	5.49459E-08	Monocyte
SOD2	0.51	0.011136958	Monocyte
TGFB1	0.49	1.05704E-05	Monocyte
CECR1	0.49	1.5599E-20	Monocyte
TREM2	0.49	6.72062E-16	Monocyte
GPR183	0.48	1.21697E-11	Monocyte
P2RY13	0.47	1.06132E-20	Monocyte
FAM96A	0.47	1	Monocyte
PTPRE	0.46	3.24836E-19	Monocyte
PLD4	0.44	2.82895E-17	Monocyte
ALDH2	0.44	1	Monocyte
BASP1	0.44	6.55416E-26	Monocyte
CHMP1B	0.43	1	Monocyte
MFSD1	0.42	1	Monocyte
CXCL16	0.42	1.26699E-15	Monocyte
NCF2	0.41	1.54711E-18	Monocyte
GRN	0.40	1	Monocyte

VAMP8	0.40	2.44647E-12	Monocyte
SMCO4	0.40	1.58439E-07	Monocyte
LACC1	0.40	2.74328E-11	Monocyte
SLC7A7	0.39	2.49757E-11	Monocyte
PPIF	0.38	1	Monocyte
CD83	0.38	6.81234E-08	Monocyte
EFHD2	0.38	1	Monocyte
F13A1	0.38	0.355308425	Monocyte
SLC20A1	0.37	5.05783E-10	Monocyte
GCA	0.37	5.90195E-12	Monocyte
SSR1	0.37	1	Monocyte
LAMTOR1	0.37	1	Monocyte
ZNF385A	0.37	1	Monocyte
ATP2B1	0.36	0.004447105	Monocyte
RGS18	0.36	1.13223E-20	Monocyte
ACTR2	0.36	0.001916704	Monocyte
B3GNT5	0.36	1	Monocyte
GLRX	0.36	2.38828E-22	Monocyte
OGFRL1	0.36	1	Monocyte
ATP6V1B2	0.35	1	Monocyte
CYBA	0.35	2.87412E-10	Monocyte
SMIM14	0.35	1	Monocyte
ACTB	0.35	2.02199E-20	Monocyte
AXL	0.35	0.020563317	Monocyte
GATM	0.35	1	Monocyte
LGALS9	0.34	6.7338E-09	Monocyte
ARPC5	0.34	2.89137E-08	Monocyte
SERPINB9	0.34	4.4386E-29	Monocyte
SLC8A1	0.33	9.17722E-09	Monocyte
PYCARD	0.33	0.002439372	Monocyte
FGR	0.33	7.49957E-09	Monocyte
GLIPR1	0.33	1.25041E-40	Monocyte
AP2S1	0.32	1	Monocyte
SIRPA	0.32	3.93416E-13	Monocyte
PLEK2	0.32	1	Monocyte
ADAP2	0.32	5.38244E-15	Monocyte
TNFSF13B	0.32	2.97451E-07	Monocyte
POU2F2	0.32	4.15708E-16	Monocyte
NAIP	0.32	5.0374E-08	Monocyte
HSPA1A	0.31	0.00069813	Monocyte
SLC43A2	0.30	2.62414E-13	Monocyte
ETV5	0.30	5.84713E-08	Monocyte
TPP1	0.30	2.56081E-12	Monocyte

C12orf45	0.30	1	Monocyte
SYK	0.30	1	Monocyte
ADAM19	0.30	2.34271E-24	Monocyte
SYNGR2	0.30	1	Monocyte
PLEKHO1	0.29	3.34293E-11	Monocyte
NAAA	0.29	1	Monocyte
NAMPT	0.29	1	Monocyte
TNFAIP8L2	0.28	1.26701E-18	Monocyte
INSIG1	0.28	0.004101411	Monocyte
VOPPI	0.27	0.173804443	Monocyte
C15orf48	0.27	5.61354E-21	Monocyte
CORO1C	0.27	1	Monocyte
HSPA6	0.27	1.99703E-13	Monocyte
PTPLAD2	0.27	0.000206642	Monocyte
BID	0.26	0.013427587	Monocyte
RPS11	0.26	9.6225E-18	Monocyte
CREBL2	0.26	0.040929166	Monocyte
DSE	0.26	1	Monocyte
ATG3	0.26	1	Monocyte
TMEM97	0.26	1	Monocyte
NFKBIE	0.26	1.46757E-11	Monocyte
RPS3A	0.26	1.04229E-12	Monocyte
RPS24	0.25	5.07816E-14	Monocyte
SSR3	0.25	1	Monocyte
PLEKHB2	0.25	1	Monocyte
SLAMF8	0.25	3.85253E-11	Monocyte
C12orf5	0.25	4.93072E-10	Monocyte
CREG1	0.25	1	Monocyte
CCDC88A	0.25	3.04359E-14	Monocyte
TPSAB1	5.33	0	Mast
CPA3	3.88	2.5272E-296	Mast
CTSG	2.98	7.2441E-147	Mast
HPGDS	2.59	1.7994E-231	Mast
KRT1	2.48	4.8802E-169	Mast
VWA5A	2.18	4.8768E-174	Mast
SLC18A2	2.15	4.2214E-161	Mast
RP11-354E11.2	2.11	8.5675E-151	Mast
NSMCE1	2.08	1.4985E-163	Mast
LTC4S	1.96	7.9779E-163	Mast
RGS13	1.86	2.3528E-124	Mast
GATA2	1.86	2.8389E-143	Mast
HPGD	1.81	6.5726E-159	Mast
UTS2	1.80	1.11175E-47	Mast

KIT	1.70	1.48617E-96	Mast
IL1RL1	1.70	1.2284E-104	Mast
GLUL	1.63	2.6039E-157	Mast
CLU	1.54	5.8497E-182	Mast
SAMSN1	1.51	3.5448E-240	Mast
HDC	1.40	3.32528E-74	Mast
SVOPL	1.27	3.366E-63	Mast
BTG2	1.24	1.3431E-111	Mast
SELK	1.21	2.9848E-100	Mast
DUSP6	1.18	7.32917E-83	Mast
NFKBIA	1.16	6.7906E-123	Mast
LIF	1.15	1.48918E-49	Mast
SOCS1	1.15	2.88369E-92	Mast
C1orf186	1.13	2.21855E-55	Mast
GCSAML	1.13	2.81673E-51	Mast
NCOA4	1.11	8.32358E-58	Mast
SRGN	1.09	3.0042E-224	Mast
AC020571.3	1.08	7.90247E-62	Mast
NFKBIZ	1.07	9.19486E-56	Mast
LEO1	1.05	5.60731E-50	Mast
SLC45A3	1.04	1.23139E-48	Mast
CLNK	1.01	1.66378E-43	Mast
SMYD3	0.99	9.88267E-46	Mast
DTNBP1	0.96	4.97884E-42	Mast
GMPR	0.93	6.76422E-44	Mast
ACOT7	0.92	3.10712E-52	Mast
CNRIP1	0.91	4.98004E-40	Mast
EXD3	0.89	6.89093E-30	Mast
DUSP10	0.84	3.52546E-47	Mast
MS4A2	0.84	2.15833E-35	Mast
FOSB	0.84	2.04033E-65	Mast
CAPG	0.83	1.005E-71	Mast
ABCC4	0.82	3.18815E-30	Mast
PTGS1	0.81	2.18249E-29	Mast
C1orf228	0.80	2.34923E-33	Mast
GALC	0.79	1.49102E-31	Mast
CTD-3203P2.2	0.78	5.73341E-27	Mast
CD69	0.77	3.0214E-102	Mast
ITGA2B	0.76	2.43648E-28	Mast
CATSPER1	0.75	1.30579E-34	Mast
PLIN2	0.75	3.09049E-29	Mast
CD44	0.74	3.71353E-80	Mast
PPP1R15A	0.74	6.50531E-31	Mast

TESPA1	0.73	1.72146E-38	Mast
OSBPL8	0.71	3.64496E-24	Mast
HS3ST1	0.71	2.5233E-13	Mast
RAB27B	0.71	0.011844994	Mast
NFATC1	0.71	6.40441E-11	Mast
CALB2	0.71	6.42695E-30	Mast
ATP6V0A2	0.68	1.93609E-30	Mast
CSF2RB	0.68	1.82452E-22	Mast
ARG2	0.67	9.05657E-19	Mast
GALNT6	0.67	9.78412E-27	Mast
MITF	0.67	5.5115E-19	Mast
CNIH1	0.66	1.05283E-05	Mast
NTRK1	0.66	1.14852E-26	Mast
ELSPBP1	0.66	6.1806E-22	Mast
LMNA	0.65	4.49913E-24	Mast
STAP1	0.65	1.89321E-21	Mast
SLC2A3	0.65	3.66984E-30	Mast
GRAP2	0.65	4.46239E-76	Mast
MANF	0.65	1.79482E-07	Mast
ADAM12	0.64	1.75362E-22	Mast
FOXP1	0.64	7.4689E-28	Mast
CPM	0.63	1.95866E-16	Mast
CMA1	0.62	5.77802E-15	Mast
LMO4	0.61	1	Mast
TWISTNB	0.59	2.7051E-13	Mast
CTNNBL1	0.59	4.336E-18	Mast
KLRG1	0.59	3.2597E-29	Mast
ZC3H12A	0.59	1.60662E-17	Mast
KCNMB1	0.57	0.000114688	Mast
GADD45B	0.57	1.28954E-09	Mast
STXBP6	0.57	2.27097E-18	Mast
CTTNBP2	0.57	1.43911E-13	Mast
BHLHE40	0.57	0.02498901	Mast
CD84	0.56	9.31356E-12	Mast
BIRC3	0.56	1.56949E-22	Mast
PRPSAP2	0.56	4.33625E-09	Mast
IER2	0.56	3.73515E-06	Mast
PLEKHF2	0.55	0.035115078	Mast
KCNH2	0.55	5.26414E-17	Mast
DNAJB9	0.54	3.99479E-16	Mast
TDRD3	0.54	1.50018E-14	Mast
RP11-620J15.3	0.53	5.26618E-10	Mast
AKAP12	0.53	1.3537E-11	Mast

ELL2	0.53	1	Mast
MLPH	0.53	2.21794E-18	Mast
C4orf48	0.53	7.47232E-13	Mast
KDM6B	0.53	3.48691E-05	Mast
GFRA3	0.53	2.03668E-17	Mast
CDK15	0.52	1.35848E-17	Mast
LYL1	0.52	5.02653E-06	Mast
PRDX6	0.52	1.88772E-20	Mast
SLC44A1	0.51	1	Mast
NR4A1	0.51	4.58193E-12	Mast
C10orf128	0.51	3.25854E-08	Mast
ABCB8	0.51	1	Mast
HSPA5	0.51	3.2856E-06	Mast
NR4A2	0.50	9.01992E-18	Mast
NUDT14	0.50	3.17529E-07	Mast
C5orf30	0.50	1.92384E-16	Mast
ALOX5AP	0.49	2.82713E-50	Mast
ARL5B	0.49	1.5923E-05	Mast
RP11-76E17.3	0.49	7.46271E-12	Mast
BMP2K	0.48	1.60337E-06	Mast
MBOAT7	0.48	2.32757E-06	Mast
C7orf73	0.48	1	Mast
ATP6V1F	0.47	8.83649E-05	Mast
TPSG1	0.47	5.77802E-15	Mast
SDF2L1	0.47	0.000490896	Mast
CLCN3	0.47	0.382642031	Mast
THAP2	0.47	1	Mast
CYCS	0.46	1	Mast
RHBDD2	0.46	1	Mast
GPR35	0.45	4.88609E-14	Mast
MAML1	0.45	1.87133E-11	Mast
DNAJC3	0.45	2.01949E-06	Mast
EGR3	0.44	2.6106E-05	Mast
THBS1	0.44	1	Mast
SLC26A2	0.44	1	Mast
BACE2	0.44	2.84637E-05	Mast
SEC61G	0.43	9.00941E-11	Mast
HES1	0.43	1	Mast
FAIM	0.43	0.318161828	Mast
RGS1	0.43	8.02289E-75	Mast
CSF1	0.43	5.15182E-08	Mast
RP11-557H15.4	0.43	5.8642E-13	Mast
SKIL	0.42	0.006389547	Mast

CTSD	0.42	1	Mast
ADRB2	0.42	0.074823	Mast
NFKBID	0.42	0.103279329	Mast
DDIT4	0.42	2.05505E-29	Mast
STARD4	0.42	1.82456E-06	Mast
LAT	0.41	6.65696E-49	Mast
AURKA	0.41	0.000438135	Mast
GPR65	0.41	9.29758E-17	Mast
LPCAT2	0.41	6.21627E-05	Mast
TMEM154	0.41	1	Mast
NEDD9	0.41	0.147315504	Mast
HSD17B12	0.40	1	Mast
SFT2D1	0.40	6.70731E-05	Mast
PCMT1	0.40	1	Mast
IDI1	0.40	1.92405E-16	Mast
TNFAIP8	0.39	2.34128E-10	Mast
RSAD2	0.39	2.52516E-12	Mast
H3F3B	0.39	2.04957E-40	Mast
ALOX5	0.39	0.14342562	Mast
FER	0.39	1.03394E-07	Mast
LAX1	0.39	1.72277E-26	Mast
PLGRKT	0.39	0.269541955	Mast
DUSP1	0.38	1.72327E-08	Mast
P2RY14	0.38	3.97775E-12	Mast
TBPL1	0.37	1.43369E-06	Mast
METTL21A	0.37	0.147995709	Mast
FTH1	0.37	2.60724E-50	Mast
VMP1	0.37	1	Mast
TNFRSF9	0.37	1.00793E-17	Mast
GPX4	0.36	1.81284E-10	Mast
EMR2	0.36	0.000429006	Mast
SVIP	0.36	0.001801776	Mast
MIR24-2	0.36	1.4462E-35	Mast
SLC4A2	0.36	6.79158E-09	Mast
FAM46A	0.36	1	Mast
AHR	0.35	1	Mast
MAFF	0.35	1	Mast
EGR1	0.35	4.84999E-08	Mast
SNX5	0.35	1	Mast
NUTM2A-AS1	0.34	1	Mast
FBP1	0.34	0.115726365	Mast
MAST4	0.34	1	Mast
TNIK	0.34	1.85979E-08	Mast

SPNS1	0.34	1	Mast
LMNB1	0.33	1	Mast
NUCB2	0.33	1	Mast
PTGS2	0.33	1	Mast
MSRA	0.33	1	Mast
NDFIP2	0.33	8.37137E-07	Mast
SEPT2	0.33	0.000848911	Mast
STX3	0.33	0.777183367	Mast
CD37	0.33	9.82904E-27	Mast
FAM110A	0.33	1	Mast
CD22	0.32	2.36218E-08	Mast
STXBP2	0.32	1	Mast
CD33	0.32	0.130792353	Mast
LINC00672	0.32	0.000524172	Mast
CAMLG	0.32	1	Mast
SLC11A1	0.32	1.37482E-06	Mast
PRKAR1A	0.32	0.083629492	Mast
FDX1	0.32	0.019927164	Mast
GNPTAB	0.31	1	Mast
FHL3	0.31	0.001816984	Mast
HSP90B1	0.31	1	Mast
HLTF	0.31	0.004581924	Mast
QPCT	0.31	0.001292313	Mast
ZFP36	0.30	1.33471E-29	Mast
C21orf91	0.30	6.53057E-07	Mast
PHLDA2	0.30	1	Mast
JUNB	0.30	2.87241E-18	Mast
DCXR	0.30	3.5319E-07	Mast
MYADM	0.30	0.001580618	Mast
PLAUR	0.29	1	Mast
SPCS1	0.29	0.002841307	Mast
ZNF331	0.29	0.836508041	Mast
BNIP3L	0.29	1	Mast
POLD4	0.29	1	Mast
RPL36AL	0.29	2.30834E-31	Mast
ATXN10	0.29	1	Mast
XBP1	0.29	1	Mast
FCER1G	0.28	6.99922E-24	Mast
LAT2	0.28	1	Mast
IRS2	0.28	0.363584343	Mast
JUN	0.28	6.09593E-18	Mast
TAF9	0.28	1	Mast
PPP1R15B	0.27	1	Mast

