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Systematic and Phylogenetic Analysis of the Ole e 1 Pollen Protein Family Members in Plants

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1. Introduction

Pollen allergens are specific substances able to cause IgE-mediated hypersensitivity (allergy) after contact with the immune system [D'Amato et al. 1998]. To date, about 50 plant species have been registered in the official allergen list of the International Union of Immunological Societies (IUIS) Allergen Nomenclature Subcommittee <http://www.allergen.org> as capable of inducing pollen allergy in atopic individuals [Mothes et al. 2004]. These plants are usually grouped as (1) trees (members of the orders: *Fagales*, *Pinales*, *Rosales*, *Arecales*, *Scrophulariales*, *Junglandales*, *Salicales*, and *Myrtales*), (2) grasses (members of the families: *Bambusoideae*, *Arundinoideae*, *Chloridoideae*, *Panicoideae*, and *Poideae*), and (3) weeds (components of families *Asteraceae*, *Chenopodiaceae* and *Urticaceae*) [Hauser et al. 2010].

Allergens are proteins with a broad range of molecular weights (~5 to 50 kDa), which exhibit different features of solubility and stability. More than 10 groups of pollen allergens have been reported. Among all groups of pollen allergens, Pollen Ole e I (Ole) domain-containing proteins are the major allergens, included like-members of the "pollen proteins of the Ole e 1 family" (Accession number: PF01190) within the Pfam protein families database [Finn et al. 2010].

Ole e 1 was the first allergen purified from *Olea europaea* L. [Lauzurica et al. 1998] and named as such according to the IUIS nomenclature [King et al. 1994]. This protein is considered the major olive pollen allergen on the basis of its high prevalence among atopic patients and the high proportion it represents within the total pollen protein content, in comparison with other olive pollen allergens. These include at present another 10 allergens already identified and classified like Ole e 2 to Ole e 11 [Rodríguez et al. 2002, Barral et al. 2004, Salamanca et al. 2010]. Ole e 1 consists of a single polypeptide chain of 145 amino acid residues with a MW of 18–22 kDa, displaying acidic pI and different forms of N-glycosylation [Villalba et al. 1990, Batanero et al. 1994]. Heterologous proteins with a relevant homology have been described in other members of the *Oleaceae* family, such as fraxinus, lilac, jasmine and privet. The polypeptides encoded by the *LAT52* gene from tomato and the *Zmc13* gene from maize pollens also exhibit a high similarity to Ole e 1 [Twell et al. 1989, Hanson et al. 1989]. These plant pollen proteins are structurally related but their biological function is not yet known; though they have been suggested to be

involved in important events of pollen physiology, such as hydration, germination and/or pollen tube growth, and other reproductive functions [Alché et al. 1999, 2004, Tang et al. 2000, Stratford et al. 2001].

Structurally, the Ole domain contains six conserved cysteines which may be involved in disulfide bonds, since no free sulfhydryl groups have been detected in the native protein [Villalba et al. 1993]. Olive Ole e 1 exhibits a high degree of microheterogeneity, mainly concentrated in the third of the molecule closer to the N- terminus. The Ole e I (Ole) domain defining the pollen proteins Ole e I family signature or consensus pattern sequences PS00925 [Sigrist et al. 2010], is characterized by the amino acid sequence [EQT]-G-x-V-Y-C-D-[TNP]-C-R, where “x” could be any residue.

There is a high diversity of proteins sharing the Ole domain among plant species. To date, eleven Ole domain-containing genes have been isolated and characterized from olive pollens [Rodríguez et al. 2002]. Ole-containing proteins include proline-rich proteins, proteins encoding extensin-like domains, phosphoglycerate mutase, tyrosine-rich hydroxyproline-rich glycoprotein, and hydroxyproline-rich glycoprotein. These Ole-containing proteins can exhibit: (1) the pollen Ole signature exclusively, e.g. the ALL1_OLEEU P19963 protein from *Olea europaea* L., (2) both the pollen Ole signature and the replication factor A protein 3 motive pattern (PF08661), e.g. the O49527 pollen-specific protein-like from *Arabidopsis thaliana* (842 residues), (3) both the pollen Ole domain and the phosphoglycerate mutase (PGAM) motif, e.g. the Q9SGZ6 protein from *Arabidopsis thaliana*., and finally (4) both the pollen Ole signature and the reverse transcriptase 2 (RVT2) motif, e.g. the A5AJL0 protein from *Vitis vinifera*.

Several efforts have been made to develop an understandable and reliable systematic classification of the diverse and increasing number of different allergen protein structures. As mentioned above, the classification system widely established for proteins that cause IgE-mediated atopic allergies in humans (allergens) was defined by Chapman et al. (2007). This system uses the first three letters of the genus; a space; the first letter of the species name; a space and an Arabic number. Despite this classification system, protein databases are full of allergen proteins lacking this systematic and comprehensive nomenclature. In other cases, many of the proteins described here have not been described as allergens, or their naming makes no reference to the Ole e 1 family that facilitates their identification. Otherwise, naming in databases is frequently given randomly, on the basis of chromosome location, addressing structural features and functional characterizations or simply using the name of the entire family. In this study, we used a combination of functional genomics and computational biology to name and classify the entire Ole e 1 family, as well as to characterize structurally and functionally the proteins of this superfamily. Our data indicate that the Ole e 1 protein family consists of at least 109 divergent families, which will likely expand as more genomic studies are undertaken, and fully sequenced plant genomes become available.

