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# **Identification of autophagy-regulated proteins by proteomic analysis of tape-stripped stratum corneum**

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Autophagy is one of the main mechanisms for the degradation of organelles and intracellular proteins. The substrates of autophagy are enclosed in vesicles which fuse with lysosomes. Autophagy is active during stress responses and terminal differentiation of keratinocytes forming the stratum corneum (SC) and skin appendages. Dysfunctions of autophagy are implicated in the etiology of skin diseases such as psoriasis [1, 2]. Methods and markers for the detection of impairments of autophagy are required to further validate the clinical significance of autophagy.

Here, we investigated whether the lack of autophagy in keratinocytes can be detected by the proteomic analysis of the SC. As a model, we utilized *Atg7<sup>f/f</sup> Krt14-Cre* mice (*Atg7-EKO* for *Atg7* epidermal knockout, n=6), in which the essential autophagy gene *Atg7* is deleted specifically in keratinocytes, in comparison to fully autophagy-competent mice (*Atg7<sup>f/f</sup>*, denoted wild-type, WT, n=5) [3]. SC was sampled by tape-stripping from the soles of sacrificed mice and subjected to label-free proteomics as previously described [4] (Supplementary Methods) (Fig. 1a). Keratins Krt2 and Krt10 were identified as the quantitatively dominant proteins in the SC of both WT and *Atg7-EKO* mice (Fig. 1b). Among more than 170 proteins detected (Suppl. Table S1), 10 proteins were significantly increased in abundance when autophagy was suppressed (adjusted P-value <0.05) (Fig. 1b, c).

Five of the proteins elevated in the absence of autophagy, namely pyruvate kinase (Pkm), elongation factor 2 (Eef2), malate dehydrogenase 2 (Mdh2), valosin-containing protein (Vcp) and galectin 7 (Lgals7), have recently been found to be elevated in autophagy-deficient hair shafts, whereas the five others are not significantly elevated or have not been quantified in hair shafts [5]. Interestingly, the increase of lamin A/C (Lmna) in *Atg7-EKO* SC is in line with the proposed role of autophagy in degrading components of the nucleus during the cornification of epidermal keratinocytes [1]. Furthermore, the skin barrier-associated protein filaggrin (Flg) and two desmosomal proteins, junction plakoglobin (Jup) and desmoplakin (Dsp), are elevated in *Atg7-EKO* samples (Fig. 1a).

These data indicate that the impairment of keratinocyte autophagy manifests in alteration of the SC that can be detected by proteomic analysis of tape-strip samples. Notably, the autophagy-dependent changes in the protein composition of the SC are less pronounced than those of hair shafts in which a broad range of proteins are significantly increased upon suppression of autophagy [5]. The lower number of autophagy-related marker proteins in the SC is likely caused by additional autophagy-independent modifications of the proteome, such as proteolysis by endogenous enzymes and proteases of commensal microbes. This study had limitations such as the incomplete sampling of the SC and the lack of a comparison with

interfollicular epidermis. We conclude that proteomics of the SC is a promising method for the analysis of autophagic activity in the epidermis, with candidate markers being provided by the present study in a genetically well-defined mouse model. Further studies on human SC and cornified skin appendages are required to determine the most useful approach for the detection of autophagy-dependent aberrations of keratinocyte differentiation in skin diseases.

#### **Ethics statement**

No experiments on live animals were performed in this study. In agreement with the national laws of Austria, a permission for killing animals for tissue preparation was not required.

#### **Data availability statement**

The raw data are available at the MassIVE Proteomics repository (<https://massive.ucsd.edu/>) with MassIVE id number MSV000095353.

#### **Author Contributions**

S.S., R.H.R. and L.E. designed the study. S.S., N.K., I.M.N., R.H.R. and L.E. collected and analyzed the data. S.S. and L.E. wrote the original draft of the manuscript. N.K., I.M.N. and R.H.R. reviewed and edited the manuscript. R.H.R. and L.E. supervised the study. All authors have read and approved the final manuscript.

#### **Competing Interests**

The authors have no competing interests.