ARHGAP18	0.27	1	Mast
TNFAIP3	0.27	1.0422E-25	Mast
USP48	0.27	1	Mast
PDIA3	0.27	1	Mast
COX17	0.26	1	Mast
FOSL2	0.26	1	Mast
DRAP1	0.26	3.5077E-21	Mast
JAZF1	0.26	0.584820999	Mast
CXXC5	0.26	1	Mast
UBA7	0.26	1	Mast
CCDC28A	0.26	1	Mast
SDCBP	0.26	0.008875505	Mast
S100A4	0.26	1.42106E-45	Mast
MAPK6	0.26	4.2199E-05	Mast
VEGFA	0.26	0.915312851	Mast
CLIC1	0.26	4.48473E-12	Mast
MT1F	0.25	3.40387E-09	Mast
NDUFB2	0.25	1	Mast
NDEL1	0.25	1	Mast
PLVAP	2.94	9.3501E-232	Endothelial
AQP1	2.72	1.4998E-229	Endothelial
RAMP2	2.55	1.0157E-224	Endothelial
DARC	2.20	1.54146E-72	Endothelial
CLDN5	2.14	3.0394E-137	Endothelial
INSR	2.09	1.44057E-82	Endothelial
EMCN	2.08	1.7019E-182	Endothelial
ECSCR	1.87	4.4313E-175	Endothelial
IFI27	1.79	4.4971E-194	Endothelial
ENG	1.75	3.4925E-153	Endothelial
ID3	1.71	7.058E-161	Endothelial
ID1	1.69	9.1114E-135	Endothelial
ELTD1	1.66	1.8323E-139	Endothelial
NPDC1	1.65	3.4315E-141	Endothelial
CRIP2	1.64	3.1786E-161	Endothelial
VWF	1.62	2.7355E-117	Endothelial
GNG11	1.56	1.0458E-198	Endothelial
RAMP3	1.55	1.7036E-125	Endothelial
PODXL	1.50	4.3146E-99	Endothelial
JAM2	1.46	5.5316E-121	Endothelial
AC011526.1	1.42	1.5102E-111	Endothelial
CD34	1.39	1.1113E-114	Endothelial
CYYR1	1.38	1.3362E-111	Endothelial
CLEC14A	1.30	2.7842E-102	Endothelial

TM4SF18	1.29	7.98159E-90	Endothelial
VWA1	1.27	1.05431E-78	Endothelial
SLCO2A1	1.27	2.37748E-85	Endothelial
SOX18	1.22	2.83317E-71	Endothelial
HSPG2	1.18	4.92809E-71	Endothelial
NOSTRIN	1.12	2.18671E-82	Endothelial
ESAM	1.12	6.32819E-93	Endothelial
CALCRL	1.11	8.24529E-73	Endothelial
ITGA6	1.11	1.6234E-103	Endothelial
CD320	1.09	4.23678E-82	Endothelial
KDR	1.09	2.43945E-67	Endothelial
EGFL7	1.08	2.417E-128	Endothelial
RDX	1.07	1.45031E-76	Endothelial
PRSS23	1.05	6.17552E-57	Endothelial
HEG1	1.04	2.52705E-61	Endothelial
FAM167B	1.03	9.29845E-61	Endothelial
ADM5	1.03	3.02654E-57	Endothelial
TXNIP	1.02	2.11404E-96	Endothelial
PCDH17	1.01	2.34743E-62	Endothelial
FLT1	1.00	1.97219E-62	Endothelial
MMRN2	1.00	8.4859E-72	Endothelial
BCAM	1.00	3.93366E-88	Endothelial
TM4SF1	0.99	5.7801E-113	Endothelial
EFNA1	0.98	1.05268E-84	Endothelial
PALMD	0.97	9.54873E-68	Endothelial
ADCY4	0.96	1.49857E-68	Endothelial
CDH5	0.96	2.77857E-65	Endothelial
FKBP1A	0.95	7.4955E-114	Endothelial
HYAL2	0.94	7.14267E-58	Endothelial
ETS2	0.92	1.69921E-67	Endothelial
DUSP23	0.92	4.35217E-49	Endothelial
LIFR	0.92	5.99779E-54	Endothelial
MYCT1	0.91	3.50934E-64	Endothelial
NOTCH4	0.90	6.05469E-54	Endothelial
NRN1	0.90	4.48618E-58	Endothelial
ICAM2	0.90	1.89409E-70	Endothelial
SLC9A3R2	0.89	1.16065E-45	Endothelial
LMO2	0.88	6.04053E-66	Endothelial
IGFBP3	0.86	3.61778E-10	Endothelial
CCDC85B	0.85	1.11276E-87	Endothelial
LMCD1	0.85	9.70914E-59	Endothelial
IL33	0.85	1.14369E-42	Endothelial
CD93	0.85	2.2913E-68	Endothelial

RAB13	0.83	1.37631E-62	Endothelial
CD200	0.82	6.87968E-52	Endothelial
RCAN1	0.82	2.85658E-41	Endothelial
RUNDC3B	0.81	1.91611E-50	Endothelial
ROBO4	0.81	1.21101E-52	Endothelial
COL15A1	0.80	8.31879E-45	Endothelial
TSPAN13	0.80	8.93742E-50	Endothelial
KLF2	0.80	8.51194E-60	Endothelial
PASK	0.79	2.18046E-29	Endothelial
RNASE1	0.79	3.1048E-115	Endothelial
TGFBR2	0.79	4.86301E-47	Endothelial
SOX17	0.78	2.71436E-44	Endothelial
HOXD9	0.77	1.85993E-48	Endothelial
PKP4	0.77	3.90335E-60	Endothelial
ELK3	0.76	2.52343E-50	Endothelial
SERTAD4-AS1	0.76	9.0073E-48	Endothelial
KANK3	0.76	1.38428E-48	Endothelial
SYNPO	0.76	2.92753E-42	Endothelial
APLNR	0.75	9.77934E-45	Endothelial
TSC22D1	0.74	4.13462E-94	Endothelial
THSD7A	0.74	1.08002E-45	Endothelial
ABCG2	0.73	1.61236E-39	Endothelial
SOCS3	0.72	1.50098E-35	Endothelial
CDC37	0.72	2.24558E-52	Endothelial
ADAM15	0.71	1.45237E-51	Endothelial
SRP14	0.71	1.23931E-50	Endothelial
MCTP1	0.70	2.10907E-38	Endothelial
LDB2	0.70	8.32882E-48	Endothelial
RASA4	0.70	1.04192E-39	Endothelial
FAM110D	0.70	4.69272E-46	Endothelial
VAMP5	0.69	4.45231E-46	Endothelial
TSHZ2	0.68	1.42624E-42	Endothelial
SELE	0.68	1.46626E-16	Endothelial
SNCG	0.67	2.25318E-41	Endothelial
LEPR	0.67	9.06401E-41	Endothelial
NFIB	0.66	2.55692E-44	Endothelial
GPR146	0.66	1.09672E-40	Endothelial
STC1	0.65	2.26067E-14	Endothelial
LIMS2	0.65	8.72551E-40	Endothelial
TIE1	0.65	2.64038E-51	Endothelial
ERG	0.65	1.35198E-44	Endothelial
SELP	0.64	9.91126E-25	Endothelial
ABCB1	0.63	1.35539E-34	Endothelial

HOXD8	0.63	8.32331E-39	Endothelial
CCL14	0.63	5.09896E-31	Endothelial
RASIP1	0.63	8.52682E-45	Endothelial
RND1	0.63	3.98496E-27	Endothelial
GIMAP7	0.62	3.8006E-123	Endothelial
PVRL2	0.62	5.01792E-38	Endothelial
SPTBN1	0.62	4.79959E-39	Endothelial
MEOX1	0.62	5.18613E-33	Endothelial
LUZP1	0.61	8.31298E-39	Endothelial
LINC01116	0.60	7.35079E-38	Endothelial
JAG2	0.60	2.72754E-29	Endothelial
PLXND1	0.60	2.22971E-33	Endothelial
EHD4	0.60	5.58878E-46	Endothelial
GIMAP4	0.60	4.35076E-98	Endothelial
ACVRL1	0.60	1.81601E-34	Endothelial
PRCP	0.59	2.27848E-15	Endothelial
IPO11	0.59	5.74274E-41	Endothelial
CTNNAL1	0.59	1.47911E-36	Endothelial
SEPW1	0.59	9.41916E-36	Endothelial
GRB10	0.59	3.4501E-29	Endothelial
RBP7	0.59	0.000610416	Endothelial
THBD	0.58	5.569E-36	Endothelial
FAM84A	0.57	0.043292936	Endothelial
EPAS1	0.57	1.30282E-44	Endothelial
FAM198B	0.57	7.22497E-30	Endothelial
ZNF385D	0.57	8.02669E-32	Endothelial
MAP3K11	0.56	3.70308E-33	Endothelial
TNFAIP1	0.56	1.44597E-34	Endothelial
S1PR1	0.56	6.48122E-33	Endothelial
SSFA2	0.56	6.90839E-33	Endothelial
ARHGEF15	0.56	3.81244E-31	Endothelial
APP	0.56	2.85657E-28	Endothelial
TMEM204	0.56	4.00088E-28	Endothelial
MKL2	0.55	2.12452E-31	Endothelial
SEC14L1	0.55	4.01117E-27	Endothelial
PIM3	0.54	3.43071E-31	Endothelial
SH3BP5	0.54	4.15071E-32	Endothelial
MAGI1	0.54	2.33661E-30	Endothelial
SMAD1	0.54	1.03113E-30	Endothelial
PTPRG	0.54	1.75707E-25	Endothelial
RAPGEF4	0.54	1.65225E-21	Endothelial
CSGALNACT1	0.54	9.82309E-30	Endothelial
PDLIM1	0.54	8.06897E-27	Endothelial

EDN1	0.53	5.09215E-21	Endothelial
PRMT1	0.53	8.30211E-31	Endothelial
BMPR2	0.53	1.03181E-27	Endothelial
C1orf115	0.53	5.9346E-34	Endothelial
PIK3R3	0.53	2.41553E-31	Endothelial
GPR116	0.53	1.47547E-35	Endothelial
TMEM88	0.53	3.42401E-32	Endothelial
UACA	0.53	7.37543E-21	Endothelial
SNHG7	0.52	1.30602E-23	Endothelial
LPAR6	0.51	1.32998E-29	Endothelial
ITGB4	0.51	1.90671E-38	Endothelial
HDAC7	0.51	4.82863E-32	Endothelial
TIMP3	0.51	9.76964E-35	Endothelial
GIMAP6	0.51	6.33098E-64	Endothelial
MCF2L	0.51	2.17334E-30	Endothelial
C16orf80	0.50	2.65481E-25	Endothelial
ITGA5	0.50	5.13375E-26	Endothelial
COL4A1	0.50	6.64201E-20	Endothelial
SORBS2	0.50	2.0046E-26	Endothelial
SPARCL1	0.50	4.9316E-45	Endothelial
LSMD1	0.49	5.75425E-28	Endothelial
TEK	0.49	4.6186E-26	Endothelial
GJA1	0.49	5.40794E-19	Endothelial
KIAA0355	0.49	8.912E-28	Endothelial
PLCB1	0.49	1.20095E-23	Endothelial
CTNNB1	0.48	6.62435E-27	Endothelial
PXN	0.48	1.89434E-27	Endothelial
SHE	0.48	1.44759E-25	Endothelial
NUAK1	0.47	3.60953E-22	Endothelial
GSN	0.47	2.73745E-20	Endothelial
NRP1	0.47	2.26232E-28	Endothelial
RAI14	0.47	1.61181E-21	Endothelial
FAM13C	0.47	2.12608E-25	Endothelial
C4orf32	0.47	1.34915E-27	Endothelial
CPLX1	0.47	1.30775E-24	Endothelial
IGFBP4	0.46	1.30276E-23	Endothelial
APLP2	0.45	3.89357E-23	Endothelial
POLE4	0.45	7.31887E-41	Endothelial
CDA	0.45	1.3129E-38	Endothelial
GNAS	0.45	6.12481E-18	Endothelial
TSPAN12	0.45	1.19157E-24	Endothelial
PTPN14	0.45	2.22663E-24	Endothelial
MATN2	0.45	1.08635E-19	Endothelial

SCARB1	0.45	2.85788E-24	Endothelial
PDE2A	0.44	3.04182E-22	Endothelial
CMTM8	0.44	9.92675E-22	Endothelial
MAPK3	0.43	1.42912E-08	Endothelial
RAPGEF3	0.43	1.29116E-21	Endothelial
VIM	0.43	1.13921E-57	Endothelial
RGCC	0.43	1.10311E-07	Endothelial
IFITM1	0.43	3.01629E-19	Endothelial
FRY	0.43	2.72158E-25	Endothelial
HSPA12B	0.42	1.74229E-21	Endothelial
COL4A2	0.42	5.21949E-17	Endothelial
AKR1C3	0.42	1.51822E-18	Endothelial
MGST2	0.41	1.18412E-36	Endothelial
GIMAP1	0.41	5.82878E-62	Endothelial
GUK1	0.41	9.25754E-36	Endothelial
ENPP2	0.41	3.04955E-09	Endothelial
PINK1	0.41	4.95965E-06	Endothelial
ACE	0.41	3.01932E-20	Endothelial
LAPTM4B	0.41	2.38933E-18	Endothelial
RP11-536O18.1	0.41	1.15431E-18	Endothelial
EDNRB	0.41	1.22433E-08	Endothelial
EFCAB4A	0.41	5.23331E-25	Endothelial
NOV	0.41	4.47351E-14	Endothelial
CEP68	0.41	1.35671E-21	Endothelial
THSD1	0.40	1.84072E-22	Endothelial
GIMAP8	0.40	1.87237E-23	Endothelial
CYB5A	0.40	3.78363E-18	Endothelial
ARRDC3	0.40	1.15802E-10	Endothelial
FKBP9	0.40	2.40031E-20	Endothelial
TMEM173	0.39	2.0975E-22	Endothelial
PTPRB	0.39	3.49126E-48	Endothelial
FGD5	0.39	2.72024E-21	Endothelial
RGL2	0.39	4.15714E-20	Endothelial
PTTG1IP	0.39	7.26545E-22	Endothelial
SLC29A1	0.39	1.23968E-21	Endothelial
CPXM2	0.39	4.08722E-20	Endothelial
KTN1	0.38	5.77773E-23	Endothelial
CDH13	0.38	4.42253E-13	Endothelial
KIAA1462	0.38	6.98484E-20	Endothelial
ICA1	0.38	2.26069E-30	Endothelial
FAM43A	0.37	1.72616E-19	Endothelial
NDST1	0.37	6.02531E-12	Endothelial
MOB2	0.37	3.80928E-06	Endothelial