2. Material and methods

2.1 Database search for Ole e 1 family genes

Sequences of Ole e 1 and Ole e 1-like genes were retrieved from the US National Center for Biotechnology Information (NCBI, <http://www.ncbi.nlm.nih.gov/>), the Uniprot database (<http://www.uniprot.org/>), and the non-redundant expressed sequence tag (EST)

databases using BLASTX, BLASTN and BLAST (low complexity filter, Blosum62 substitution matrix) [Altschul et al. 1997]. Searches were conducted using previously characterized *Olea europaea* L. Ole e 1 (GenBank Accession number P19963), *Solanum lycopersicum* LAT52 (GenBank Accession number P13447), *Zea mays* Zmc13 (GenBank Accession number B6T1A9), *Arabidopsis thaliana* pollen-specific protein-like (GenBank Accession number O49527), *Arabidopsis thaliana* PGAM containing domain protein (GenBank Accession number Q9SGZ6), and *Vitis vinifera* RVT2 containing domain protein (GenBank Accession number A5AJL0). Full-length amino acid sequences for Ole e 1 proteins were compiled and aligned using ClustalW [Thompson et al. 1994]. Genetic distances between pairs of amino acid sequences were calculated with Bioedit V7.0.5.3 [Hall 1999]. Consensus protein sequences were derived from these original alignment, and further analyzed for the presence of putative functional motifs using the PROSITE database [Sigrist et al. 2010], of biologically meaningful motif descriptors derived from multiple alignments and the ScanProsite program [de Castro et al. 2006], from the Expert Protein Analysis System (ExPASy) proteomics server of the Swiss Institute of Bioinformatics [Gasteiger et al. 2003]. Finally, the consensus protein sequences were submitted to BLASTP analysis to identify homologous proteins from other plant species.

2.2 Revised/unified nomenclature

In order to provide a revised and unified nomenclature for Ole e 1-like gene superfamily, we developed a sequence-based similarity approach to classify all the retrieved sequences using a previously developed gene nomenclature model [Kotchoni et al. 2010]. For this new nomenclature, Ole e 1 protein sequences that are more than 40% identical to previously identified Ole e 1 sequences compose a family, and sequences more than 60% identical within a family, compose a gene subfamily. Protein sequences that are less than 40% identical would describe a new Ole e 1 gene family. Taking olive protein Ole e 1_57A9 (previous name Ole e 1, major olive pollen allergen) as an example for the revised nomenclature (Table 1), Ole e 1 indicates the root; the digits (57) indicates a family and the first letter (A) a subfamily, while the final number (9) identifies an individual gene within a subfamily. The revised nomenclature is therefore composed of an assigned gene symbol (Ole e 1) (abbreviated gene name) for the whole gene superfamily. The gene symbol must be (i) unique and representative of the gene superfamily; (ii) contain only Latin letters and/or Arabic numerals, (iii) not contain punctuation, and (iv) without any reference to species. These newly developed criteria have been applied to database curators to generate the unified Ole e 1 gene families/classes regardless of the source of the cloned gene(s).

2.3 Sequence alignments and phylogenetic analyses

The retrieved Ole e 1 protein families were used to generate a phylogenetic tree using ClustalW [Thompson et al. 1994]. The alignment was created using the Gonnet protein weight matrix, multiple alignment gap opening/extension penalties of 10/0.5 and pairwise gap opening/extension penalties of 10/0.1. These alignments were adjusted using Bioedit V7.0.5.3 [Hall 1999]. Portions of sequences that could not be reliably aligned were eliminated. Phylogenetic tree was generated by the neighbourjoining method (NJ), and the branches were tested with 1,000 bootstrap replicates. The tree was visualized using Treedyn program [Chevenet et al. 2006].

2.4 Ole e 1 superfamily: Protein modeling and structural characterization

In order to study the structural and conformational variability between the Ole e 1 protein families, selected members of the Ole e 1 superfamily were modelled using SWISS-MODEL server, via the ExPASy web server [Gasteiger et al. 2003]. The initial modelled Ole e 1 structures were subjected to energy minimization with GROMOS96 force field energy [van Gunsteren et al. 1996] implemented in DeepView/Swiss-PDBViewer v3.7 [Guex and Peitsch 1997] to improve the van der Waals contacts and to correct the stereochemistry of the improved models. The quality of the models was assessed by checking the protein stereology with PROCHECK [Laskowski et al. 1993] and the protein energy with ANOLEA [Melo et al. 1997, 1998]. Ramachandran plot statistics for the models were calculated to show the number of protein residues in the favoured regions.

3. Results

3.1 The Ole e 1 protein families: Revised and unified nomenclature

In order to provide a revised/international consensus and unified nomenclature for the Ole e 1 gene superfamily, we first retrieved all the Ole e 1 and Ole e 1-like gene sequences using PS00925 as the major molecular consensus defining the entire superfamily of Ole e 1 proteins. We next verified all annotated plant Ole e 1 open reading frames (ORFs) using Ole e 1 sequence domains. A complementary and comparative study was developed by using Uniprot database to validate the molecular function and previous denomination of each Ole e 1 protein. Our searches resulted in the identification of 571 sequences encoding Ole e 1 and Ole e 1 like proteins from a wide variety of plant species, with the diagnostic motif PS00925 (Table 1). According to the established criteria (see Material and Methods), these sequences integrated 109 Ole e 1 gene families which have been attributed to different functional categories including extensins and extensin-like proteins, proline-rich proteins, hydroxyproline-rich glycoproteins, tyrosine-rich/hydroxyproline-rich glycoproteins, hydrolases, phosphoglycerate mutases, arabinogalactan proteins, etc. (Table 1).

Among the sequences retrieved, Ole e 1₄₈ is the most extensive family with 63 gene members encoding for different pollen-specific protein C13 homologues, followed by Ole e 1₅₇ family with 42 gene homologues encoding Ole e 1 (the olive major pollen allergen), Ole e 1₁₆ with 26 gene members encoding proline-rich proteins, and Ole e 1₅₂ with 22 members encoding LAT52 homologues (Table 1). The number of Ole e 1 genes greatly varied from one plant species to another. The genus *Oryza* included the highest number of Ole e 1 genes (143), followed by *Arabidopsis* with 95 genes (Table 1). At present, more than half of the catalogued Ole e 1 families encoded a single Ole e 1/Ole e 1-like gene, which was in most cases “uncharacterized” (Table 1).

The total number of genes in the Ole e 1 superfamily is expected to increase steadily with time, mainly due to the genomic sequencing of additional species like *Olea europaea* L. (http://www.gen-es.org/11_proyectos/PROYECTOS.CFM?pg=0106&n=1). Regardless of the plethora of Ole e 1 genes yet to be identified/characterized, their classification and relationship to the entire extended Ole e 1 gene superfamily will be easy owing to this nomenclature building block that catalogues newly identified/characterized Ole e 1 gene products only on the basis of sequence similarity to previously characterized Ole e 1 gene products.