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## Figure legend

**Figure 1. Proteomic analysis of sole skin stratum corneum (SC) from wildtype (WT) and *Atg7* epidermal knockout (EKO) mice. (a)** Schematic depiction of the study design. **(b)** The normalized protein abundance is shown for the predominant keratins of sole skin and ten proteins that differed significantly (adjusted *P*-values <0.05, \* and <0.01, \*\*) in abundance in WT and EKO SC. Bars and error bars show means and standard deviations, respectively. **(c)** Fold changes (EKO/WT) of the proteins shown in panel **b**. Note that the vertical axes in both panels show dimensionless quantities. ns, not significant.

## **Supplementary methods**

### **Mice**

*Atg7<sup>fl/fl</sup> K14-Cre* (EKO) and *Atg7<sup>fl/fl</sup>* (WT) mice were maintained under standard housing conditions [3, 5]. Male mice were sacrificed at an age of 9-10 weeks immediately before samples were prepared.

### **Tape-stripping of stratum corneum**

Stratum corneum was prepared from the soles of hind limb feet by repeated application of D-Squame discs (Cuderm, Dallas, TX, USA). The first adhesive disc containing the most superficial layer of the stratum corneum was excluded from further analysis. The next three discs containing deeper layers of the stratum corneum were collected and processed for subsequent proteomic analysis as previously described [4].

### **Mass spectrometry and protein identification**

The trypsin-digested samples were analyzed by liquid chromatography – tandem mass spectrometry (LC-MS/MS) on a Thermo Scientific Dionex UltiMate 3000 RSLC system according to a published method [5]. The raw data were analyzed using PEAKS Studio (Bioinformatics Solutions Inc., Waterloo, ON, Canada) as previously described [5].

### **Statistical analysis**

The statistical analysis was performed using GraphPad Prism version 8.0.1 for Windows (GraphPad Software, San Diego, CA, USA). Two-tailed t-tests with a correction for multiple comparisons using the Holm-Šídák method (alpha = 0.05) were performed to determine the significance of differences.

**Supplementary Table S1.** Proteomic analysis of the stratum corneum of wildtype (WT) and Atg7 epidermal knockout (EKO) mice: Normalized abundance values