ADAMTS9	0.37	7.67913E-17	Endothelial
CLDN15	0.37	1.07179E-18	Endothelial
LAMA5	0.37	1.57701E-18	Endothelial
BCL6B	0.37	1.08139E-17	Endothelial
GIMAP5	0.36	2.05529E-65	Endothelial
AFAP1L1	0.36	1.29419E-17	Endothelial
MTUS1	0.36	5.80989E-15	Endothelial
CPNE2	0.36	2.46099E-19	Endothelial
IFITM2	0.35	6.01358E-30	Endothelial
OLFML2A	0.35	2.49363E-15	Endothelial
CMIP	0.35	2.10696E-15	Endothelial
RASGRP3	0.35	1.03859E-10	Endothelial
PLK2	0.35	7.86666E-15	Endothelial
EFNB2	0.35	1.17017E-11	Endothelial
SHC1	0.35	1.51741E-16	Endothelial
RALGAPA2	0.35	6.52452E-22	Endothelial
HSD17B11	0.34	3.61562E-21	Endothelial
ARL15	0.34	2.90472E-12	Endothelial
SLC44A2	0.34	1	Endothelial
GLTSCR2	0.34	4.62008E-11	Endothelial
CFI	0.34	1.18406E-21	Endothelial
FSCN1	0.34	4.08828E-16	Endothelial
IFI44L	0.34	3.32918E-15	Endothelial
PLA2G16	0.34	4.11249E-32	Endothelial
CYTL1	0.34	2.10667E-25	Endothelial
CLIC4	0.33	2.84508E-16	Endothelial
MESDC1	0.33	2.08977E-13	Endothelial
GIPC2	0.33	2.97111E-19	Endothelial
PLSCR1	0.33	1.5073E-13	Endothelial
EPHB4	0.33	2.44498E-15	Endothelial
TBC1D15	0.33	1.56295E-17	Endothelial
LAYN	0.33	1.11392E-13	Endothelial
HECW2	0.33	1.0244E-13	Endothelial
NOVA2	0.33	3.97622E-17	Endothelial
MLEC	0.33	3.66844E-08	Endothelial
LSR	0.33	1	Endothelial
RPS6KA2	0.32	2.50162E-16	Endothelial
MECOM	0.32	1	Endothelial
FAM107A	0.32	1.71939E-16	Endothelial
RHOC	0.32	3.65088E-15	Endothelial
FLI1	0.32	2.54256E-36	Endothelial
SLC3A2	0.32	0.001228368	Endothelial
DYSF	0.32	2.46722E-16	Endothelial

HTRA1	0.32	7.71849E-12	Endothelial
SLC35G2	0.32	3.68159E-15	Endothelial
NUCB1	0.31	2.09881E-17	Endothelial
PTRF	0.31	2.2885E-14	Endothelial
VAMP3	0.31	9.64812E-07	Endothelial
ADAMTSL2	0.31	1.59663E-10	Endothelial
TRIOBP	0.31	1	Endothelial
URM1	0.31	1	Endothelial
MMP15	0.31	2.64694E-19	Endothelial
SLC30A1	0.31	6.1993E-11	Endothelial
ATOX1	0.31	6.05319E-15	Endothelial
FAM101B	0.31	4.03254E-24	Endothelial
C1orf54	0.31	4.52902E-17	Endothelial
DLL4	0.31	9.18159E-14	Endothelial
HLA-E	0.30	8.31271E-43	Endothelial
ATOH8	0.30	8.05432E-14	Endothelial
SCARF1	0.30	3.90869E-10	Endothelial
GRAMD1A	0.30	9.3368E-24	Endothelial
FZD4	0.30	1.47567E-14	Endothelial
GFOD2	0.30	2.96125E-07	Endothelial
COMMD2	0.30	1.0633E-10	Endothelial
MSX1	0.30	1.3067E-13	Endothelial
MRPL17	0.30	1	Endothelial
CFLAR	0.30	2.47476E-11	Endothelial
SLC39A10	0.30	1.5749E-16	Endothelial
CPNE8	0.30	1.0339E-09	Endothelial
CLEC1A	0.30	7.81884E-17	Endothelial
TACR1	0.30	8.24248E-18	Endothelial
LCN6.1	0.30	7.10476E-15	Endothelial
CD151	0.29	5.21392E-18	Endothelial
RILPL2	0.29	1.95716E-12	Endothelial
SEMA6A	0.29	2.87428E-12	Endothelial
PPM1F	0.29	1.40379E-11	Endothelial
UBE2J1	0.29	2.65988E-12	Endothelial
MAPK11	0.28	3.24185E-15	Endothelial
RNF7	0.28	0.143253007	Endothelial
LEF1	0.28	2.73726E-13	Endothelial
RPL3	0.28	1.40897E-50	Endothelial
FAM65A	0.28	4.98168E-13	Endothelial
KIF9	0.28	4.13246E-13	Endothelial
A2M	0.28	2.0308E-21	Endothelial
MYBBP1A	0.28	8.13507E-17	Endothelial
PPFIBP1	0.28	6.08767E-11	Endothelial

CASKIN2	0.28	1.36204E-13	Endothelial
TAOK2	0.28	2.80798E-13	Endothelial
HRH1	0.28	5.54227E-15	Endothelial
ZNF467	0.28	8.13103E-14	Endothelial
ABCD4	0.28	1.10676E-16	Endothelial
NES	0.27	2.85721E-12	Endothelial
SPTAN1	0.27	1	Endothelial
EXOC3L2	0.27	3.30769E-14	Endothelial
EBF3	0.27	4.27088E-14	Endothelial
CRIM1	0.27	6.38617E-12	Endothelial
PCGF2	0.27	6.55672E-14	Endothelial
SLC16A14	0.27	1.17937E-09	Endothelial
TTC28	0.27	2.45987E-08	Endothelial
NOS3	0.27	5.75218E-16	Endothelial
GALNT18	0.27	6.16986E-17	Endothelial
ARHGAP29	0.26	7.49418E-19	Endothelial
TRIM47	0.26	1.28318E-11	Endothelial
HIPK3	0.26	7.64411E-07	Endothelial
HLX	0.26	3.03424E-11	Endothelial
DOCK6	0.26	3.22228E-10	Endothelial
DOCK9	0.26	1	Endothelial
CAV1	0.26	1.70243E-16	Endothelial
PIK3C2A	0.26	1.73764E-15	Endothelial
MIER2	0.26	1.79621E-11	Endothelial
CCM2L	0.26	9.76428E-13	Endothelial
PSMB4	0.26	1	Endothelial
ITIH5	0.26	7.90855E-06	Endothelial
ANGPT2	0.26	0.452929812	Endothelial
ANKRD29	0.26	7.99517E-12	Endothelial
MTIF3	0.26	1	Endothelial
CPD	0.25	1.09245E-10	Endothelial
PLEC	0.25	0.303589401	Endothelial
FIS1	0.25	6.60329E-14	Endothelial
PKN3	0.25	5.43489E-13	Endothelial
LUM	3.84	1.2744E-144	Fibroblast
DCN	3.74	2.1532E-222	Fibroblast
COL3A1	3.50	1.8558E-177	Fibroblast
RGS5	3.46	2.3745E-99	Fibroblast
PTGDS	3.33	7.13566E-82	Fibroblast
APOD	3.23	4.2657E-112	Fibroblast
COL1A2	3.16	2.1359E-186	Fibroblast
FBLN1	2.87	1.5339E-115	Fibroblast
MFAP4	2.79	1.2463E-115	Fibroblast

C1S	2.77	6.394E-182	Fibroblast
COL1A1	2.68	2.3297E-134	Fibroblast
COL6A1	2.64	3.574E-158	Fibroblast
COL6A2	2.61	1.0333E-168	Fibroblast
CPE	2.59	1.4631E-117	Fibroblast
CFD	2.47	0.001779623	Fibroblast
SFRP2	2.43	2.41796E-91	Fibroblast
SOD3	2.32	1.191E-136	Fibroblast
C1R	2.29	4.6013E-147	Fibroblast
FAM162B	2.25	3.68982E-79	Fibroblast
HIGD1B	2.23	1.0125E-57	Fibroblast
RARRES2	2.21	5.8032E-133	Fibroblast
ACTA2	2.20	1.08342E-66	Fibroblast
COL6A3	2.18	1.4185E-104	Fibroblast
CCL11	2.17	3.22321E-52	Fibroblast
PCOLCE	2.13	2.3544E-132	Fibroblast
ABCA8	2.08	2.50084E-88	Fibroblast
TAGLN	1.99	3.71465E-62	Fibroblast
MYL9	1.98	2.27897E-78	Fibroblast
ASPN	1.90	2.97883E-69	Fibroblast
TPM2	1.89	2.3049E-101	Fibroblast
NDUFA4L2	1.81	4.52596E-16	Fibroblast
CTSK	1.78	1.49316E-92	Fibroblast
CCDC80	1.76	1.46551E-93	Fibroblast
CALD1	1.76	3.3402E-184	Fibroblast
COL6A5	1.72	1.66131E-64	Fibroblast
FRZB	1.68	3.8219E-52	Fibroblast
PDGFRB	1.68	2.65259E-71	Fibroblast
COX4I2	1.63	5.25073E-44	Fibroblast
CXCL14	1.60	1.31689E-67	Fibroblast
SERPING1	1.57	4.9003E-110	Fibroblast
FN1	1.54	2.83585E-59	Fibroblast
LHFP	1.54	1.15888E-97	Fibroblast
IGFBP5	1.50	1.397E-37	Fibroblast
DPT	1.45	3.20173E-54	Fibroblast
CYR61	1.42	8.14641E-16	Fibroblast
FXYD1	1.41	1.81517E-75	Fibroblast
SERPINF1	1.37	2.23558E-55	Fibroblast
MFGE8	1.36	3.57422E-64	Fibroblast
PLAC9	1.32	1.62124E-68	Fibroblast
ADH1B	1.31	5.6715E-32	Fibroblast
CLDN11	1.29	1.32172E-53	Fibroblast
LTBP4	1.29	4.38112E-54	Fibroblast

POSTN	1.27	9.59078E-24	Fibroblast
NBL1	1.25	1.87714E-45	Fibroblast
NR2F1	1.21	7.62154E-60	Fibroblast
COL5A1	1.20	8.82926E-59	Fibroblast
WFDC1	1.20	4.69808E-39	Fibroblast
MMP2	1.20	4.19629E-42	Fibroblast
MEG3	1.19	3.51547E-53	Fibroblast
TPM1	1.16	5.77575E-14	Fibroblast
THY1	1.16	3.23825E-72	Fibroblast
COL5A2	1.15	1.22372E-58	Fibroblast
TFPI	1.14	2.30725E-64	Fibroblast
PLEKHH2	1.14	2.30169E-47	Fibroblast
RERG	1.13	3.07115E-59	Fibroblast
PTN	1.12	1.7222E-10	Fibroblast
IGFBP6	1.11	1.68461E-48	Fibroblast
SELM	1.11	7.29621E-66	Fibroblast
MEST	1.11	7.40119E-38	Fibroblast
SMOC2	1.09	8.2632E-36	Fibroblast
AEBP1	1.08	3.24714E-66	Fibroblast
PLXDC1	1.07	1.36427E-60	Fibroblast
PDGFRA	1.07	2.4203E-51	Fibroblast
CSRP2	1.07	1	Fibroblast
NOTCH3	1.06	1	Fibroblast
TDO2	1.06	1.98712E-37	Fibroblast
PPP1R14A	1.05	2.22471E-23	Fibroblast
LGALS3BP	1.02	4.58484E-31	Fibroblast
CLEC11A	1.00	1.91403E-32	Fibroblast
NDN	0.99	1.61323E-42	Fibroblast
NR2F2	0.99	8.14324E-31	Fibroblast
COL12A1	0.99	4.21072E-37	Fibroblast
SEPP1	0.96	5.34889E-34	Fibroblast
SDC2	0.93	1.49343E-40	Fibroblast
TPPP3	0.93	4.28969E-33	Fibroblast
F10	0.92	5.25073E-44	Fibroblast
SGCE	0.91	2.21288E-39	Fibroblast
EMILIN1	0.91	1.63006E-41	Fibroblast
ISYNA1	0.91	7.72072E-19	Fibroblast
COL14A1	0.90	4.21073E-37	Fibroblast
TNC	0.90	1.75239E-24	Fibroblast
OGN	0.89	8.63576E-25	Fibroblast
SPON2	0.89	3.30512E-23	Fibroblast
PPAP2A	0.89	6.89498E-28	Fibroblast
PLEKHA5	0.89	1.23482E-14	Fibroblast

CDH6	0.88	8.63576E-25	Fibroblast
ISLR	0.88	5.16547E-42	Fibroblast
APCDD1	0.88	1.26123E-22	Fibroblast
PLTP	0.88	2.66783E-25	Fibroblast
TNFRSF21	0.88	3.33496E-31	Fibroblast
TCF21	0.87	2.21288E-39	Fibroblast
FMO1	0.87	1.19994E-22	Fibroblast
EFEMP2	0.86	8.0882E-47	Fibroblast
FXYD6	0.86	4.61929E-40	Fibroblast
MXRA8	0.86	8.87595E-37	Fibroblast
TIMP2	0.85	4.70846E-23	Fibroblast
NKD2	0.85	2.11109E-38	Fibroblast
CRISPLD2	0.83	3.06332E-39	Fibroblast
CCDC102B	0.83	9.07486E-22	Fibroblast
ANTXR1	0.82	8.52317E-36	Fibroblast
MOXD1	0.82	2.49181E-31	Fibroblast
CHN1	0.81	1.01622E-20	Fibroblast
EDNRA	0.80	3.09457E-33	Fibroblast
THBS2	0.80	3.3365E-34	Fibroblast
DKK3	0.79	8.30797E-40	Fibroblast
STEAP4	0.79	6.39301E-20	Fibroblast
ABI3BP	0.78	1.04421E-30	Fibroblast
SEPT4	0.78	3.08029E-28	Fibroblast
CYGB	0.78	3.02939E-16	Fibroblast
FMOD	0.77	1.49319E-33	Fibroblast
C1QTNF1	0.77	4.25172E-25	Fibroblast
PMP22	0.76	1.7254E-15	Fibroblast
NUPR1	0.75	1.40967E-11	Fibroblast
PRRX1	0.74	1.21775E-31	Fibroblast
OSR2	0.74	2.90379E-27	Fibroblast
RP11-14N7.2	0.73	1.05375E-11	Fibroblast
MMP23B	0.73	6.52692E-33	Fibroblast
ABCA6	0.73	1.71279E-22	Fibroblast
C3	0.72	5.05026E-06	Fibroblast
CYBRD1	0.72	3.06832E-18	Fibroblast
BMP4	0.72	6.96972E-34	Fibroblast
PCDH18	0.72	6.92649E-28	Fibroblast
VCAM1	0.71	2.08914E-26	Fibroblast
IL34	0.71	1.09533E-11	Fibroblast
SYNPO2	0.70	2.04637E-24	Fibroblast
LPPR4	0.70	5.93705E-27	Fibroblast
DDR2	0.69	1.21334E-31	Fibroblast
RASD1	0.69	2.30977E-20	Fibroblast