Ole e 1 Family	Revised annotation	Previous annotation	GeneBank Accession Number	Source
1	Ole e 1_1A1	A44g17215	Q6RXZ6	ARATH
1	Ole e 1_1A2	-	Q8LRV8	ARATH
1	Ole e 1_1A3	ARALYDRAFT_493155	D7MC15	ARALY
1	Ole e 1_1A4	40.100006	Q2A9B5	BRAOL
1	Ole e 1_1A5	31.100008	Q2A9F3	BRAOL
1	Ole e 1_1B1	ARALYDRAFT_493053	D7LEF7	ARALY
1	Ole e 1_1B2	A12g40113	Q58FY6	ARATH
1	Ole e 1_1B3	-	Q1LE62	ARATH
1	Ole e 1_1B4	A15g47635	Q29PT1	ARATH
1	Ole e 1_1B5	ARALYDRAFT_330672	D7MP26	ARALY
2	Ole e 1_2A1	POPTRDRAFT_818926	B9HCD0	POPTR
2	Ole e 1_2A2	POPTRDRAFT_776772	B9IH16	POPTR
2	Ole e 1_2B1	VIT_00003138001	D7SSK6	VITVI
2	Ole e 1_2C1	-	C6T3E9	SOYBN
2	Ole e 1_2D1	RCOM_0860870	B8SA60	RICCO
3	Ole e 1_3A1	Osl_33016	B9BG44	ORYSI
3	Ole e 1_3A2	Os10g0206500	Q109X3	ORYSJ
3	Ole e 1_3B1	OSJNBa0014J14.3	Q7G7E7	ORYSJ
3	Ole e 1_3B2	OJ1004_F92.9	Q8RV11	ORYSJ
3	Ole e 1_3C1	OSJNBa014J14.28	Q8S6U0	ORYSJ
3	Ole e 1_3D1	Os10g0209600	Q109X1	ORYSJ
3	Ole e 1_3D2	Osl_33026	B9BG53	ORYSI
3	Ole e 1_3E1	SORBI DRAFT_01g013620	C5WR76	SORBI
3	Ole e 1_3F1	-	B4FE66	MAIZE
4	Ole e 1_4A1	SELMODRAFT_444621	D8SBK5	SELML
4	Ole e 1_4A2	SELMODRAFT_443315	D8S0X9	SELML
5	Ole e 1_5A1	ARALYDRAFT_401639	D7LGX1	ARALY
5	Ole e 1_5A2	A12g27385	Q6NLE8	ARATH
5	Ole e 1_5B1	-	C6SVU9	SOYBN
5	Ole e 1_5B2	-	C6T0F4	SOYBN
5	Ole e 1_5C1	-	C6SZ03	SOYBN
5	Ole e 1_5D1	POPTRDRAFT_821599	A9PI57	POPTR
5	Ole e 1_5D2	RCOM_1281170	B9SCW4	RICCO
5	Ole e 1_5D3	VITISV_031097	A5BY12	VITVI
5	Ole e 1_5E1	A15g22430	Q9FMQ8	ARATH
5	Ole e 1_5E2	-	Q8L9I4	ARATH
5	Ole e 1_5E3	ARALYDRAFT_351256	D7M0X5	ARALY
6	Ole e 1_6A1	-	B6TL01	MAIZE
6	Ole e 1_6A2	-	B4FQ86	MAIZE

Ole e 1 Family	Revised annotation	Previous annotation	GeneBank Accession Number	Source
6	Ole e 1_6B1	-	B6TXH9	MAIZE
6	Ole e 1_6C1	Sl04lg021840	C5X7Z8	SORBI
6	Ole e 1_6D1	B1136H02.23	Q6EPW8	ORYSJ
7	Ole e 1_7A1	SELMODRAFT_405039	D8QY58	SELML
7	Ole e 1_7A2	SELMODRAFT_414878	D8RTV5	SELML
8	Ole e 1_8A1	SELMODRAFT_4148129	D8T4Z3	SELML
8	Ole e 1_8B1	SELMODRAFT_408805	D8RC11	SELML
8	Ole e 1_8C1	SELMODRAFT_4148128	D8T4Z1	SELML
9	Ole e 1_9A1	A12g21140	Q8SKP9	ARATH
9	Ole e 1_9A2	Proline-rich protein 2	Q9M7P0	ARATH
9	Ole e 1_9A3	ARALYDRAFT_900523	D7LL03	ARALY
9	Ole e 1_9B1	Extensin-like protein	Q9M6T6	ARATH
9	Ole e 1_9B2	Proline-rich protein 4	Q9M7N8	ARATH
9	Ole e 1_9B3	AT4g38770/T9A14_50	Q9T0U5	ARATH
9	Ole e 1_9B4	ARALYDRAFT_490841	D7MFM2	ARALY
10	Ole e 1_10A1	Proline-rich protein	Q9M6T7	NICGL
10	Ole e 1_10B1	VIT_00024051001	D7U5A0	VITVI
10	Ole e 1_10B2	POPTRDRAFT_700888	B9HRA6	POPTR
10	Ole e 1_10C2	POPTRDRAFT_105015	B9H154	POPTR
10	Ole e 1_10D2	RCOM_0660490	B8BTC5	RICCO
11	Ole e 1_11A1	Proline-rich protein	Q82066	SOLTU
12	Ole e 1_12A1	VITISV_029041	A5BQP2	VITVI
13	Ole e 1_13A1	VITISV_029038	A5BQP1	VITVI
13	Ole e 1_13A2	VITISV_029037	A5BQP0	VITVI
13	Ole e 1_13B1	VIT_00024076001	D7U5B7	VITVI
14	Ole e 1_14A1	proline-rich protein	Q93WF4	ORYSA
14	Ole e 1_14A2	Os10g0149100	C7J7T1	ORYSJ
14	Ole e 1_14A3	proline-rich protein	Q93WL9	ORYSA
14	Ole e 1_14A4	Os10g0149009	Q7XGT3	ORYSJ
14	Ole e 1_14A5	proline-rich protein	Q94H18	ORYSA
14	Ole e 1_14A6	Os10g0149200	Q7XGT1	ORYSJ
14	Ole e 1_14A7	OsJ_30733	A3CZJ8	ORYSJ
14	Ole e 1_14A8	Osl_12924	A2XKE8	ORYSI
14	Ole e 1_14A9	Osl_12923	A2XKE7	ORYSI
14	Ole e 1_14A10	Osl_12921	B9AP23	ORYSI
14	Ole e 1_14A11	OSJNBa0031A07.6	Q84H17	ORYSA
14	Ole e 1_14A12	OsJ_30737	A3CZK3	ORYSJ
14	Ole e 1_14A13	Os10g0148400	Q7XGT0	ORYSJ
14	Ole e 1_14A14	OsJ_30734	A3CZK0	ORYSJ