Protein	Description	Accession	Abundance (normalized area)				Abundance (normalized area) EKO				WT mean	EKO mean	WT SD	EKO SD	END/WT	P value	Adjusted P value	Significance			
			WT1	WT2	WT3	WT5	EKO1	EKO2	EKO3	EKO4											
Krt2	Keratin type I cytoskeletal 4 Osmus-musculus CX0-10900 GN-Krt2 PE=1 SV=1	Q31755	4.13E-06	3.81E-06	4.30E-06	4.16E-06	3.09E-06	4.05E-06	4.05E-06	4.05E-06	4.06E-06	4.06E-06	2.28E-06	2.69E-06	1.02	0.373483	<0.000999	n.s.			
Homoem	Keratin type I cytoskeletal 10 Osmus-musculus CX0-10900 GN-Homoem PE=1 SV=1	P01166	1.04E-06	1.04E-06	1.04E-06	1.04E-06	1.04E-06	1.04E-06	1.04E-06	1.04E-06	1.04E-06	1.04E-06	1.04E-06	1.04E-06	1.04E-06	1.04E-06	0.000000	0.000000	n.s.		
Homoem	Osmus-musculus CX0-10900 GN-Homoem PE=1 SV=1	E86K9P3	8.72E-06	1.04E-02	1.24E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	n.s.	
Krt1	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt1 PE=1 SV=4	P01406	5.02E-02	4.18E-02	7.02E-02	4.36E-02	4.78E-02	3.87E-02	4.32E-02	4.00E-02	3.93E-02	3.40E-02	4.12E-02	5.47E-02	3.94E-02	1.05E-02	2.82E-02	0.72	0.012827	0.383913	n.s.
Krt181	Keratin type II cuticular Hb3 Osmus-musculus CX0-10900 GN-Krt181 PE=1 SV=2	Q9REZ2	1.35E-05	1.15E-05	4.64E-05	2.75E-04	7.04E-05	2.11E-04	2.26E-04	2.00E-04	2.03	0.005591	0.999406	n.s.							
Krt183	Keratin type I cuticular H3 Osmus-musculus CX0-10900 GN-Krt183 PE=1 SV=2	E9V1Q9	8.50E-04	6.73E-04	2.51E-04	2.11E-04	6.13E-04	5.34E-04	5.14E-04	1.13E-04	1.23E-04	1.10E-04	1.58E-04	6.79E-04	5.24E-04	1.06E-04	2.44E-04	0.24	0.04959	0.997071	n.s.
Krt183b	Keratin type I cuticular H3 Osmus-musculus CX0-10900 GN-Krt183b PE=1 SV=2	P01897	8.25E-03	4.04E-03	1.81E-03	1.81E-03	4.56E-03	2.45E-03	8.06E-03	2.78E-03	1.28E-03	1.00E-03	6.01E-04	4.19E-03	7.24E-03	2.28E-03	2.65E-03	1.74	0.00968	0.999483	n.s.
Krt186	Keratin type II cuticular Hb3 Osmus-musculus CX0-10900 GN-Krt186 PE=1 SV=2	P01781	7.68E-05	8.71E-05	1.21E-05	2.35E-05	1.01E-04	2.45E-05	1.54E-04	2.24E-04	1.79E-04	1.07E-04	8.28E-05	6.00E-05	1.24E-04	3.55E-05	9.10E-05	2.70	0.01206	0.999513	n.s.
Krt187	Keratin type II cuticular 87 Osmus-musculus CX0-10900 GN-Krt187 PE=2 SV=2	Q9GMF0	5.33E-03	4.06E-03	2.07E-03	1.38E-03	3.35E-03	1.87E-03	6.81E-03	7.14E-03	7.27E-03	9.41E-03	4.11E-03	3.77E-03	6.15E-03	1.41E-03	2.46E-03	1.88	0.006089	0.999406	n.s.
Krt184	Keratin type I cuticular H4 Osmus-musculus CX0-10900 GN-Krt184 PE=2 SV=2	P01898	5.23E-03	4.06E-03	2.07E-03	1.38E-03	3.35E-03	1.87E-03	6.81E-03	7.14E-03	7.27E-03	9.41E-03	4.11E-03	3.77E-03	6.15E-03	1.41E-03	2.46E-03	1.88	0.006089	0.999406	n.s.
Krt188	Keratin type II cuticular 87 Osmus-musculus CX0-10900 GN-Krt188 PE=2 SV=2	P01781	7.68E-05	8.71E-05	1.21E-05	2.35E-05	1.01E-04	2.45E-05	1.54E-04	2.24E-04	1.79E-04	1.07E-04	8.28E-05	6.00E-05	1.24E-04	3.55E-05	9.10E-05	2.70	0.01206	0.999513	n.s.
Krt189	Keratin type I cuticular H4 Osmus-musculus CX0-10900 GN-Krt189 PE=1 SV=1	Q9D64W	2.52E-02	1.98E-02	4.63E-02	3.80E-02	3.97E-02	1.12E-02	4.88E-03	4.77E-02	5.93E-02	3.08E-02	1.04E-02	4.88E-03	3.83E-02	8.02E-02	1.40E-02	2.34	0.014721	0.993988	n.s.
Krt189	Keratin type II cuticular 10 Osmus-musculus CX0-10900 GN-Krt189 PE=1 SV=1	P01898	2.52E-02	1.98E-02	4.63E-02	3.80E-02	3.97E-02	1.12E-02	4.88E-03	4.77E-02	5.93E-02	3.08E-02	1.04E-02	4.88E-03	3.83E-02	8.02E-02	1.40E-02	2.32	0.030581	0.999599	n.s.
Krt190	Keratin type I cytoskeletal 24 Osmus-musculus CX0-10900 GN-Krt190 PE=1 SV=1	A13171	3.87E-03	1.66E-03	7.95E-04	3.84E-04	3.54E-03	3.16E-03	4.75E-03	4.63E-03	3.53E-03	1.89E-03	2.91E-03	2.91E-03	2.91E-03	2.91E-03	2.91E-03	0.000000	0.000000	0.000000	
Krt191	Keratin type II cytoskeletal 25 Osmus-musculus CX0-10900 GN-Krt191 PE=1 SV=1	Q9D64W	6.57E-02	3.89E-02	5.00E-02	4.07E-02	5.78E-02	6.63E-02	4.50E-02	5.67E-02	4.99E-02	5.75E-02	5.54E-02	5.51E-02	5.51E-02	5.51E-02	5.51E-02	0.000000	0.000000	0.000000	
Krt193	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt193 PE=1 SV=1	Q9D64W	3.82E-03	3.84E-03	1.58E-03	3.08E-03	2.31E-03	7.32E-03	6.75E-03	3.76E-03	3.09E-03	2.76E-03	5.34E-03	5.26E-03	5.26E-03	5.26E-03	5.26E-03	0.000000	0.000000	0.000000	