LRP1	0.69	4.75407E-15	Fibroblast
ADIRF	0.69	6.00429E-05	Fibroblast
RBP1	0.68	1	Fibroblast
LAMA4	0.68	3.12164E-13	Fibroblast
SELENBP1	0.67	1.18088E-05	Fibroblast
MT1M	0.66	8.44819E-23	Fibroblast
SEMA5A	0.66	3.67163E-13	Fibroblast
DIO2	0.65	4.99106E-07	Fibroblast
LGALS1	0.65	1.16352E-52	Fibroblast
COL18A1	0.65	7.56703E-12	Fibroblast
SERPINE2	0.64	0.000656116	Fibroblast
CRYAB	0.64	1	Fibroblast
MLTK	0.63	1.0644E-08	Fibroblast
LAPTM4A	0.63	6.49401E-44	Fibroblast
KANK2	0.62	2.61565E-24	Fibroblast
F2R	0.62	4.32511E-13	Fibroblast
LBH	0.61	1.63795E-26	Fibroblast
ZNF503	0.61	6.04227E-06	Fibroblast
GUCY1A3	0.61	6.45572E-16	Fibroblast
SERPINI1	0.61	1	Fibroblast
FGFR1	0.60	3.364E-14	Fibroblast
NFATC4	0.60	9.80714E-22	Fibroblast
TMEM98	0.60	1	Fibroblast
GUCY1B3	0.59	7.11733E-13	Fibroblast
TMEM176B	0.59	4.05956E-09	Fibroblast
GSTM3	0.58	1	Fibroblast
CDH11	0.58	1.21272E-26	Fibroblast
FBN1	0.58	1.70408E-29	Fibroblast
GEM	0.57	8.05975E-08	Fibroblast
CBX6	0.56	0.009344946	Fibroblast
IGFBP2	0.56	1	Fibroblast
MDK	0.56	1	Fibroblast
VCAN	0.56	1.15787E-21	Fibroblast
FGF7	0.56	1.47569E-19	Fibroblast
ID4	0.56	1	Fibroblast
MRVI1	0.56	1.54039E-18	Fibroblast
FMO3	0.56	2.47E-16	Fibroblast
GPNMB	0.55	0.047006953	Fibroblast
SPATS2L	0.55	1	Fibroblast
SEPT7	0.55	1.11241E-18	Fibroblast
ECM2	0.55	2.55461E-19	Fibroblast
TGFB11	0.54	5.62752E-06	Fibroblast
PRSS12	0.54	5.53916E-22	Fibroblast

MYLK	0.54	0.529893419	Fibroblast
GPR124	0.53	1.02282E-24	Fibroblast
PTK7	0.53	0.001047708	Fibroblast
VSTM4	0.53	2.55461E-19	Fibroblast
FBLN2	0.53	3.76346E-20	Fibroblast
MRGPRF	0.53	6.39301E-20	Fibroblast
FBLN5	0.53	4.47027E-25	Fibroblast
MAP1B	0.52	0.250531544	Fibroblast
PTPRS	0.52	1	Fibroblast
PDE5A	0.52	3.19388E-20	Fibroblast
LOXL1	0.52	2.41927E-22	Fibroblast
SLITRK6	0.52	1.27852E-19	Fibroblast
RP11-572C15.6	0.51	1.24692E-16	Fibroblast
FBLIM1	0.51	7.9319E-08	Fibroblast
GAS6	0.50	1	Fibroblast
WLS	0.50	1	Fibroblast
RCN3	0.50	4.18003E-23	Fibroblast
RUNX1T1	0.50	0.193568503	Fibroblast
TMEM45A	0.50	1.75717E-22	Fibroblast
RNASE4	0.50	2.84578E-13	Fibroblast
APOE	0.49	1	Fibroblast
NID1	0.49	2.43333E-10	Fibroblast
SSPN	0.49	1.76892E-09	Fibroblast
PHPT1	0.49	1	Fibroblast
NENF	0.49	0.060062207	Fibroblast
LURAP1L	0.48	3.66651E-20	Fibroblast
FHL2	0.48	1	Fibroblast
NOVA1	0.48	2.96026E-14	Fibroblast
PGF	0.48	1.60429E-13	Fibroblast
PALLD	0.48	1	Fibroblast
TINAGL1	0.48	1	Fibroblast
CCL2	0.48	0.076142343	Fibroblast
PODN	0.48	6.2894E-17	Fibroblast
PTEN	0.48	1	Fibroblast
PKIG	0.47	1	Fibroblast
EDIL3	0.47	0.005165082	Fibroblast
ADH5	0.47	1	Fibroblast
ZCCHC24	0.47	3.71957E-10	Fibroblast
C2	0.47	2.05937E-11	Fibroblast
GSTM5	0.47	3.16965E-17	Fibroblast
TGM2	0.47	1.04138E-09	Fibroblast
ADRA2A	0.46	7.24133E-09	Fibroblast
PAG1	0.46	2.59502E-10	Fibroblast

FOXF2	0.46	1.24692E-16	Fibroblast
PTK2	0.46	1	Fibroblast
MRC2	0.46	1	Fibroblast
C1orf21	0.46	1	Fibroblast
RBMS3	0.46	7.86588E-05	Fibroblast
LSAMP	0.45	3.16965E-17	Fibroblast
IFI27L2	0.45	1	Fibroblast
GFRA1	0.45	2.02715E-18	Fibroblast
HCFC1R1	0.45	1	Fibroblast
SSBP2	0.44	1	Fibroblast
EPHX1	0.44	1	Fibroblast
PAM	0.44	0.055541946	Fibroblast
IL15RA	0.44	2.97977E-11	Fibroblast
P4HA2	0.44	1	Fibroblast
EPB41L2	0.44	6.5276E-07	Fibroblast
RCAN2	0.43	1	Fibroblast
ADCY3	0.43	9.76664E-09	Fibroblast
TMEM176A	0.43	0.000442301	Fibroblast
PFN2	0.43	0.987308615	Fibroblast
FILIP1L	0.43	5.82169E-06	Fibroblast
GREM2	0.43	8.02969E-18	Fibroblast
SCPEP1	0.42	1	Fibroblast
RRBP1	0.42	1	Fibroblast
FSTL1	0.42	0.955434237	Fibroblast
SH3D19	0.42	1	Fibroblast
RNF150	0.42	9.66764E-16	Fibroblast
REV3L	0.42	0.005656279	Fibroblast
CPQ	0.41	0.00047134	Fibroblast
OLFML1	0.41	1.59603E-17	Fibroblast
LTBP1	0.41	1.01554E-13	Fibroblast
NTM	0.41	1.5942E-20	Fibroblast
TNXB	0.41	1	Fibroblast
FKBP7	0.41	1	Fibroblast
PDLIM3	0.41	7.94357E-05	Fibroblast
SKP1	0.41	1.25423E-11	Fibroblast
WNT5A	0.41	1	Fibroblast
CTSF	0.40	0.113936918	Fibroblast
PID1	0.40	1.19225E-09	Fibroblast
C12orf57	0.40	0.005853205	Fibroblast
MYO1B	0.40	1	Fibroblast
PMEPA1	0.40	1.79601E-11	Fibroblast
C10orf10	0.39	1	Fibroblast
CALM2	0.39	3.43374E-16	Fibroblast

LOXL2	0.39	0.134214576	Fibroblast
HOXA3	0.39	1.0709E-10	Fibroblast
ST5	0.39	1	Fibroblast
ARPC1A	0.38	1	Fibroblast
TWSG1	0.38	1.70047E-07	Fibroblast
PTOV1	0.38	1	Fibroblast
UBA2	0.38	1	Fibroblast
GPX3	0.37	1	Fibroblast
ITGB1	0.37	0.014020394	Fibroblast
KITLG	0.37	1	Fibroblast
RAB34	0.37	1	Fibroblast
TPBG	0.37	0.103893521	Fibroblast
RP11-553L6.5	0.37	1	Fibroblast
RBP5	0.37	1	Fibroblast
PAMR1	0.37	6.2894E-17	Fibroblast
C1QTNF2	0.37	4.6118E-06	Fibroblast
PRR24	0.37	1.37537E-06	Fibroblast
SNHG18	0.37	1	Fibroblast
SMTN	0.37	0.000106304	Fibroblast
GULP1	0.37	1	Fibroblast
RP11-834C11.4	0.36	0.000324851	Fibroblast
LAMP1	0.36	1	Fibroblast
TTC3	0.36	1	Fibroblast
ARHGAP12	0.36	1	Fibroblast
EHD2	0.36	1	Fibroblast
SAT2	0.36	1	Fibroblast
SGCB	0.36	1.27127E-05	Fibroblast
HNMT	0.36	0.108736213	Fibroblast
CERCAM	0.35	1.16649E-10	Fibroblast
SPRY1	0.35	1	Fibroblast
TUSC3	0.35	1	Fibroblast
SNAI2	0.35	1	Fibroblast
RHOB	0.34	1	Fibroblast
SGIP1	0.34	0.41015116	Fibroblast
SEC31A	0.34	1	Fibroblast
GLT8D2	0.34	0.001546911	Fibroblast
KCNQ1OT1	0.34	1	Fibroblast
C20orf27	0.33	1	Fibroblast
PPIB	0.33	1	Fibroblast
IRF2BPL	0.33	1	Fibroblast
EBF1	0.33	1	Fibroblast
S100A6	0.33	1.46161E-09	Fibroblast
C5orf15	0.33	1	Fibroblast

PTMS	0.33	1	Fibroblast
KLHL42	0.33	1	Fibroblast
CHD9	0.33	1	Fibroblast
RRAS	0.32	1	Fibroblast
ARID5A	0.32	1	Fibroblast
PPP1R12A	0.32	1	Fibroblast
PIGT	0.32	1	Fibroblast
FOXF1	0.32	0.000106285	Fibroblast
MAP1LC3A	0.32	1	Fibroblast
ZBTB20	0.32	1	Fibroblast
HOXB-AS1	0.32	0.600778722	Fibroblast
LTBP3	0.31	1	Fibroblast
FKBP10	0.31	1	Fibroblast
TNS1	0.31	1	Fibroblast
GNAI1	0.31	1	Fibroblast
OLFML3	0.31	0.027246456	Fibroblast
FAM114A1	0.31	1	Fibroblast
GSTM4	0.31	0.561000802	Fibroblast
SPARC	0.31	2.85682E-06	Fibroblast
FARP1	0.31	1	Fibroblast
PLD3	0.31	0.128702054	Fibroblast
SOD1	0.31	0.468686523	Fibroblast
GPX8	0.31	1	Fibroblast
BST2	0.31	0.50736153	Fibroblast
ESD	0.31	1	Fibroblast
CD59	0.30	1	Fibroblast
FAM92A1	0.30	0.181987421	Fibroblast
NUCKS1	0.30	1	Fibroblast
TPST1	0.30	0.22171985	Fibroblast
COX7A1	0.30	1	Fibroblast
ARF4	0.30	1	Fibroblast
CXCL12	0.30	1	Fibroblast
PARVA	0.29	1	Fibroblast
PPIC	0.29	1	Fibroblast
TMEM59	0.29	0.068857555	Fibroblast
IL1R1	0.29	1	Fibroblast
LAMB2	0.29	1	Fibroblast
COPS6	0.29	1	Fibroblast
CTSL	0.29	1	Fibroblast
PEBP1	0.29	1	Fibroblast
FERMT2	0.29	1	Fibroblast
C1orf122	0.28	1	Fibroblast
CISD1	0.28	1	Fibroblast

REEP3	0.28	1	Fibroblast
PRNP	0.28	1	Fibroblast
ADD3	0.28	1	Fibroblast
MGP	0.27	1	Fibroblast
ROBO1	0.27	1	Fibroblast
PTP4A3	0.27	1	Fibroblast
LRPAP1	0.27	1	Fibroblast
LY6E	0.27	1	Fibroblast
FAP	0.27	1	Fibroblast
OAF	0.27	1	Fibroblast
GADD45A	0.27	1	Fibroblast
CNBP	0.27	1	Fibroblast
MANBAL	0.27	1	Fibroblast
NFIC	0.26	1	Fibroblast
CASC4	0.26	1	Fibroblast
EMC2	0.26	1	Fibroblast
CFH	0.26	1	Fibroblast
EID1	0.26	0.685160755	Fibroblast
MAN1A1	0.26	1	Fibroblast
SEC63	0.26	1	Fibroblast
EFHC1	0.26	1	Fibroblast
AK3	0.26	1	Fibroblast
C1orf86	0.25	1	Fibroblast
PCYOX1	0.25	1	Fibroblast

Supplemental Table 2. Markers of the human esophageal epithelial subpopulations

gene	logfc_min	adjp_max	epithelial subpopulation
DST	0.92	7.48997E-49	Quiescent
DLK2	0.85	3.47075E-39	Quiescent
KRT15	0.84	1.32928E-65	Quiescent
IL1R2	0.75	1.33512E-25	Quiescent
TXNIP	0.75	1.87494E-28	Quiescent
GPNMB	0.74	2.77492E-33	Quiescent
WNT10A	0.71	1.4448E-28	Quiescent
TSLP	0.70	3.16207E-22	Quiescent
ZFP36L2	0.70	9.44526E-44	Quiescent
GLTSCR2	0.69	1.16263E-51	Quiescent
MIR205HG	0.68	9.93853E-47	Quiescent
ZFAS1	0.68	3.59398E-53	Quiescent
CXCL14	0.67	4.85406E-06	Quiescent
FOS	0.66	1	Quiescent
IFITM3	0.64	3.04676E-35	Quiescent
RPL34	0.63	1.70876E-94	Quiescent
SNHG8	0.62	7.59164E-35	Quiescent
EIF3E	0.59	2.96091E-55	Quiescent
LAMB3	0.59	1.22126E-16	Quiescent
CIRBP	0.59	5.07074E-31	Quiescent
IGFBP5	0.58	0.000491458	Quiescent
APP	0.57	4.57556E-22	Quiescent
EEF2	0.57	1.62148E-52	Quiescent
RPL12	0.57	6.66966E-82	Quiescent
BCAM	0.57	1.3959E-19	Quiescent
PNRC1	0.57	4.02995E-17	Quiescent
EPB41L4A-AS1	0.56	1.81417E-17	Quiescent
SNHG7	0.56	1.52609E-15	Quiescent
RPL13	0.55	9.29588E-94	Quiescent
EFEMP1	0.55	3.21601E-13	Quiescent
RPS27	0.54	1.57924E-80	Quiescent
ASS1	0.53	5.18492E-17	Quiescent
RPL17	0.53	1.1738E-26	Quiescent
FST	0.52	6.06752E-08	Quiescent
COL17A1	0.51	1.24156E-14	Quiescent
CAV1	0.51	8.19134E-17	Quiescent
SLC3A2	0.51	2.09646E-16	Quiescent

TSC22D1	0.50	3.7541E-05	Quiescent
DDIT4	0.50	2.15327E-06	Quiescent
CH25H	0.50	9.94118E-11	Quiescent
GNB2L1	0.49	1.46291E-71	Quiescent
PPP1R16A	0.49	1.14133E-12	Quiescent
RPL31	0.48	3.35905E-74	Quiescent
ETS2	0.48	1.05861E-09	Quiescent
RPL35A	0.48	1.15094E-85	Quiescent
EIF4A2	0.47	3.12024E-25	Quiescent
PFDN5	0.47	5.17922E-38	Quiescent
RPL30	0.46	1.96175E-69	Quiescent
DLL1	0.45	1.48027E-14	Quiescent
FHL2	0.45	1.47008E-10	Quiescent
SLC7A5	0.45	3.13913E-10	Quiescent
RPL13A	0.44	2.70841E-80	Quiescent
PHY ^{HIGH} P	0.44	1.79519E-12	Quiescent
RPS9	0.43	3.36622E-71	Quiescent
SAT2	0.43	5.42766E-10	Quiescent
RPL3	0.43	2.96982E-68	Quiescent
RPS19	0.43	7.64202E-76	Quiescent
RPL5	0.42	6.26793E-62	Quiescent
BTF3	0.42	2.96688E-56	Quiescent
RSL24D1	0.42	1.67186E-16	Quiescent
COMMD6	0.42	9.00622E-28	Quiescent
EIF2A	0.41	1.34121E-11	Quiescent
NOB1	0.41	5.28707E-08	Quiescent
C1R	0.41	6.6278E-07	Quiescent
KRT32	0.41	3.88995E-06	Quiescent
PTRF	0.41	1.26335E-08	Quiescent
SLC1A3	0.41	0.008117268	Quiescent
RPL10A	0.40	8.55871E-72	Quiescent
ST13	0.39	5.05953E-17	Quiescent
EEF1D	0.39	1.32929E-32	Quiescent
C6orf48	0.39	3.1084E-08	Quiescent
ATP1B3	0.39	2.51318E-19	Quiescent
WNT5B	0.39	5.99296E-07	Quiescent
CCDC3	0.39	6.32005E-07	Quiescent
Z83851.1	0.39	1.3287E-05	Quiescent
RSL1D1	0.39	5.93653E-12	Quiescent
PRNP	0.39	1.66805E-07	Quiescent
DHRS3	0.39	4.6796E-08	Quiescent
HSPA2	0.38	2.35567E-06	Quiescent
BLCAP	0.38	0.001426013	Quiescent