Table 1. The Ole e 1 protein superfamily: new and unified nomenclature. ARATH: *Arabidopsis thaliana*; ARALY: *Arabidopsis lyrata*; BETPN: *Betula pendula*; BRAOL: *Brassica oleracea*; BRARP: *Brassica rapa*; CAPAN: *Capsicum annuum*; CARAS: *Cardaminopsis arenosa*; CHE1: *Chenopodium album*; CROSA: *Crocus sativus*; DAUCA: *Daucus carota*; EUPPU: *Euphorbia pulcherrima*; FRAEX: *Fraxinus excelsior*; GOSBA: *Gossypium barbadense*; GOSHE: *Gossypium herbaceum*; GOSHI: *Gossypium hirsutum*; GOSKI: *Gossypioides kirkii*; HYAOR: *Hyacinthus orientalis*; LigVu: *Ligustrum vulgare*; LILLO: *Lilium longiflorum*; LOLPE : *Lolium perenne*; MAIZE: *Zea mays*; MEDTR: *Medicago truncatula*; NICAL: *Nicotiana alata*; NICGL: *Nicotiana glauca*; NicLa: *Vitis pseudoreticulata*; OleEu: *Olea europaea*; ORYSI: *Oryza sativa*; PETCR: *Petroselinum crispum*; PETHY: *Petunia hybrida*; PHAVU: *Phaseolus vulgaris*; PHEPR : *Phleum pratense*; PHYPA: *Physcomitrella patens*; PICSI: *Picea sitchensis*; PLALA: *Platanus lanceolata*; POPTR: *Populus trichocarpa*; RICCO: *Ricinus communis*; SALKa: *Salsola kali*; SAMNI: *Sambucus nigra*; SELML: *Selaginella moellendorffii*; SOLLI: *Solanum lycopersicum*; SOLTU: *Solanum tuberosum*; SORBI: *Sorgum bicolor*; SOYBN: *Glycine max*; TOBAC: *Nicotiana tabacum*; TRISU: *Trifolium subterraneum*; VITVI: *Vitis vinifera*; 9ROSI: *Cleome spinosa*; (-): uncharacterized.