Krt194	Keratin type II cytoskeletal 14 Osmus-musculus CX0-10900 GN-Krt194 PE=1 SV=1	Q9D64W	2.01E-02	3.19E-02	1.66E-02	1.74E-02	2.04E-02	1.04E-02	3.04E-03	3.66E-02	2.98E-02	2.86E-02	1.21E-02	1.35E-02	2.08E-02	2.30E-02	2.94E-02	1.11	0.060929	0.999999	n.s.
Krt195	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt195 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt196	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt196 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt197	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt197 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt198	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt198 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt199	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt199 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt200	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt200 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt201	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt201 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt202	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt202 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt203	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt203 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt204	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt204 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt205	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt205 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt206	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt206 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt207	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt207 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt208	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt208 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt209	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt209 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt210	Keratin type II cytoskeletal 10 Osmus-musculus CX0-10900 GN-Krt210 PE=1 SV=1	Q9D64W	1.96E-02	1.03E-02	6.98E-03	1.35E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	1.04E-02	0.000000	0.000000	0.000000	
Krt211	Keratin associated protein 13 Osmus-musculus CX0-10900 GN-Krt211 PE=1 SV=1	P01455	1.20E-02	2.77E-02	7.94E-03	1.03E-02	2.11E-02	4.88E-03	4.74E-02	5.14E-02	4.54E-02	4.74E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	0.000000	0.000000	0.000000	
Krt212	Keratin associated protein 13 Osmus-musculus CX0-10900 GN-Krt212 PE=1 SV=1	Q9D64W	1.20E-02	2.77E-02	7.94E-03	1.03E-02	2.11E-02	4.88E-03	4.74E-02	5.14E-02	4.54E-02	4.74E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	0.000000	0.000000	0.000000	
Krt213	Keratin associated protein 13 Osmus-musculus CX0-10900 GN-Krt213 PE=1 SV=1	Q9D64W	1.20E-02	2.77E-02	7.94E-03	1.03E-02	2.11E-02	4.88E-03	4.74E-02	5.14E-02	4.54E-02	4.74E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	0.000000	0.000000	0.000000	
Krt214	Keratin associated protein 13 Osmus-musculus CX0-10900 GN-Krt214 PE=1 SV=1	Q9D64W	1.20E-02	2.77E-02	7.94E-03	1.03E-02	2.11E-02	4.88E-03	4.74E-02	5.14E-02	4.54E-02	4.74E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	0.000000	0.000000	0.000000	
Krt215	Keratin associated protein 13 Osmus-musculus CX0-10900 GN-Krt215 PE=1 SV=1	Q9D64W	1.20E-02	2.77E-02	7.94E-03	1.03E-02	2.11E-02	4.88E-03	4.74E-02	5.14E-02	4.54E-02	4.74E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	0.000000	0.000000	0.000000	
Krt216	Keratin associated protein 13 Osmus-musculus CX0-10900 GN-Krt216 PE=1 SV=1	Q9D64W	1.20E-02	2.77E-02	7.94E-03	1.03E-02	2.11E-02	4.88E-03	4.74E-02	5.14E-02	4.54E-02	4.74E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	4.54E-02	0.00000			

Anxa5	Annexin A5 OS=Mus musculus OX=10090 GN=Anxa5 PE=1 SV=1	P48036	2,45E-05	3,23E-07	7,62E-05	7,28E-05	1,3
Dusp14	Dual specificity protein phosphatase 14 OS=Mus musculus OX=10090 GN=Dusp14 PE=2 SV=2	Q9JLY7	5,97E-06	7,29E-07	3,53E-07	6,24E-06	1,3