THSD4	0.38	0.00775339	Quiescent
TAX1BP3	0.38	5.5822E-17	Quiescent
LIMA1	0.37	0.009687125	Quiescent
JUN	0.37	6.17868E-08	Quiescent
TP53AIP1	0.37	4.29868E-10	Quiescent
KLK5	0.37	5.40929E-05	Quiescent
RPL32	0.37	2.33896E-72	Quiescent
RPL36	0.37	5.59493E-66	Quiescent
RPLP1	0.36	5.24859E-67	Quiescent
RPL11	0.36	1.03682E-69	Quiescent
RPL21	0.36	7.81747E-70	Quiescent
EEF1A1	0.36	2.74736E-49	Quiescent
ARPC1B	0.36	1.81962E-06	Quiescent
GAMT	0.36	0.000485216	Quiescent
NME3	0.36	6.04173E-06	Quiescent
CDH13	0.36	4.81752E-05	Quiescent
RPL37	0.35	4.60744E-40	Quiescent
IP6K2	0.35	0.005519206	Quiescent
RIN2	0.35	1	Quiescent
RPS5	0.35	3.79718E-53	Quiescent
RPL15	0.35	2.94012E-61	Quiescent
RPS18	0.35	6.62346E-76	Quiescent
DKK3	0.35	0.000477722	Quiescent
RPL7	0.35	6.97894E-58	Quiescent
RPS28	0.34	6.43676E-56	Quiescent
RPS20	0.34	1.06148E-44	Quiescent
FAM132A	0.34	0.004682244	Quiescent
RPS15A	0.34	3.02566E-61	Quiescent
RPL18A	0.34	1.61277E-61	Quiescent
LMO4	0.34	0.013369467	Quiescent
COL18A1	0.34	0.000303439	Quiescent
N4BP2L2	0.33	4.72305E-08	Quiescent
GPX4	0.33	2.76469E-16	Quiescent
PTPRS	0.33	1	Quiescent
RPS6	0.33	8.48526E-60	Quiescent
RPS8	0.33	9.91581E-56	Quiescent
BTG1	0.33	0.149421146	Quiescent
RPL9	0.32	2.47731E-49	Quiescent
NBEAL1	0.32	0.037573443	Quiescent
EIF3L	0.32	3.03949E-14	Quiescent
RPL38	0.32	2.9322E-34	Quiescent
RPS15	0.32	1.55097E-66	Quiescent
WNT7B	0.31	0.001243749	Quiescent

CCDC80	0.31	1.33174E-06	Quiescent
NACA	0.31	5.40818E-40	Quiescent
MOXD1	0.31	0.013818295	Quiescent
IRF1	0.31	1	Quiescent
SLC40A1	0.31	0.472414631	Quiescent
RPS12	0.30	2.81877E-47	Quiescent
RPS25	0.30	2.0571E-52	Quiescent
AKAP9	0.30	0.315277852	Quiescent
RPL18	0.30	5.42634E-52	Quiescent
PDLIM1	0.30	2.4791E-07	Quiescent
KMT2E	0.29	1	Quiescent
MUM1	0.29	1	Quiescent
RPL41	0.29	1.46028E-59	Quiescent
RARRES3	0.29	0.118962006	Quiescent
EIF3D	0.29	6.69354E-07	Quiescent
RPL14	0.29	2.21657E-42	Quiescent
RPS27A	0.29	8.52334E-54	Quiescent
CD74	0.29	1	Quiescent
RAMP1	0.29	1.38389E-05	Quiescent
RPL23A	0.29	9.51275E-44	Quiescent
KTN1	0.29	5.60723E-06	Quiescent
GPX1	0.29	1.66762E-06	Quiescent
RPS13	0.28	1.32047E-45	Quiescent
EEF1G	0.28	1	Quiescent
RPS7	0.28	2.90589E-42	Quiescent
RPL23	0.28	4.45955E-36	Quiescent
NUDT14	0.28	1	Quiescent
TOMM7	0.28	3.5231E-19	Quiescent
RPS14	0.28	3.0011E-49	Quiescent
SNAI2	0.28	1	Quiescent
CYB5R1	0.28	1	Quiescent
RPL6	0.28	2.07339E-41	Quiescent
NAP1L1	0.27	3.31482E-09	Quiescent
NPR3	0.27	1	Quiescent
BTG2	0.27	1	Quiescent
RPL29	0.27	6.67842E-43	Quiescent
CTSH	0.27	1	Quiescent
ABCC3	0.27	1	Quiescent
NSRP1	0.27	1	Quiescent
VAMP5	0.27	1	Quiescent
RPLP0	0.27	1.53877E-34	Quiescent
HCFC1R1	0.26	1	Quiescent
ORAI3	0.26	1	Quiescent

RPL24	0.26	2.21919E-33	Quiescent
EIF3H	0.26	1.415E-08	Quiescent
BOC	0.26	0.03879264	Quiescent
ASCL2	0.26	0.065813538	Quiescent
NTF4	0.26	1	Quiescent
C1S	0.25	0.00077026	Quiescent
HOOK2	0.25	1	Quiescent
RIN1	0.25	1	Quiescent
HMGB2	1.78	2.4695E-116	Proliferating
H2AFZ	1.69	8.31E-102	Proliferating
TUBA1B	1.52	5.32919E-85	Proliferating
ST1H4C	1.45	1.84075E-39	Proliferating
STMN1	1.43	3.83469E-94	Proliferating
UBE2C	1.32	2.78788E-94	Proliferating
TOP2A	1.22	7.93203E-95	Proliferating
TUBB	1.21	2.73343E-78	Proliferating
RRM2	1.15	2.18721E-93	Proliferating
CCNB1	1.13	7.85883E-74	Proliferating
HMGN2	1.13	1.07776E-63	Proliferating
CKS2	1.12	1.36871E-85	Proliferating
BIRC5	1.12	2.1405E-113	Proliferating
KIAA0101	1.11	4.72969E-97	Proliferating
KPNA2	1.11	2.57027E-63	Proliferating
CDK1	1.07	6.1104E-99	Proliferating
TK1	1.07	4.9636E-111	Proliferating
HMGB1	1.02	2.41707E-77	Proliferating
ARL6IP1	1.01	7.81013E-33	Proliferating
CENPF	1.00	7.77879E-88	Proliferating
PTTG1	0.98	1.98482E-56	Proliferating
NUSAP1	0.95	1.1848E-103	Proliferating
CENPW	0.88	1.289E-109	Proliferating
MKI67	0.87	2.6852E-102	Proliferating
CDC20	0.85	8.98004E-75	Proliferating
MAD2L1	0.84	5.5293E-104	Proliferating
CCNB2	0.82	9.98237E-88	Proliferating
H2AFV	0.79	5.93649E-72	Proliferating
CDKN3	0.78	5.43421E-91	Proliferating
TYMS	0.77	9.6321E-89	Proliferating
CALM2	0.76	4.68346E-37	Proliferating
KIF20B	0.76	5.03256E-80	Proliferating
RANBP1	0.75	3.51975E-58	Proliferating
PBK	0.74	3.5004E-101	Proliferating
ASPM	0.73	1.77697E-85	Proliferating

PCNA	0.71	5.34923E-25	Proliferating
ZWINT	0.70	1.93143E-87	Proliferating
HNRNPA2B1	0.69	3.92441E-51	Proliferating
CCNA2	0.68	1.08486E-87	Proliferating
CKS1B	0.68	2.52711E-44	Proliferating
PTMA	0.67	1.78757E-75	Proliferating
DUT	0.66	1.23244E-30	Proliferating
PRC1	0.65	5.4032E-94	Proliferating
SMC2	0.64	4.578E-67	Proliferating
AKR1C1	0.63	5.94575E-33	Proliferating
AURKB	0.63	2.54332E-77	Proliferating
TPX2	0.62	2.51659E-85	Proliferating
HSP90AA1	0.61	1.37882E-42	Proliferating
KRT5	0.59	1.00298E-30	Proliferating
NUDT1	0.58	2.22623E-57	Proliferating
DTYMK	0.58	8.82219E-73	Proliferating
PLK1	0.58	7.44939E-58	Proliferating
H2AFX	0.58	1.01156E-89	Proliferating
UBE2T	0.58	3.49937E-90	Proliferating
KRT14	0.58	1	Proliferating
TMEM106C	0.57	4.37693E-42	Proliferating
LMNB1	0.56	4.59228E-90	Proliferating
AKR1C2	0.56	2.44877E-08	Proliferating
BUB3	0.55	3.08376E-38	Proliferating
CCDC34	0.55	8.94707E-54	Proliferating
SRSF3	0.55	3.60336E-39	Proliferating
CENPM	0.55	2.77003E-83	Proliferating
CENPA	0.54	1.71648E-57	Proliferating
CENPE	0.53	1.9246E-64	Proliferating
RAN	0.52	7.82124E-25	Proliferating
SPC25	0.52	2.01643E-79	Proliferating
AKR1B10	0.52	1	Proliferating
STRA13	0.52	2.27428E-34	Proliferating
CENPN	0.52	1.46408E-93	Proliferating
ANP32E	0.51	1.01264E-54	Proliferating
RPA3	0.51	2.23865E-42	Proliferating
HMMR	0.51	1.60349E-68	Proliferating
LSM5	0.51	3.45358E-37	Proliferating
SRSF2	0.50	1.25584E-37	Proliferating
PTGES3	0.50	2.91115E-28	Proliferating
GMNN	0.49	1.27214E-49	Proliferating
SIVA1	0.49	2.87537E-30	Proliferating
TMPO	0.49	1.62369E-54	Proliferating

DDX39A	0.48	5.82698E-49	Proliferating
SGOL1	0.48	7.3066E-81	Proliferating
ASF1B	0.48	1.51618E-77	Proliferating
RNASEH2A	0.46	2.23664E-53	Proliferating
HNRNPA3	0.46	1.91125E-36	Proliferating
PHGDH	0.46	6.63525E-22	Proliferating
FEN1	0.46	8.23995E-56	Proliferating
CDCA3	0.46	4.14886E-64	Proliferating
RRM1	0.46	3.63091E-29	Proliferating
RHEB	0.46	2.52656E-34	Proliferating
LSM4	0.45	1.9905E-49	Proliferating
DEK	0.45	1.44817E-27	Proliferating
YWHAH	0.45	2.48006E-44	Proliferating
SNRPB	0.44	1.28694E-28	Proliferating
MCM7	0.44	5.59056E-21	Proliferating
SNRPD1	0.44	3.62688E-37	Proliferating
SNRPG	0.44	4.93593E-30	Proliferating
CDCA8	0.44	8.48539E-69	Proliferating
BCL7C	0.44	3.52054E-34	Proliferating
SGOL2	0.44	1.31526E-64	Proliferating
RAD21	0.43	4.52237E-30	Proliferating
CDCA4	0.43	2.25052E-35	Proliferating
MZT1	0.43	9.84046E-48	Proliferating
RAD51AP1	0.43	9.22348E-67	Proliferating
DNAJC9	0.42	1.64285E-35	Proliferating
RACGAP1	0.42	3.96012E-65	Proliferating
TUBB4B	0.42	1.55705E-15	Proliferating
SFPQ	0.41	7.28943E-23	Proliferating
MZT2B	0.41	4.78974E-34	Proliferating
CBX3	0.41	1.66332E-26	Proliferating
DHFR	0.41	3.41162E-53	Proliferating
CACYBP	0.40	4.81356E-22	Proliferating
LSM2	0.40	8.95973E-24	Proliferating
HNRNPR	0.40	3.14733E-23	Proliferating
HMGN1	0.39	3.6711E-28	Proliferating
KIFC1	0.39	1.09228E-66	Proliferating
TMEM14A	0.39	1.24163E-27	Proliferating
UBE2S	0.39	2.01181E-46	Proliferating
CKAP2L	0.38	4.18294E-64	Proliferating
ANLN	0.38	4.18789E-67	Proliferating
CKAP2	0.37	3.68784E-29	Proliferating
DEPDC1	0.37	9.31405E-65	Proliferating
CENPU	0.37	5.26041E-44	Proliferating

HNRNPAB	0.37	5.14848E-22	Proliferating
NDC80	0.36	7.00341E-57	Proliferating
NUF2	0.36	3.59691E-68	Proliferating
TAGLN2	0.36	4.3027E-23	Proliferating
CENPH	0.36	3.96245E-30	Proliferating
SLBP	0.36	3.31041E-22	Proliferating
PPIH	0.35	2.58127E-33	Proliferating
ILF2	0.35	2.85998E-31	Proliferating
HADH	0.35	6.22676E-23	Proliferating
CSE1L	0.35	1.32408E-23	Proliferating
CENPK	0.35	3.84603E-55	Proliferating
BOLA3	0.35	1.61676E-26	Proliferating
SKA2	0.35	2.1481E-22	Proliferating
LSMD1	0.34	1.6727E-23	Proliferating
CALM3	0.34	1.26299E-16	Proliferating
POLE3	0.34	8.10415E-27	Proliferating
AURKA	0.34	3.54241E-51	Proliferating
LMNB2	0.34	3.72237E-41	Proliferating
ANP32B	0.34	1.13424E-18	Proliferating
CRNDE	0.34	3.02274E-20	Proliferating
KIF22	0.34	1.35006E-27	Proliferating
GIN52	0.34	2.99044E-19	Proliferating
BANF1	0.34	1.4458E-17	Proliferating
ACTL6A	0.34	3.67081E-27	Proliferating
DBF4	0.34	2.54685E-48	Proliferating
KIF23	0.34	4.78926E-53	Proliferating
TEX30	0.34	6.70087E-43	Proliferating
BSG	0.34	1.82332E-15	Proliferating
CCT5	0.33	6.45661E-17	Proliferating
TACC3	0.33	1.4266E-68	Proliferating
PA2G4	0.33	9.80168E-18	Proliferating
FAM96A	0.33	1.64704E-23	Proliferating
NASP	0.33	1.74864E-08	Proliferating
KNSTRN	0.33	5.22341E-51	Proliferating
NCAPG	0.33	6.36041E-61	Proliferating
ENO1	0.33	5.37822E-16	Proliferating
CDCA5	0.33	1.22621E-61	Proliferating
TCP1	0.33	1.27113E-18	Proliferating
YBX1	0.33	1.29417E-25	Proliferating
CEP55	0.32	1.89115E-55	Proliferating
ERH	0.32	1.34156E-19	Proliferating
ARHGAP11A	0.32	4.50146E-60	Proliferating
PIF1	0.32	8.4387E-32	Proliferating