14	Ole e 1_14A15	OSJNBa0031A07.3	Q84H14	ORYSA	19	Ole e 1_15B2	-	B4FM91	MAIZE
14	Ole e 1_14A16	Os10g0149900	Q7XG57	ORYSJ	19	Ole e 1_19B3	Proline-rich protein	B6TZN9	MAIZE
14	Ole e 1_14A17	Osl_32754	A2Z52R	ORYSI	19	Ole e 1_19B4	Proline-rich protein	C5WP20	SORBI
14	Ole e 1_14B1	proline-rich protein	Q84H15	ORYSA	19	Ole e 1_19C1	Osl_10729	A2XE42	ORYSI
14	Ole e 1_14C1	Os10g0149800	Q7XG58	ORYSJ	19	Ole e 1_19D1	Os03g0245200	Q10P65	ORYSJ
14	Ole e 1_14D1	Osl_30735	A3C2K6	ORYSJ	19	Ole e 1_19E1	Sb01g041230	C5WQZ7	SORBI
14	Ole e 1_14E1	Osl_32753	A2Z527	ORYSI	19	Ole e 1_19E2	Proline-rich protein	B6T564	MAIZE
15	Ole e 1_15A1	Osl_30735	A3C2K1	ORYSJ	19	Ole e 1_19E3	Proline-rich protein	B4FQ36	MAIZE
16	Ole e 1_16A1	proline-rich protein	Q84H12	ORYSA	20	Ole e 1_20A1	proline-rich protein	Q94GB4	ORYSA
16	Ole e 1_16A2	proline-rich protein	A6N1C2	ORYSI	20	Ole e 1_20A2	Os10g0148700	Q7XGT6	ORYSJ
16	Ole e 1_16A3	Os10g0150400	Q7XG54	ORYSJ	20	Ole e 1_20A3	Osl_32750	B8BFR4	ORYSI
16	Ole e 1_16A4	Osl_32757	A2Z531	ORYSI	21	Ole e 1_21A1	Osl_10730	A2XE43	ORYSI
16	Ole e 1_16A5	proline-rich protein	Q84H09	ORYSA	21	Ole e 1_21A2	Os03g0245300	Q10P64	ORYSJ
16	Ole e 1_16A6	Os10g0150800	Q7XG32	ORYSJ	21	Ole e 1_21B1	Sb01g041220	C5WQZ6	SORBI
16	Ole e 1_16A7	proline-rich protein	Q8RVW6	ORYSA	21	Ole e 1_21B2	Proline-rich protein	B6TJK1	MAIZE
16	Ole e 1_16A8	proline-rich protein	Q84H10	ORYSA	22	Ole e 1_22A1	Osl_04802	A2W4Z6	ORYSI
16	Ole e 1_16A9	Os10g0150700	Q7XG53	ORYSJ	22	Ole e 1_22A2	Os01g0899700	Q5N8V8	ORYSJ
16	Ole e 1_16A10	Osl_32759	A2Z533	ORYSI	22	Ole e 1_22A3	Sb03g042800	C5XF54	SORBI
16	Ole e 1_16A11	proline-rich protein	A6M2D0	ORYSI	23	Ole e 1_23A1	SELMODRAFT_448X71	D8TAV1	SEML
16	Ole e 1_16A12	proline-rich protein	Q84H11	ORYSA	24	Ole e 1_24A1	SELMODRAFT_449Z07	D1TDP8	SEML
16	Ole e 1_16A13	Os10g0150600	Q7GBX3	ORYSJ	25	Ole e 1_25A1	OH-proline-rich glycoprotein	Q09085	PHAVU
16	Ole e 1_16A14	Proline-rich protein	A6N177	ORYSI	26	Ole e 1_26A1	Tyr-, OH-proline-rich glycoprot.	Q40793	PETCR
16	Ole e 1_16A15	Osl_32758	A2Z537	ORYSI	27	Ole e 1_27A1	SELMODRAFT_419497	D8S950	SEML
16	Ole e 1_16A16	Osl_32768	B8BFR7	ORYSI	27	Ole e 1_27A2	SELMODRAFT_427121	D8SVK5	SEML
16	Ole e 1_16A17	LOC_Os10g05990	Q33B16	ORYSJ	28	Ole e 1_28A1	SELMODRAFT_441903	D8RHM0	SEML
16	Ole e 1_16B1	Proline-rich protein	Q84H13	ORYSA	28	Ole e 1_28A2	SELMODRAFT_430905	D8T809	SEML
16	Ole e 1_16B2	Os10g0150300	Q7XG55	ORYSJ	28	Ole e 1_28B1	SELMODRAFT_432063	D8R002	SEML
16	Ole e 1_16B3	Osl_32756	A2Z530	ORYSI	28	Ole e 1_28B2	SELMODRAFT_449336	D8TF68	SEML
16	Ole e 1_16C1	-	B6SJA4	MAIZE	28	Ole e 1_29A1	SELMODRAFT_438058	D8R0D9	SEML
16	Ole e 1_16C2	-	B8TBY5	MAIZE	29	Ole e 1_29A2	SELMODRAFT_439721	D8R5C7	SEML
16	Ole e 1_16C3	Proline-rich protein	B6TL13	MAIZE	30	Ole e 1_30A1	SELMODRAFT_448085	D8T4Q2	SEML
16	Ole e 1_16C4	Sb01g026180	C5WP19	SORBI	31	Ole e 1_31A1	SELMODRAFT_413728	D8RQ13	SEML
16	Ole e 1_16D1	-	B6U9A5	MAIZE	31	Ole e 1_31A2	SELMODRAFT_416536	D8RZL3	SEML
16	Ole e 1_16E1	-	C0PAE2	MAIZE	32	Ole e 1_32A1	SELMODRAFT_418534	D8RZL1	SEML
17	Ole e 1_17A1	Sb01g025970	C3WP14	SORBI	32	Ole e 1_32A2	SELMODRAFT_413730	D8RQ15	SEML
17	Ole e 1_17A2	Proline-rich protein	Q8S8X4	MAIZE	33	Ole e 1_33A1	ARALYDRAFT_488422	D7M7G1	ARALY
18	Ole e 1_18A1	Sb01g026170	C5WP16	SORBI	33	Ole e 1_33A2	At5g15780	Q9LFU8	ARATH
19	Ole e 1_19A1	proline-rich protein	Q84GB6	ORYSA	33	Ole e 1_33B1	-	Q1KUY6	9ROSI
19	Ole e 1_19A2	Os10g0148100	Q7XGT9	ORYSJ	34	Ole e 1_34A1	Pollen Ole e 1 allergen/vegetansin	Q2H8E9	MEDTR
19	Ole e 1_19A3	Osl_30727	B8GTJ2	ORYSJ	34	Ole e 1_34B1	-	B7FKI5	MEDTR
19	Ole e 1_19A4	Osl_32749	A2Z524	ORYSI	34	Ole e 1_34C1	RCOM_0790500	B9SVV7	RICCO
19	Ole e 1_19B1	-	C4JAB8	MAIZE	34	Ole e 1_34D1	VIT_00036543001	D78MN1	VITVI