PSMA4	0.32	1.41904E-27	Proliferating
CSRP2	0.32	2.5727E-16	Proliferating
NUDC	0.32	2.3872E-22	Proliferating
TPM3	0.32	2.67936E-15	Proliferating
SNRPC	0.32	8.59175E-20	Proliferating
KIF2C	0.32	1.10726E-49	Proliferating
XRCC5	0.31	2.49143E-16	Proliferating
DLGAP5	0.31	5.07359E-48	Proliferating
TTK	0.31	1.29564E-55	Proliferating
LSM3	0.31	3.24605E-16	Proliferating
GCSH	0.31	3.32689E-16	Proliferating
ARHGAP11B	0.31	1.52424E-51	Proliferating
USP1	0.31	4.89453E-24	Proliferating
KIF11	0.31	1.03544E-56	Proliferating
VRK1	0.31	6.64127E-43	Proliferating
CYBA	0.31	3.35532E-28	Proliferating
HNRNPF	0.31	5.61549E-14	Proliferating
SRSF7	0.31	5.03983E-14	Proliferating
BCL2L12	0.31	2.12323E-53	Proliferating
ID3	0.31	7.66292E-35	Proliferating
DNMT1	0.30	7.11928E-23	Proliferating
SNRPE	0.30	2.26942E-16	Proliferating
SPC24	0.30	3.24349E-46	Proliferating
SAC3D1	0.30	2.84855E-36	Proliferating
TUBG1	0.30	4.02186E-30	Proliferating
POLD2	0.30	4.83974E-14	Proliferating
HP1BP3	0.30	1.6638E-14	Proliferating
MIS18A	0.30	2.16568E-43	Proliferating
SRP9	0.30	5.20423E-17	Proliferating
GGH	0.30	3.80001E-36	Proliferating
PAFAH1B3	0.29	5.49494E-17	Proliferating
NUCKS1	0.29	1.01878E-10	Proliferating
CKLF	0.29	6.4576E-35	Proliferating
ORC6	0.29	4.70333E-53	Proliferating
TFDP1	0.29	1.27818E-17	Proliferating
CDT1	0.29	1.54137E-23	Proliferating
PSRC1	0.29	4.62564E-40	Proliferating
FAM111B	0.29	5.53959E-34	Proliferating
RUVBL2	0.29	2.43361E-14	Proliferating
UQCRC1	0.28	1.38227E-14	Proliferating
EXOSC8	0.28	2.37744E-26	Proliferating
GTSE1	0.28	8.34438E-51	Proliferating
LYAR	0.28	1.67912E-27	Proliferating

TROAP	0.28	8.64907E-47	Proliferating
NME1	0.28	9.34276E-15	Proliferating
PSMA3	0.28	3.24653E-17	Proliferating
ECT2	0.28	2.17159E-54	Proliferating
HNRNPD	0.28	8.46034E-18	Proliferating
SAE1	0.28	7.90512E-25	Proliferating
HJURP	0.28	7.02847E-53	Proliferating
SRM	0.28	2.06357E-16	Proliferating
WDR34	0.28	9.94818E-18	Proliferating
PXMP2	0.28	2.27492E-21	Proliferating
GSTO1	0.28	1.6431E-12	Proliferating
HAT1	0.28	7.03242E-18	Proliferating
TRA2B	0.28	2.58729E-12	Proliferating
SNRPA1	0.27	2.68681E-18	Proliferating
MND1	0.27	9.60542E-51	Proliferating
CHCHD2	0.27	3.85876E-09	Proliferating
H3F3A	0.27	5.07465E-24	Proliferating
ISOC2	0.27	1.14041E-13	Proliferating
RPL22L1	0.27	1.41366E-12	Proliferating
U2AF1	0.27	1.41952E-14	Proliferating
MAGOH	0.27	7.93847E-14	Proliferating
TUFM	0.27	1.61166E-12	Proliferating
OIP5	0.27	3.26453E-56	Proliferating
GPAA1	0.27	6.45895E-13	Proliferating
MXD3	0.27	2.56345E-42	Proliferating
NCAPD2	0.27	3.52008E-46	Proliferating
KPNB1	0.27	1.75035E-16	Proliferating
MELK	0.27	4.15472E-56	Proliferating
HNRNPM	0.27	4.04699E-12	Proliferating
HSPA8	0.26	3.17449E-13	Proliferating
CNIH4	0.26	1.5272E-14	Proliferating
NCL	0.26	3.53418E-05	Proliferating
RFC2	0.26	4.06538E-21	Proliferating
CDC25B	0.26	1.67578E-44	Proliferating
PSMA2.1	0.26	2.30249E-15	Proliferating
MRPL11	0.26	1.50117E-13	Proliferating
PSMG1	0.26	1.51682E-16	Proliferating
JTB	0.26	6.99943E-11	Proliferating
ANXA5	0.26	4.51867E-20	Proliferating
ZDHHC12	0.26	1.82107E-18	Proliferating
NEK2	0.25	4.22482E-49	Proliferating
MTHFD2	0.25	6.15613E-31	Proliferating
ZWILCH	0.25	1.92442E-35	Proliferating

COMMD4	0.25	5.1198E-17	Proliferating
HSPE1	0.25	6.80518E-20	Proliferating
NBL1	0.25	3.63088E-12	Proliferating
SMC3	0.25	3.11469E-15	Proliferating
LSM6	0.25	1.4999E-16	Proliferating
DSC2	1.06	1.05178E-77	Trans1
DSP	0.79	1.53007E-50	Trans1
DSG3	0.70	6.99232E-40	Trans1
CDH1	0.47	1.17001E-17	Trans1
PKP1	0.47	5.94721E-44	Trans1
TRIM29	0.42	1.26406E-12	Trans1
MAST4	0.42	1.57409E-13	Trans1
ELL2	0.39	5.64738E-24	Trans1
RP11-408H20.1	0.37	3.18558E-21	Trans1
DHCR24	0.36	2.95446E-06	Trans1
GJA1	0.36	7.92891E-20	Trans1
PPM1K	0.36	4.09013E-14	Trans1
MAF	0.35	6.12177E-07	Trans1
CTTNBP2	0.35	4.71444E-16	Trans1
DSG1	0.34	2.13705E-17	Trans1
RAPGEFL1	0.34	6.07697E-08	Trans1
KANK1	0.34	2.94728E-16	Trans1
ZNF770	0.34	6.81825E-10	Trans1
HIGH F1A	0.31	1.45412E-08	Trans1
MTMR10	0.31	6.98599E-14	Trans1
ADH7	0.30	7.16747E-10	Trans1
PLEKHN1	0.30	2.98314E-17	Trans1
EIF4G1	0.30	5.98345E-05	Trans1
MT-CO2	0.30	1	Trans1
JAG1	0.29	8.14319E-07	Trans1
NBEAL2	0.29	4.7587E-08	Trans1
CLCA2	0.29	5.4925E-22	Trans1
HIGH PK2	0.28	5.12921E-05	Trans1
NOTCH3	0.28	0.000291883	Trans1
PVRL1	0.28	2.02868E-07	Trans1
DLG1	0.28	7.40998E-08	Trans1
SLC26A2	0.27	2.43219E-07	Trans1
ATP2A2	0.27	0.00018642	Trans1
SAMD5	0.27	3.41606E-10	Trans1
LINC00657	0.27	1.02031E-06	Trans1
PROM2	0.26	6.62674E-06	Trans1
DUOX1	0.26	2.37656E-18	Trans1

ZHX1	0.26	1.9529E-06	Trans1
FGFR3	0.25	0.003061579	Trans1
WNT5A	0.25	2.42432E-13	Trans1
MYH14	0.25	1.60835E-20	Trans1
SERPINB3	0.57	1.04147E-07	Trans2
ACTB	0.49	1.3611E-25	Trans2
CSTA	0.47	1.77326E-30	Trans2
HSPB1	0.46	4.8733E-62	Trans2
MSMO1	0.41	1	Trans2
PRDX5	0.39	1	Trans2
SH3BGRL3	0.38	1	Trans2
CST3	0.38	1	Trans2
SERPINB4	0.35	0.111596147	Trans2
CRABP2	0.35	0.004516629	Trans2
CTNNBIP1	0.34	1	Trans2
NUCB2	0.33	1	Trans2
RAB25	0.33	1	Trans2
S100A16	0.32	9.60046E-17	Trans2
S100A11	0.32	8.58917E-38	Trans2
ORMDL2	0.31	1	Trans2
ARPC3	0.31	1	Trans2
GNAI3	0.30	1	Trans2
SLPI	0.30	1	Trans2
TUBA4A	0.29	0.031452933	Trans2
LYPD3	0.28	1	Trans2
ANXA2	0.28	2.2072E-07	Trans2
FAM162A	0.27	1	Trans2
PI3	0.27	1	Trans2
AP2S1	0.27	1	Trans2
CXCL17	0.27	1	Trans2
TMED2	0.27	1	Trans2
S100A2	0.26	1.88365E-12	Trans2
FAM3B	0.25	1	Trans2
ENSA	0.25	1	Trans2
SULT2B1	0.25	1	Trans2
PIM1	1.14	3.71391E-86	Differentiated ^{low}
AIM1	1.04	4.27103E-60	Differentiated ^{low}
FAM3D	0.92	1.15966E-93	Differentiated ^{low}
CLCA4	0.91	2.35425E-74	Differentiated ^{low}
DIO2	0.91	8.52733E-65	Differentiated ^{low}
ATP1B1	0.79	6.59538E-70	Differentiated ^{low}
RP11-	0.77	2.51701E-65	Differentiated ^{low}

7K24.3			
WDR26	0.71	8.50069E-85	Differentiated ^{low}
WNK1	0.70	2.9824E-31	Differentiated ^{low}
RP11-351J23.1	0.69	4.96673E-32	Differentiated ^{low}
MLLT4	0.68	4.11017E-86	Differentiated ^{low}
CTSV	0.65	3.90909E-31	Differentiated ^{low}
PADI1	0.65	1.28083E-31	Differentiated ^{low}
TGM3	0.64	3.0029E-115	Differentiated ^{low}
EVPL	0.63	2.20309E-28	Differentiated ^{low}
TACSTD2	0.63	5.77961E-57	Differentiated ^{low}
LL22NC03-2H8.5	0.63	1.68602E-11	Differentiated ^{low}
CRNN	0.61	4.9504E-123	Differentiated ^{low}
GRHL1	0.60	1.3496E-33	Differentiated ^{low}
TJP1	0.60	1.32298E-48	Differentiated ^{low}
DOCK9	0.59	9.37259E-59	Differentiated ^{low}
TMPRSS11B	0.59	6.60168E-61	Differentiated ^{low}
NPEPPS	0.58	7.91988E-38	Differentiated ^{low}
EPS8L2	0.57	2.295E-63	Differentiated ^{low}
GRB7	0.57	6.514E-16	Differentiated ^{low}
H1FO	0.56	2.01831E-58	Differentiated ^{low}
MPZL3	0.55	4.07675E-54	Differentiated ^{low}
CLDN10	0.55	7.13639E-18	Differentiated ^{low}
ATG9B	0.55	1.80075E-15	Differentiated ^{low}
CD46	0.55	1.17146E-22	Differentiated ^{low}
CCDC64B	0.54	1.00987E-45	Differentiated ^{low}
HECTD1	0.54	2.62926E-43	Differentiated ^{low}
KLK13	0.54	8.8706E-52	Differentiated ^{low}
AL627309.1	0.53	2.37389E-13	Differentiated ^{low}
UACA	0.53	1.11175E-15	Differentiated ^{low}
CEACAM6	0.52	2.30033E-33	Differentiated ^{low}
PPL	0.52	1.34749E-43	Differentiated ^{low}
ST3GAL4	0.52	2.01672E-44	Differentiated ^{low}
SPINK5	0.51	7.7957E-92	Differentiated ^{low}
ARRDC3	0.51	5.13454E-37	Differentiated ^{low}
MUC1	0.51	0.078125016	Differentiated ^{low}
ERBB3	0.50	1.03113E-23	Differentiated ^{low}
PLEKHM1	0.50	3.99258E-20	Differentiated ^{low}

EPS8L1	0.50	1.5691E-30	Differentiated ^{low}
GPX3	0.49	2.65715E-55	Differentiated ^{low}
DUSP1	0.48	2.53063E-28	Differentiated ^{low}
VSIG10L	0.47	8.49657E-34	Differentiated ^{low}
ARHGAP27	0.46	1.02355E-19	Differentiated ^{low}
ABLIM3	0.46	3.04214E-15	Differentiated ^{low}
RBM47	0.46	2.03497E-32	Differentiated ^{low}
NAPRT1	0.46	1.16303E-54	Differentiated ^{low}
NRBP1	0.45	6.53605E-09	Differentiated ^{low}
EMP1	0.45	1.0178E-114	Differentiated ^{low}
ITPRIPL2	0.45	1.50581E-17	Differentiated ^{low}
VPS4B	0.45	1.37607E-46	Differentiated ^{low}
SFT2D2	0.45	1.10461E-24	Differentiated ^{low}
CRYAB	0.45	3.95604E-27	Differentiated ^{low}
GMDS	0.45	5.69423E-33	Differentiated ^{low}
LPIN1	0.44	0.000227592	Differentiated ^{low}
ABLIM1	0.44	5.56916E-43	Differentiated ^{low}
FAM129B	0.44	7.64142E-32	Differentiated ^{low}
ZNF117	0.44	6.57707E-30	Differentiated ^{low}
CAPN14	0.44	3.23936E-20	Differentiated ^{low}
SLK	0.43	2.79346E-41	Differentiated ^{low}
NDUFA4L2	0.43	1.60071E-40	Differentiated ^{low}
SHROOM3	0.42	2.61493E-28	Differentiated ^{low}
SLC16A3	0.42	3.89557E-41	Differentiated ^{low}
CLIP1	0.42	1.13881E-25	Differentiated ^{low}
NABP1	0.41	5.06094E-16	Differentiated ^{low}
CEACAM1	0.41	1.64916E-31	Differentiated ^{low}
JMJD1C	0.41	6.11933E-23	Differentiated ^{low}
ATP6V1C2	0.41	4.16364E-17	Differentiated ^{low}
RANBP9	0.41	4.23437E-31	Differentiated ^{low}
RP11-575H3.1	0.40	1.47681E-12	Differentiated ^{low}
MALL	0.40	1.1152E-60	Differentiated ^{low}
FAM83A	0.39	3.94753E-39	Differentiated ^{low}
ARHGAP5	0.39	1.6199E-11	Differentiated ^{low}
LY6G6C	0.39	8.47691E-18	Differentiated ^{low}
AFF4	0.39	1.36615E-18	Differentiated ^{low}
RNF222	0.39	4.13585E-38	Differentiated ^{low}
LRP10	0.39	2.73329E-34	Differentiated ^{low}

DTX2	0.39	1.76824E-12	Differentiated ^{low}
KLK10	0.39	2.26262E-15	Differentiated ^{low}
NCOA2	0.38	5.58231E-16	Differentiated ^{low}
VAT1	0.38	3.16942E-20	Differentiated ^{low}
MARCKS	0.38	3.51552E-18	Differentiated ^{low}
MROH6	0.38	3.41472E-31	Differentiated ^{low}
CAST	0.38	2.91517E-44	Differentiated ^{low}
C2orf54	0.38	2.56431E-26	Differentiated ^{low}
ULK3	0.38	1.24452E-20	Differentiated ^{low}
DENND2C	0.37	1.32618E-24	Differentiated ^{low}
CPEB4	0.37	3.01937E-21	Differentiated ^{low}
ZDHHC13	0.37	2.10048E-06	Differentiated ^{low}
PRKCI	0.37	4.20553E-08	Differentiated ^{low}
PKN2	0.37	4.3275E-05	Differentiated ^{low}
PADI3	0.36	5.4888E-07	Differentiated ^{low}
PPP4R1	0.36	2.49557E-24	Differentiated ^{low}
ANXA9	0.36	8.99583E-15	Differentiated ^{low}
CSTB	0.36	1.14729E-84	Differentiated ^{low}
MKNK2	0.36	1	Differentiated ^{low}
NUP214	0.36	0.00400625	Differentiated ^{low}
SLURP1	0.35	3.08587E-05	Differentiated ^{low}
MUC4	0.35	0.14969306	Differentiated ^{low}
PRDM1	0.35	1.30239E-11	Differentiated ^{low}
LMO7	0.35	1.10079E-39	Differentiated ^{low}
ANGPTL4	0.35	4.3316E-12	Differentiated ^{low}
CXXC5	0.35	1.02069E-19	Differentiated ^{low}
SORBS2	0.35	8.66183E-12	Differentiated ^{low}
PDCD6	0.35	2.00005E-13	Differentiated ^{low}
KIF21A	0.35	1	Differentiated ^{low}
CLDND1	0.34	2.27093E-07	Differentiated ^{low}
GPT2	0.34	8.11925E-15	Differentiated ^{low}
RAB11A	0.34	3.14782E-23	Differentiated ^{low}
FCHO2	0.34	4.19246E-11	Differentiated ^{low}
EIF4G2	0.34	6.51801E-22	Differentiated ^{low}
KIAA0247	0.34	1.1621E-12	Differentiated ^{low}
TSC22D4	0.33	2.81845E-08	Differentiated ^{low}
BNIP1	0.33	1.26293E-23	Differentiated ^{low}
ARHGEF10L	0.33	5.59722E-13	Differentiated ^{low}