35	Ole e 1_35A1	MirDRAFT_AC172742g2v1	A2O629	MEDTR	47	Ole e 1_47A2	Os12g0472800	Q2Q852	ORYSJ
36	Ole e 1_36A1	POPTRDRAFT_584E21	B8N7M0	POPTR	47	Ole e 1_47B1	-	B4FY56	MAIZE
37	Ole e 1_37A1	Osl_33013	A2Z5T3	ORYSI	47	Ole e 1_47B2	-	B6TZW5	MAIZE
37	Ole e 1_37A2	Os10g0205700	Q0RV00	ORYSJ	47	Ole e 1_47B3	Sb0011s012840	C6JRP6	SORBI
37	Ole e 1_37A3	Osl_26257	A2YMD0	ORYSI	47	Ole e 1_47C1	-	C0PAV0	MAIZE
37	Ole e 1_37B1	Osl_31017	A3C3E5	ORYSJ	48	Ole e 1_48A1	Pollen ole e 1 allergen	D7M279	ARALY
37	Ole e 1_37C1	Sb05g003610	C5V4M4	SORBI	48	Ole e 1_48A2	At5G0130310a protein	B7U699	CARAS
37	Ole e 1_37C2	-	B4FWB4	MAIZE	48	Ole e 1_48A3	At5g10130	Q8LX15	ARATH
38	Ole e 1_38A1	-	A9NKB0	PICSI	48	Ole e 1_48A4	Putative pollen Ole e 1 allergen	C3UJ86	ARALY
38	Ole e 1_38A2	-	A9NZN8	PICSI	48	Ole e 1_48A5	89A08_10	Q4AB07	BRARP
38	Ole e 1_38A3	-	A9NYX9	PICSI	48	Ole e 1_48B1	-	B9HFN2	POPTR
39	Ole e 1_39A1	-	A9NZS6	PICSI	48	Ole e 1_48B2	-	B9H553	POPTR
39	Ole e 1_39A2	-	C0PTE0	PICSI	48	Ole e 1_48B3	Pollen-specific protein C13	B874H0	RICCO
39	Ole e 1_39A3	-	A9NTZ8	PICSI	48	Ole e 1_48C1	-	D7M8H5	ARALY
40	Ole e 1_40A1	ARALYDRAFT_664511	D7LRC1	ARALY	48	Ole e 1_48C2	Allergen-like protein BRSn20	Q9SZY5	ARATH
40	Ole e 1_40A2	At3g26960	Q8L853	ARATH	48	Ole e 1_48C3	Pollen specific protein	Q42077	ARATH
40	Ole e 1_40A3	Pollen proteins Ole e 1 family	BKSLJ6	MAIZE	48	Ole e 1_48D1	-	A9P956	POPTR
40	Ole e 1_40A4	ARALYDRAFT_355871	D7MI27	ARALY	48	Ole e 1_48D2	-	A9P960	POPTR
40	Ole e 1_40A5	At5g41050	Q8FLM4	ARATH	48	Ole e 1_48D3	-	A9PCW2	POPTR
40	Ole e 1_40B1	-	C6T792	SOYBN	48	Ole e 1_48D4	-	A9PHV1	POPTR
40	Ole e 1_40B2	-	C6S215	SOYBN	48	Ole e 1_48D5	Pollen-specific protein C13	B9RJG6	RICCO
40	Ole e 1_40B3	-	B7FIQ2	MEDTR	48	Ole e 1_48D6	Pollen-specific protein	Q21007	NICLA
40	Ole e 1_40B4	POPTRDRAFT_1069266	B9GF61	POPTR	48	Ole e 1_48D7	-	A5BPK1	VITVI
40	Ole e 1_40B5	POPTRDRAFT_174592	B9GF59	POPTR	48	Ole e 1_48D8	scaffold_357 assembly12x	D7TRB4	VITVI
40	Ole e 1_40B6	POPTRDRAFT_568673	A9PAE7	POPTR	48	Ole e 1_48D9	-	E2LMG1	CRUPE
40	Ole e 1_40B7	RCOM_1447040	B9RHJ8	RICCO	48	Ole e 1_48D10	Allergen-like protein BRSn20	Q9SE54	SAMNI
40	Ole e 1_40B8	VIT_00033047001	D7SVM0	VITVI	48	Ole e 1_48E1	Putative SAH7 protein	Q84PK7	GOSBA
41	Ole e 1_41A1	P1 clone: MOJ10	Q9LSD9	ARATH	48	Ole e 1_48E2	Putative SAH7 protein	Q84PK9	GOSHE
42	Ole e 1_42A1	At5g13140	Q9FY96	ARATH	48	Ole e 1_48E3	Putative SAH7 protein	Q84PK6	GOSBA
42	Ole e 1_42A2	-	Q8LEU2	ARATH	48	Ole e 1_48E4	Putative SAH7 protein	Q84PK8	GOSRA
42	Ole e 1_42A3	ARALYDRAFT_488130	D7M572	ARALY	48	Ole e 1_48E5	Putative SAH7 protein	Q84PK5	GOSKI
43	Ole e 1_43A1	VITISV_011139	A5AJL0	VITVI	48	Ole e 1_48F1	-	C6SVN7	SOYBN
44	Ole e 1_44A1	POPTRDRAFT_841726	B9GMF5	POPTR	48	Ole e 1_48F2	-	C6SVR9	SOYBN
44	Ole e 1_44B1	Hydrolase	B9RM98	RICCO	48	Ole e 1_48F3	-	B7FN25	MEDTR
44	Ole e 1_44C1	POPTRDRAFT_413678	B9GZC8	POPTR	48	Ole e 1_49G1	LLP-B3 protein	Q8QZ82	LILLO
45	Ole e 1_45A1	Ep60	A5Y558	EUPPU	48	Ole e 1_48H1	H0209H04_4 protein	Q0HL34	O8YBA
46	Ole e 1_46A1	Osl_31975	B8BDC0	ORYSI	48	Ole e 1_48H2	-	A2XSZ2	ORYSI
46	Ole e 1_46A2	Os09g0508200	Q0J011	ORYSJ	48	Ole e 1_48H3	Os04g0398700 protein	Q7XLS2	ORYSJ
46	Ole e 1_46A3	Osl_28955	B9G4H1	ORYSJ	48	Ole e 1_48H4	Pollen specific gene protein	Q40715	ORYSA
46	Ole e 1_46A4	Sb02g029470	C5X5H6	SORBI	48	Ole e 1_49H5	Sb06g014740	C5VF43	SORBI
46	Ole e 1_46A5	-	B4FS91	MAIZE	48	Ole e 1_48H6	Pollen-specific protein C13	P33050	MAIZE
47	Ole e 1_47A1	Osl_39287	B8BPK9	ORYSI	48	Ole e 1_48H7	Pollen-specific protein C13	B6T1A9	MAIZE

Table 1. (continued). The Ole e 1 protein superfamily: new and unified nomenclature.