ARHGAP40	0.33	8.36316E-15	Differentiated ^{low}
TMEM45B	0.33	1.37623E-21	Differentiated ^{low}
RAB5B	0.33	6.69505E-08	Differentiated ^{low}
SERPINB6	0.33	1.16779E-20	Differentiated ^{low}
TPRG1	0.33	3.88243E-21	Differentiated ^{low}
KIF1C	0.33	1.08286E-10	Differentiated ^{low}
ASPG	0.33	4.11526E-21	Differentiated ^{low}
C1orf116	0.33	1.77821E-25	Differentiated ^{low}
RERE	0.32	9.15348E-12	Differentiated ^{low}
INPPL1	0.32	1.43885E-06	Differentiated ^{low}
PMM1	0.32	1.16197E-09	Differentiated ^{low}
TJP2	0.32	3.93541E-09	Differentiated ^{low}
ANXA1	0.32	1.64292E-21	Differentiated ^{low}
NCCRP1	0.32	3.59165E-47	Differentiated ^{low}
KAZN	0.32	5.9939E-10	Differentiated ^{low}
CCNG2	0.32	9.25839E-30	Differentiated ^{low}
SAMD4B	0.32	5.92667E-08	Differentiated ^{low}
DAPP1	0.31	1.79959E-11	Differentiated ^{low}
TOM1L2	0.31	0.000256163	Differentiated ^{low}
KIAA0232	0.31	3.05554E-09	Differentiated ^{low}
MCL1	0.31	5.42829E-15	Differentiated ^{low}
PLEKHA6	0.31	7.43158E-26	Differentiated ^{low}
CNOT1	0.31	6.61897E-10	Differentiated ^{low}
SCNN1B	0.31	4.59246E-14	Differentiated ^{low}
EPB41L3	0.31	7.61157E-34	Differentiated ^{low}
TRNP1	0.31	2.16512E-14	Differentiated ^{low}
SH3PXD2A	0.30	3.4902E-05	Differentiated ^{low}
ARHGAP32	0.30	0.318569094	Differentiated ^{low}
NCKAP1	0.30	5.65326E-07	Differentiated ^{low}
NUMA1	0.30	1	Differentiated ^{low}
CYTH1	0.30	7.55777E-08	Differentiated ^{low}
ABHD17C	0.30	5.22026E-13	Differentiated ^{low}
AMFR	0.30	2.65433E-10	Differentiated ^{low}
EPHA2	0.30	0.000604687	Differentiated ^{low}
CEACAM5	0.29	1.35401E-17	Differentiated ^{low}
ADD3	0.29	1	Differentiated ^{low}
CAMSAP3	0.29	2.51739E-13	Differentiated ^{low}
CTNNA1	0.29	1.06202E-09	Differentiated ^{low}

FNDC4	0.29	4.48239E-31	Differentiated ^{low}
CLCN3	0.29	8.67392E-05	Differentiated ^{low}
CANT1	0.29	4.60768E-17	Differentiated ^{low}
SPINK7	0.29	0.068676449	Differentiated ^{low}
CALM1	0.29	2.65019E-19	Differentiated ^{low}
AGFG2	0.28	6.37418E-20	Differentiated ^{low}
TUBB6	0.28	1	Differentiated ^{low}
ATP13A4	0.28	3.97232E-17	Differentiated ^{low}
HBP1	0.28	1.33203E-18	Differentiated ^{low}
GALE	0.28	0.002099859	Differentiated ^{low}
CPNE3	0.28	1.91481E-06	Differentiated ^{low}
PLXNB2	0.28	1	Differentiated ^{low}
SH3GL1	0.28	2.95449E-16	Differentiated ^{low}
KCTD11	0.28	2.36223E-11	Differentiated ^{low}
CCNYL1	0.28	5.94757E-24	Differentiated ^{low}
UGCG	0.28	1.94603E-10	Differentiated ^{low}
UPK1A	0.28	2.26985E-21	Differentiated ^{low}
MYO6	0.27	0.042130871	Differentiated ^{low}
GLTPD1	0.27	0.019923133	Differentiated ^{low}
YPEL3	0.27	0.009928825	Differentiated ^{low}
KAT2B	0.27	1.46067E-28	Differentiated ^{low}
SLC11A2	0.27	1.65931E-13	Differentiated ^{low}
ACADM	0.27	1.3789E-08	Differentiated ^{low}
SNX21	0.27	8.76865E-08	Differentiated ^{low}
DGKA	0.27	1	Differentiated ^{low}
SGPL1	0.27	0.66637086	Differentiated ^{low}
AIM1L	0.27	1.08546E-06	Differentiated ^{low}
CLIC3	0.26	2.54119E-13	Differentiated ^{low}
IST1	0.26	1	Differentiated ^{low}
SLC8A1-AS1	0.26	6.54852E-11	Differentiated ^{low}
HCAR2	0.26	1.03068E-13	Differentiated ^{low}
DGAT2	0.26	1.96477E-10	Differentiated ^{low}
INO80C	0.26	4.67924E-06	Differentiated ^{low}
FRMD4B	0.26	0.227635752	Differentiated ^{low}
FBXO34	0.26	4.6945E-10	Differentiated ^{low}
KLHL2	0.26	8.71428E-08	Differentiated ^{low}
KATNBL1	0.26	3.75333E-08	Differentiated ^{low}
AIFM2	0.26	0.001273961	Differentiated ^{low}

C9orf169	0.25	2.77737E-19	Differentiated ^{low}
ITSN2	0.25	1.60796E-11	Differentiated ^{low}
MPRIIP	0.25	8.16542E-05	Differentiated ^{low}
ESPL1	0.25	0.009032713	Differentiated ^{low}
NPAS2	0.25	6.76628E-12	Differentiated ^{low}
B3GNT3	0.25	1.6332E-13	Differentiated ^{high}
MT1G	3.18	2.53104E-28	Differentiated ^{high}
MT1E	2.16	1.47469E-10	Differentiated ^{high}
MT1H	2.02	5.8043E-11	Differentiated ^{high}
RNASE7	1.84	6.3068E-103	Differentiated ^{high}
MT2A	1.81	4.23694E-05	Differentiated ^{high}
KRT16	1.47	1.72756E-66	Differentiated ^{high}
^{HIGH} LPDA	1.46	1.9407E-99	Differentiated ^{high}
SPRR2D	1.45	3.2634E-129	Differentiated ^{high}
DKK1	1.18	4.105E-15	Differentiated ^{high}
KRTAP3-2	1.16	0.042555029	Differentiated ^{high}
ACTG1	1.06	1.51505E-87	Differentiated ^{high}
MT1M	1.01	0.289291817	Differentiated ^{high}
KPRP	0.99	2.4605E-38	Differentiated ^{high}
NFKBIA	0.96	6.89534E-32	Differentiated ^{high}
RND3	0.92	1.9069E-123	Differentiated ^{high}
BPGM	0.91	4.59498E-10	Differentiated ^{high}
SPRR2E	0.90	1.48452E-46	Differentiated ^{high}
DUSP5	0.90	2.0004E-135	Differentiated ^{high}
GLUL	0.89	6.07694E-51	Differentiated ^{high}
FTH1	0.86	1.0511E-136	Differentiated ^{high}
HOTAIRM1	0.86	1.97495E-22	Differentiated ^{high}
GADD45B	0.85	1.33179E-52	Differentiated ^{high}
MT1F	0.84	1	Differentiated ^{high}
NR1D1	0.81	1.19702E-32	Differentiated ^{high}
SPRR2A	0.81	1.9337E-136	Differentiated ^{high}
ANKRD37	0.81	2.62073E-18	Differentiated ^{high}
CHAC1	0.75	7.30852E-66	Differentiated ^{high}
C15orf48	0.74	1.9277E-101	Differentiated ^{high}
CITED2	0.68	5.16325E-53	Differentiated ^{high}
IL23A	0.66	1.66613E-13	Differentiated ^{high}
PMAIP1	0.65	1.54453E-34	Differentiated ^{high}
SPRR2F	0.64	1.16406E-09	Differentiated ^{high}

ADM	0.64	1.256E-36	Differentiated ^{high}
S100P	0.63	5.6071E-56	Differentiated ^{high}
GABARAPL2	0.63	2.30301E-75	Differentiated ^{high}
FLG	0.61	6.60747E-27	Differentiated ^{high}
UBC	0.59	4.37389E-80	Differentiated ^{high}
PCBP1	0.58	7.18424E-66	Differentiated ^{high}
PPDPF	0.57	2.8362E-127	Differentiated ^{high}
FAM25A	0.56	8.49985E-94	Differentiated ^{high}
SQSTM1	0.56	2.70482E-76	Differentiated ^{high}
IER3	0.55	9.03366E-21	Differentiated ^{high}
GADD45A	0.55	0.011069541	Differentiated ^{high}
SPRR2B	0.54	6.14324E-11	Differentiated ^{high}
KRT17	0.53	1	Differentiated ^{high}
PHLDA1	0.52	6.50015E-54	Differentiated ^{high}
UPP1	0.51	1.90523E-25	Differentiated ^{high}
CRCT1	0.51	3.50242E-91	Differentiated ^{high}
ADIRF	0.51	1.33511E-66	Differentiated ^{high}
MT1X	0.49	1	Differentiated ^{high}
MAFF	0.47	3.87193E-54	Differentiated ^{high}
PPIF	0.47	1	Differentiated ^{high}
FAM45A	0.46	2.00669E-41	Differentiated ^{high}
MAP1LC3B	0.46	1.12909E-68	Differentiated ^{high}
ALDH1A3	0.46	4.32153E-45	Differentiated ^{high}
ZFP36	0.44	3.58478E-20	Differentiated ^{high}
RFK	0.44	1.73549E-56	Differentiated ^{high}
RASGEF1B	0.43	6.92539E-49	Differentiated ^{high}
MGAT1	0.42	2.66911E-47	Differentiated ^{high}
JUNB	0.41	1.06847E-15	Differentiated ^{high}
LGALS3	0.40	1.9962E-21	Differentiated ^{high}
TUFT1	0.40	1.23162E-48	Differentiated ^{high}
YOD1	0.40	5.34224E-38	Differentiated ^{high}
VMP1	0.40	3.52077E-28	Differentiated ^{high}
SPRR1B	0.38	1.73537E-30	Differentiated ^{high}
CXCL2	0.38	0.610362532	Differentiated ^{high}
DEFB4A	0.37	1.54524E-05	Differentiated ^{high}
LCN2	0.36	2.62347E-27	Differentiated ^{high}
NDFIP2	0.36	1.6065E-42	Differentiated ^{high}
CXCL3	0.35	1	Differentiated ^{high}

TM9SF2	0.34	1	Differentiated ^{high}
ISG15	0.34	1	Differentiated ^{high}
UBE2V1	0.33	2.13951E-34	Differentiated ^{high}
DHRS9	0.33	1.30631E-42	Differentiated ^{high}
ATP8B1	0.33	2.46045E-07	Differentiated ^{high}
PRSS22	0.33	4.23968E-16	Differentiated ^{high}
TPM4	0.32	2.50065E-29	Differentiated ^{high}
MAPK8	0.32	2.23438E-33	Differentiated ^{high}
RAP2B	0.32	1.98361E-30	Differentiated ^{high}
DUOXA2	0.32	3.81058E-21	Differentiated ^{high}
EIF1	0.32	1.09893E-21	Differentiated ^{high}
TTC9	0.32	1.05084E-30	Differentiated ^{high}
IL1A	0.32	9.06695E-17	Differentiated ^{high}
HSPB8	0.31	1.15077E-24	Differentiated ^{high}
UBE2D3	0.31	4.24245E-10	Differentiated ^{high}
HLA-E	0.31	1.94936E-07	Differentiated ^{high}
RMND5A	0.31	4.9753E-35	Differentiated ^{high}
ZNF812	0.30	1.0142E-12	Differentiated ^{high}
HLCS	0.30	2.748E-21	Differentiated ^{high}
RP11-532F12.5	0.30	1.45457E-32	Differentiated ^{high}
TMEM159	0.29	1.6899E-10	Differentiated ^{high}
FEM1C	0.27	4.64417E-06	Differentiated ^{high}
DUSP14	0.27	3.99427E-22	Differentiated ^{high}
GRPEL2	0.27	6.48333E-09	Differentiated ^{high}
RP11-390E23.6	0.27	3.86342E-22	Differentiated ^{high}
AVPI1	0.27	2.0135E-11	Differentiated ^{high}
NFKBIZ	0.27	2.44796E-38	Differentiated ^{high}
RNF145	0.27	4.95091E-23	Differentiated ^{high}
POLR1D	0.27	2.48118E-14	Differentiated ^{high}
SERTAD2	0.26	1.20923E-34	Differentiated ^{high}
ARL4C	0.26	3.68277E-18	Differentiated ^{high}

Supplemental Table 3. Markers of the human esophageal basal epithelial layers

basal layer markers *	RPKM basal	RPKM suprabasal	ratio basal/suprabasal
IGFBP3	6.21	0.01	620.58
VIT	9.13	0.18	51.93
CH25H	7.29	0.16	44.44
ABI3BP	5.15	0.15	35.25
DKK3	7.03	0.20	34.40
COL17A1	81.54	2.39	34.10
BGN	9.80	0.33	29.26
CDH13	9.63	0.34	28.38
TNS3	6.86	0.34	20.09
CAV1	11.40	0.61	18.80
EFEMP1	13.35	0.75	17.70
CYR61	9.36	0.58	16.08
MXRA5	27.39	1.72	15.96
TPM2	6.63	0.42	15.64
HOPX	5.42	0.36	14.91
BASP1	8.45	0.58	14.58
DST	125.92	8.68	14.51
CYP2S1	12.03	0.86	13.94
ASS1	18.44	1.33	13.82
CCDC3	17.63	1.30	13.53
TNS1	8.47	0.63	13.42
ADH1C	6.04	0.46	13.03
DLK2	5.76	0.45	12.91
SLC7A5	21.60	1.89	11.43
FHL2	5.84	0.51	11.37
NTRK2	5.68	0.51	11.20
LAMB3	18.93	1.76	10.76
ABCC3	8.43	0.80	10.55
MOXD1	17.34	1.89	9.18
SLC40A1	6.58	0.76	8.66
CFB	5.33	0.64	8.31
BOC	7.38	0.90	8.16
GPNMB	103.75	13.00	7.98
FOXQ1	7.57	0.95	7.97
IGFBP5	20.10	2.72	7.40
ZFP36L2	8.98	1.23	7.29
ABCA1	9.40	1.29	7.28
TP53I11	7.24	0.99	7.28

WNT4	15.05	2.08	7.25
IFITM1	6.80	0.98	6.94
TIMP1	7.94	1.18	6.72
NPR3	17.53	2.63	6.67
SLC1A3	20.29	3.12	6.50
PCDH7	6.88	1.12	6.16
TFAP2B	5.34	0.87	6.11
ANKH	6.29	1.04	6.05
LEPREL1	9.42	1.56	6.04
CXCL14	52.82	8.95	5.90
GABRE	5.09	0.88	5.76
KRT14	14.60	2.56	5.71
HIST1H3I	7.45	1.34	5.58
TNS4	33.36	5.99	5.56
SLC1A4	11.75	2.12	5.53
ITGB4	11.45	2.16	5.30
CYBRD1	7.49	1.42	5.27
AP2B1	11.20	2.19	5.11
NPNT	6.26	1.23	5.07
ANTXR1	7.40	1.47	5.04
ZMYM6NB	15.10	3.02	5.01
BEX2	8.03	1.65	4.88
GLUL	12.82	2.63	4.87
SOX6	5.05	1.05	4.83
FAT1	7.85	1.64	4.78
PINLYP	6.79	1.48	4.59
MEGF6	8.09	1.78	4.53
SLC3A2	10.22	2.28	4.47
PTRF	12.02	2.86	4.21
FLNA	6.82	1.65	4.13
CDHR1	9.14	2.28	4.01
IL18	29.31	7.50	3.91
KRT19	53.41	13.73	3.89
TXNIP	30.89	7.95	3.88
TFCP2L1	8.98	2.31	3.88
SESN3	14.93	3.86	3.86
PTPN14	6.67	1.74	3.83
BTG2	10.77	2.82	3.81
EHD3	7.58	2.04	3.72
KRT15	702.82	189.20	3.71
TANC2	6.26	1.71	3.66
PTPRS	8.34	2.29	3.64
SH3PXD2A	9.20	2.54	3.62

PRNP	11.98	3.33	3.60
LAPTM4B	13.82	3.90	3.55
C21orf91	6.81	1.92	3.54
MEF2A	5.05	1.45	3.47
ETS2	7.87	2.33	3.38
CTDSPL	6.91	2.04	3.38
NRM	7.08	2.10	3.37
CLSTN1	9.04	2.68	3.37
SLC2A1	29.74	9.15	3.25
TPBG	8.73	2.70	3.23
PTPRZ1	10.43	3.24	3.22
CRIM1	6.28	1.95	3.22
PRKAB2	5.00	1.55	3.22
ZNF91	5.23	1.65	3.16
GLTSCR2	13.93	4.44	3.14
BEX4	5.57	1.79	3.12
AJUBA	5.50	1.79	3.08
LAMB2	5.30	1.73	3.06
SNAI2	17.40	5.72	3.04
ARL4C	5.50	1.83	3.01
RBM4B	5.24	1.74	3.01
DHRS3	14.83	4.95	3.00
LGALS8	8.11	2.72	2.99
LAMC1	5.11	1.71	2.99
CCND2	9.56	3.20	2.98
LAMA3	7.64	2.60	2.93
RBBP8	11.22	3.88	2.89
ZNF395	5.46	1.90	2.88
APCDD1	20.11	7.04	2.86
SLC43A3	12.24	4.33	2.83
NAP1L1	13.98	4.94	2.83
CROT	5.08	1.82	2.80
AHCYL2	8.71	3.13	2.79
C2CD2	6.39	2.30	2.79
GSR	6.28	2.26	2.78
IFITM3	33.82	12.20	2.77
LIMA1	11.12	4.05	2.75
HLF	11.61	4.24	2.74
SELENBP1	6.39	2.36	2.71
SP100	5.75	2.12	2.71
EGR1	45.41	16.78	2.71
CRTAP	7.64	2.83	2.70
MXRA7	5.83	2.17	2.68

ITGB1	8.12	3.04	2.67
STOM	9.69	3.64	2.66
FTH1	62.96	23.67	2.66
FBXW7	5.14	1.95	2.64
CD74	7.23	2.75	2.63
TLR3	5.09	1.94	2.62
FGD6	6.09	2.33	2.62
CTDSP2	7.93	3.07	2.58
HAUS4	5.54	2.18	2.54
HSPA2	8.23	3.27	2.52
NF1	5.14	2.05	2.51
ST6GALNAC2	11.95	4.80	2.49
CDCA7	6.30	2.54	2.48
LDB1	9.70	3.93	2.47
DSG2	6.04	2.48	2.44
THSD4	21.51	8.87	2.43
DTX3L	5.01	2.09	2.40
STON2	7.57	3.18	2.38
PBX2	8.95	3.78	2.36
SLC7A1	49.11	20.98	2.34
PHF3	9.64	4.21	2.29
CALCOCO1	13.01	5.70	2.28
KDM6A	5.34	2.34	2.28
PARP14	7.41	3.26	2.27
AMOTL1	7.08	3.15	2.25
GSTM2	10.07	4.58	2.20
CHD3	8.38	3.83	2.19

* the green font denotes esophagus-specific genes

Supplemental Table 4. Markers of the human esophageal suprabasal epithelial layers

suprabasal layer markers*	RPKM basal	RPKM suprabasal	ratio basal/suprabasal
SERPINB3	2.18	36.71	0.06
KRT4	34.91	586.30	0.06
ALDH1A1	0.45	6.69	0.07
TGM3	1.11	13.07	0.08
GPX3	0.66	7.34	0.09
CXCL17	3.04	32.80	0.09
A2ML1	3.58	36.68	0.10
RHCG	3.52	34.55	0.10
ALDH3B2	0.96	9.13	0.11
SPRR1B	2.80	26.53	0.11
KRT6C	3.02	27.51	0.11
EPHX3	1.16	10.16	0.11
KRT6B	1.73	15.13	0.11
C2orf54	0.63	5.36	0.12
S100A8	38.84	330.82	0.12
CLCA4	0.62	5.21	0.12
SPINK5	7.43	61.98	0.12
CYP2C18	0.61	5.05	0.12
SPRR3	29.11	238.55	0.12
MUC15	0.79	5.93	0.13
KRT6A	20.25	149.68	0.14
S100A9	5.07	36.57	0.14
DSG1	1.53	11.01	0.14
KRT1	0.80	5.53	0.14
SCEL	1.04	7.20	0.15
C10orf99	1.95	12.43	0.16
CSTA	76.50	447.69	0.17
SPARCL1	1.48	8.60	0.17
SAMHD1	2.09	11.96	0.17
CSTB	32.53	185.73	0.18
SERPINB13	2.34	12.72	0.18
ZNF750	3.00	16.21	0.19
KRT13	307.29	1575.82	0.20
RHOV	1.26	6.43	0.20
SLC39A2	1.10	5.40	0.20
KLK13	8.57	41.85	0.20
SCNN1A	1.73	7.95	0.22
CRABP2	12.92	57.13	0.23

CTTNBP2	1.18	5.22	0.23
GRHL3	3.73	16.13	0.23
SLPI	1.69	7.14	0.24
S100A11	254.83	998.88	0.26
DSC2	12.12	47.40	0.26
SCIN	2.23	8.71	0.26
BARX2	4.84	18.59	0.26
LPAR5	2.43	9.34	0.26
PTGS1	1.62	6.12	0.26
VPS25	2.12	7.90	0.27
BBOX1	1.74	6.35	0.27
PVRL4	1.72	6.16	0.28
KLK11	3.16	11.16	0.28
LYPD3	10.39	36.64	0.28
SERPINB1	3.02	10.48	0.29
FGFBP1	2.45	8.06	0.30
ANXA1	90.94	298.35	0.30
NUCB2	1.80	5.89	0.31
AQP3	62.14	202.78	0.31
FABP5	42.59	138.72	0.31
CALML3	4.28	13.89	0.31
NAGK	2.16	6.95	0.31
DYNLT3	1.76	5.63	0.31
CNN3	1.82	5.67	0.32
IL1RN	13.93	43.39	0.32
CDKN1A	4.79	14.86	0.32
TUBA4A	5.09	15.76	0.32
MAL2	11.51	35.11	0.33
NOTCH3	4.31	13.10	0.33
SMAGP	1.93	5.80	0.33
UGT1A7	6.37	19.01	0.34
THBD	1.70	5.03	0.34
ZNF185	10.98	32.46	0.34
AKR1C3	1.79	5.23	0.34
PDE6D	1.84	5.37	0.34
AP1B1	1.74	5.03	0.35
ICT1	5.56	15.95	0.35
MSMO1	2.36	6.74	0.35
LY6D	30.32	86.32	0.35
MTSS1	2.92	8.18	0.36
DBI	22.14	61.98	0.36
SFN	43.84	122.22	0.36
TIMM8B	2.72	7.56	0.36

ACPP	6.23	17.27	0.36
NDUFS6	3.57	9.70	0.37
SCD	2.85	7.70	0.37
CCND1	31.60	84.93	0.37
KLF8	2.27	6.05	0.38
CCDC56	4.44	11.80	0.38
SERPINB2	2.22	5.85	0.38
ACAA2	4.00	10.53	0.38
RAB25	26.37	69.09	0.38
AKR1B10	4.67	12.22	0.38
S100A16	13.43	34.62	0.39
BDH1	2.90	7.38	0.39
CES2	2.20	5.60	0.39
SLC9A3R1	14.03	34.98	0.40
S100A14	33.90	84.07	0.40
PLD1	2.55	6.31	0.40
TXN	37.76	92.32	0.41
NDUFAF2	2.39	5.81	0.41
DDAH1	2.32	5.65	0.41
ELOVL1	3.19	7.74	0.41
NDUFB3	10.41	25.11	0.41
CYP4B1	2.09	5.03	0.42
RPS26	10.85	26.01	0.42
TPD52L1	5.86	13.95	0.42
EMP1	16.94	39.90	0.42
NDUFS8	2.82	6.59	0.43
C7orf25	2.50	5.85	0.43
NAA20	3.49	8.13	0.43
NDUFAF3	2.19	5.06	0.43
PGD	34.13	78.36	0.44
MTMR10	4.29	9.83	0.44
USMG5	9.76	22.33	0.44
TCEA3	2.63	5.94	0.44
PTGR1	10.10	22.75	0.44
CLDN7	2.87	6.44	0.45
MPZL2	24.32	54.60	0.45
ADRB2	5.44	12.20	0.45
MYCBP	3.62	8.08	0.45
DSP	103.30	230.15	0.45
GLTP	5.09	11.32	0.45
DUOX1	3.92	8.69	0.45
UGDH	8.34	18.44	0.45
CAPNS2	8.34	18.32	0.46

TRIM29	61.30	133.28	0.46
B4GALT5	3.02	6.54	0.46
SUCLG1	5.30	11.48	0.46
ACAT2	3.18	6.88	0.46
GPD1L	4.13	8.92	0.46
ATP5J2	16.09	34.55	0.47
FAM162A	5.24	11.24	0.47
PDCD5	8.34	17.89	0.47
SUCLG2	3.38	7.21	0.47
MGST2	7.99	17.05	0.47
CYCS	7.89	16.76	0.47
TJP1	7.75	16.41	0.47
TAF13	2.55	5.39	0.47
MFSD6	3.32	7.01	0.47
CLTB	3.00	6.32	0.48
NOP10	3.36	7.07	0.48
PKP1	15.18	31.71	0.48
BHLHE40	21.34	44.56	0.48
FAM127A	4.27	8.86	0.48
PPIC	4.65	9.60	0.48
ANXA2	92.29	190.33	0.48
CDH1	7.09	14.58	0.49
MRPS22	5.63	11.42	0.49
DYNLT1	13.59	27.55	0.49
SH3RF2	5.60	11.35	0.49
CHMP4B	4.26	8.61	0.50
CTSC	4.22	8.46	0.50
PGAM1	3.29	6.60	0.50
PRELID1	5.92	11.86	0.50
NDRG2	3.42	6.82	0.50
CIB1	2.53	5.04	0.50
PSMB6	7.10	14.13	0.50
GSTP1	32.41	64.47	0.50
PPL	6.08	12.09	0.50
PGM2	3.38	6.71	0.50
IDH2	3.66	7.23	0.51
MPP7	4.17	8.22	0.51
MRPL20	2.66	5.23	0.51
NDUFB2	17.95	35.20	0.51
JUP	26.38	51.67	0.51
TFRC	4.27	8.32	0.51
DYNLL1	44.34	86.40	0.51
LAD1	8.80	17.11	0.51

GPX2	11.91	23.05	0.52
MIEN1	5.85	11.31	0.52
BRP44L	4.16	8.00	0.52
MRPL13	14.15	27.10	0.52
EZR	11.71	22.32	0.52
UQCRQ	3.56	6.77	0.53
ENSA	29.02	54.95	0.53
OGFRL1	3.79	7.17	0.53
DSG3	45.09	84.90	0.53
CYB5A	3.37	6.34	0.53
FAM206A	3.35	6.28	0.53
SFT2D2	7.11	13.26	0.54
RAB11A	3.74	6.96	0.54
DLG1	3.47	6.45	0.54
MINOS1	3.47	6.44	0.54
MANSC1	3.66	6.79	0.54
FKBP4	7.60	14.08	0.54
NDUFA7	2.87	5.31	0.54
ATP6V0D1	4.76	8.79	0.54
TMSB4X	6.49	11.93	0.54
HSD17B4	8.97	16.43	0.55
PERP	53.86	97.98	0.55
POMP	7.20	13.08	0.55
DHRS1	3.14	5.68	0.55
UBE2T	4.13	7.44	0.56
CAPZB	4.54	8.18	0.56
SLC35A4	2.83	5.09	0.56
ATP5J	23.35	41.95	0.56
ADH7	28.55	50.92	0.56
TMEM154	3.30	5.87	0.56
PTN	22.14	39.28	0.56
C21orf59	7.62	13.51	0.56
ELL2	7.75	13.70	0.57
PSMC2	7.94	14.03	0.57
SUSD4	7.31	12.91	0.57
COX6A1	24.15	42.29	0.57
TIMM21	3.26	5.70	0.57
MDH2	12.11	21.18	0.57
COX8A	10.87	19.00	0.57
ARF6	4.51	7.89	0.57
SLIRP	10.28	17.96	0.57
DAPL1	34.00	59.29	0.57
PPIB	15.23	26.38	0.58

COMT	5.05	8.74	0.58
EMP2	19.88	34.32	0.58
TECR	42.59	73.52	0.58
RAB10	12.17	20.98	0.58
HMGCR	3.78	6.50	0.58
GTF3C6	2.96	5.06	0.58
EIF2B1	6.12	10.43	0.59
ADI1	4.32	7.34	0.59
OSTF1	3.95	6.69	0.59
ERMP1	3.58	6.06	0.59
JAG1	4.69	7.93	0.59
SERPINB5	13.09	22.01	0.59
CMAS	5.80	9.75	0.60
ARPC3	6.57	10.99	0.60
MOCS2	3.93	6.58	0.60
NDUFS1	5.03	8.36	0.60
RAB5C	3.10	5.14	0.60
RFFL	3.06	5.08	0.60
PSMD14	4.19	6.89	0.61
DNAJC8	4.39	7.18	0.61
ALDH9A1	12.85	20.98	0.61
AIM1	11.61	18.73	0.62
EPHX1	9.07	14.55	0.62
CA12	7.79	12.44	0.63
TM4SF1	5.47	8.70	0.63
MTX2	5.08	8.07	0.63
LMAN2	4.18	6.62	0.63
SLC25A5	28.68	45.13	0.64
YWHAZ	90.00	140.48	0.64
MRPS10	7.45	11.58	0.64
ATP5H	12.00	18.55	0.65
TIMM23	7.04	10.80	0.65
CLCA2	20.43	31.24	0.65
HNRNPAB	20.73	30.72	0.67
CAPZA1	8.34	12.33	0.68
ANXA7	11.41	16.81	0.68
TOMM70A	4.05	5.87	0.69
MT1X	30.03	43.49	0.69

* the green font denotes esophagus-specific genes