48	Ole e 1_48H8	-	B4FKQ2	MAIZE	52	Ole e 1_52C1	Ole e1-like protein	O49613	BETPN
48	Ole e 1_48H8	Pollen-specific protein C13	B6T7Z0	MAIZE	52	Ole e 1_52D1	Pollen allergen Che a 1	B9S0A6	RICCO
48	Ole e 1_48I1	Putative pollen specific prot.C13	Q8RU50	ORYSJ	52	Ole e 1_52E1	PN40024	D7TJL1	VITV1
48	Ole e 1_48I2	Os10g0371000 protein	Q8Y39	ORYSJ	52	Ole e 1_52F1	-	C6TL27	SOYBN
48	Ole e 1_48I3	-	A2Z6J6	ORYSJ	52	Ole e 1_52F2	-	B7FGN2	MEDTR
48	Ole e 1_48I4	Pollen-specific protein C13	B6S340	MAIZE	52	Ole e 1_52G1	Pollen allergen Che a 1	Q8LGR0	CHE1
48	Ole e 1_48I5	Pollen-specific protein C13	B6T394	MAIZE	52	Ole e 1_52G2	Pollen allergen Cro s 1	Q29W25	CROSA
48	Ole e 1_48I6	Sb0012s014630	C6JRR2	SORBI	52	Ole e 1_52H1	Sal k 4	E2D0Z0	SALKA
48	Ole e 1_48I7	Pollen-specific protein	Q677C4	HYAOR	52	Ole e 1_52I1	-	B9N635	POPTR
48	Ole e 1_48J1	Major pollen allergen Lol p 11	Q7M1X5	LOLPR	52	Ole e 1_52I2	-	B9P9Z0	POPTR
48	Ole e 1_48J2	Pollen allergen Phi p 11	Q8H6L7	PHLPR	52	Ole e 1_52I3	-	B9I1V1	POPTR
48	Ole e 1_48J3	Sb03g001020	C5KK86	SORBI	52	Ole e 1_52J1	Anther-specific prot. LAT52	B9S8K9	RICCO
48	Ole e 1_48J4	Pollen allergen Phi p 11	B6T7Z8	MAIZE	52	Ole e 1_52K1	As1	D7R0W3	GOSHI
48	Ole e 1_48J5	-	A2YE17	ORYSJ	52	Ole e 1_52L1	Anther-specific prot. LAT52	P13447	SOILL
48	Ole e 1_48J6	Os06g0556800 protein	Q5Z7N0	ORYSJ	53	Ole e 1_53A1	-	D7KDG6	ARALY
48	Ole e 1_48K1	Sb08g007260	C5YU02	SORBI	54	Ole e 1_54A1	Pollen-specific protein - like	O49527	ARATH
48	Ole e 1_48K2	-	B4FCC1	MAIZE	55	Ole e 1_55A1	Putative Ole e 1-like protein	A3F4A6	NICLI
48	Ole e 1_48K3	Pollen allergen Phi p 11	B6TN05	MAIZE	56	Ole e 1_56A1	Major pollen allergen Pla 1	P82242	PLALA
48	Ole e 1_48L1	-	B6BEU6	ORYSJ	57	Ole e 1_57A1	Allergen Fra e 1,0101	Q7XAV4	FRAEX
48	Ole e 1_48L2	-	A3C1R9	ORYSJ	57	Ole e 1_57A2	Fra e 1,0102 major allergen	Q5EXJ6	FRAEX
48	Ole e 1_48L3	Putative Pollen specific protein C13	Q650Z4	ORYSJ	57	Ole e 1_57A3	Major pollen allergen Lig v 1	O82015	LigVu
48	Ole e 1_48L4	Os09g0572800 protein	Q0ZF0	ORYSJ	57	Ole e 1_57A4	Ole e 1 olive pollen allergen	X75387	OleEu
48	Ole e 1_48L5	Os07g0500500 protein	Q6ZLH6	ORYSJ	57	Ole e 1_57A5	Ole e 1 olive pollen allergen	AF532765	OleEu
48	Ole e 1_48L6	-	A3BLQ7	ORYSJ	57	Ole e 1_57A6	Ole e 1 olive pollen allergen	AF532766	OleEu
48	Ole e 1_48L7	-	A2YN03	ORYSJ	57	Ole e 1_57A7	Ole e 1 olive pollen allergen	AF532767	OleEu
48	Ole e 1_48L8	Sb02g042930	C5X6P8	SORBI	57	Ole e 1_57A8	Ole e 1 olive pollen allergen	X76306	OleEu
48	Ole e 1_49A1	-	C6T355	SOYBN	57	Ole e 1_57A9	Ole e 1 olive pollen allergen	P19963	OleEu
50	Ole e 1_50A1	Pollen ole e 1 allergen	D7KV62	ARALY	57	Ole e 1_57A10	Ole e 1 olive pollen allergen	Ole e 1 Edman	OleEu
50	Ole e 1_50A2	Pollen ole e 1 allergen	D7KV08	ARALY	57	Ole e 1_57A11	Ole e 1 olive pollen allergen	X76395	OleEu
50	Ole e 1_50A3	P-glycerate mutase 1 like prot.	Q8LDM5	ARATH	57	Ole e 1_57A12	Ole e 1 olive pollen allergen	Y12426	OleEu
50	Ole e 1_50A4	-	Q8M709	ARATH	57	Ole e 1_57A13	Ole e 1 olive pollen allergen	Y12477	OleEu
50	Ole e 1_50A5	Pollen specific protein	Q42043	ARATH	57	Ole e 1_57A14	Ole e 1 olive pollen allergen	AF500908	OleEu
51	Ole e 1_51A1	F25K19.26 protein	Q9SGZ6	ARATH	57	Ole e 1_57A15	Ole e 1 olive pollen allergen	AF515277	OleEu
52	Ole e 1_52A1	A1g29140	Q84WD6	ARATH	57	Ole e 1_57A16	Ole e 1 olive pollen allergen	AF515278	OleEu
52	Ole e 1_52A2	F28N24.16 protein	Q8LPM4	ARATH	57	Ole e 1_57A17	Ole e 1 olive pollen allergen	AF515280	OleEu
52	Ole e 1_52B1	A5g45080	Q680L9	ARATH	57	Ole e 1_57A18	Ole e 1 olive pollen allergen	AF515279	OleEu
52	Ole e 1_52B2	Ole e 1-like protein	Q8L9P9	ARATH	57	Ole e 1_57A19	Ole e 1 olive pollen allergen	AF515281	OleEu
52	Ole e 1_52B3	-	D7MSQ6	ARALY	57	Ole e 1_57A20	Ole e 1 olive pollen allergen	AF532755	OleEu
52	Ole e 1_52B4	A4g18596	Q8NMJ2	ARATH	57	Ole e 1_57A21	Ole e 1 olive pollen allergen	AF532756	OleEu
52	Ole e 1_52B5	Pollen ole e 1 allergen	D7MCQ3	ARALY	57	Ole e 1_57A22	Ole e 1 olive pollen allergen	AF532757	OleEu
52	Ole e 1_52B6	Ole e 1-like protein	Q9FJ48	ARATH	57	Ole e 1_57A23	Ole e 1 olive pollen allergen	AF532760	OleEu

57	Ole e 1_57A24	Ole e 1 olive pollen allergen	AF532753	OleEu	61	Ole e 1_61A2	A2g16630	Q08LF4	ARATH
57	Ole e 1_57A25	Ole e 1 olive pollen allergen	AF532754	OleEu	61	Ole e 1_61A3	-	D7L7M3	ARALY
57	Ole e 1_57A26	Ole e 1 olive pollen allergen	AY137467	OleEu	61	Ole e 1_61B1	-	B9H158	POPTR
57	Ole e 1_57A28	Ole e 1 olive pollen allergen	AY137468	OleEu	61	Ole e 1_61B2	-	A9PG40	POPTR
57	Ole e 1_57A29	Ole e 1 olive pollen allergen	AY137469	OleEu	61	Ole e 1_61B3	-	B9SQJ5	RICCO
57	Ole e 1_57A30	Ole e 1 olive pollen allergen	B75766	OleEu	61	Ole e 1_61B4	-	D7U593	VITV1
57	Ole e 1_57A31	Ole e 1 olive pollen allergen	Y12426	OleEu	62	Ole e 1_62A1	PN40024	A2WZ69	ORYSJ
57	Ole e 1_57A32	Ole e 1 olive pollen allergen	AF532758	OleEu	62	Ole e 1_62A2	-	A3A255	ORYSJ
57	Ole e 1_57A33	Ole e 1 olive pollen allergen	AF532761	OleEu	62	Ole e 1_62B1	-	B6TF27	MAIZE
57	Ole e 1_57A34	Ole e 1 olive pollen allergen	AF532762	OleEu	62	Ole e 1_62B2	-	B4FZU6	MAIZE
57	Ole e 1_57A35	Ole e 1 olive pollen allergen	AF532759	OleEu	62	Ole e 1_62B3	-	B6TR02	MAIZE
57	Ole e 1_57A36	Ole e 1 olive pollen allergen	AF532764	OleEu	63	Ole e 1_63A1	-	B6UF60	MAIZE
57	Ole e 1_57A37	Ole e 1 olive pollen allergen	AF532763	OleEu	64	Ole e 1_64A1	-	ASRQ15	PHYPA
57	Ole e 1_57A38	Ole e 1 olive pollen allergen	AY159880	OleEu	64	Ole e 1_64B1	-	ASSH00	PHYPA
57	Ole e 1_57A39	Ole e 1 olive pollen allergen	AY159881	OleEu	65	Ole e 1_65A1	-	D8TAV2	SEML
57	Ole e 1_57A40	Allergen Fra e 1	Q6U740	FraEx	65	Ole e 1_65A2	-	D8TDP3	SEML
57	Ole e 1_57A41	Ole e 1 olive pollen allergen	X76541	OleEu	66	Ole e 1_66A1	-	D7MY20	ARALY
57	Ole e 1_57A42	Ole e 1 olive pollen allergen	X76540	OleEu	66	Ole e 1_66A2	proline-rich glycoprotein.	O64586	ARATH
57	Ole e 1_57A43	Ole e 1 olive pollen allergen	X76539	OleEu	66	Ole e 1_66A3	-	D7LH37	ARALY
58	Ole e 1_58A1	-	B7FNF5	MEDTR	67	Ole e 1_67A1	-	D7LGE2	ARALY
58	Ole e 1_58A2	-	B7FNF3	MEDTR	67	Ole e 1_67A2	A2g33790	P93013	ARATH
58	Ole e 1_58B1	-	C6SYE3	SOYBN	67	Ole e 1_67B1	A1g28290	Q9FZA2	ARATH
58	Ole e 1_59A1	Extensin-like protein	A9NMR0	PICSI	67	Ole e 1_67B2	proline-rich protein	Q0WPA7	ARATH
58	Ole e 1_59A2	-	A9NPL2	PICSI	67	Ole e 1_67B3	-	D7KCU8	ARALY
58	Ole e 1_59A3	Extensin-like protein	E0ZE62	PICSI	67	Ole e 1_67C1	HyPRP1	Q0PIW3	GOSHI
58	Ole e 1_59A4	Extensin-like protein	E0ZE90	PICSI	67	Ole e 1_67D1	Arabinogalactan protein	C6YQU7	GOSHI
58	Ole e 1_59A5	Extensin-like protein	E0ZE78	PICSI	68	Ole e 1_68A1	-	C6TL02	SOYBN
60	Ole e 1_60A1	AT1g27100/T7N9_16	Q94EJ3	ARATH	68	Ole e 1_68A2	proline-rich protein	Q41122	PHAVU
60	Ole e 1_60A2	-	Q8L322	ARATH	68	Ole e 1_68B1	-	B7F559	MEDTR
60	Ole e 1_60A3	Pollen ole e 1 allergen	D7MUX1	ARALY	68	Ole e 1_68C1	-	A9PAW5	POPTR
60	Ole e 1_60A4	-	C6SVQ8	SOYBN	68	Ole e 1_68C2	-	A9PA42	POPTR
60	Ole e 1_60A5	-	C6TA74	SOYBN	68	Ole e 1_68D1	-	B9NQ07	POPTR
60	Ole e 1_60A6	-	A9PBA0	POPTR	68	Ole e 1_68D2	-	B9H2T3	POPTR
60	Ole e 1_60A7	-	A9PFL1	POPTR	68	Ole e 1_68D3	-	A9P945	POPTR
60	Ole e 1_60A8	-	B9SAF8	RICCO	68	Ole e 1_68E1	Structural constituent of cell wall	B9RBC9	RICCO
60	Ole e 1_60A9	PN40024	D7T895	VITV1	68	Ole e 1_68F1	PN40024	D7TGB4	VITV1
60	Ole e 1_60A10	-	A2X417	ORYSJ	68	Ole e 1_69G1	Arabinogalactan protein	Q9FSW5	DAUCA
60	Ole e 1_60A11	Os02g0317800 protein	Q6Z441	ORYSJ	69	Ole e 1_69A1	hybrid proline-rich protein PRP1	Q87884	TRISU
60	Ole e 1_60A12	Sb07g009530	C5YJW7	SORBI	70	Ole e 1_70A1	Proline-rich protein	Q87084	NICAL
60	Ole e 1_60A13	-	B6T3A4	MAIZE	70	Ole e 1_70A2	-	C0LLS3	PETHY
60	Ole e 1_60B1	-	B6LRF7	PICSI	70	Ole e 1_70A3	Proline-rich protein 1	Q6QNA3	CAPAN
61	Ole e 1_61A1	-	Q8RWG5	ARATH					

Table 1. (continued). The Ole e 1 protein superfamily: new and unified nomenclature.

71	Ole e 1_71A1	Pistil extensin-like protein	Q40385	NICAL	80	Ole e 1_80A2	-	Q22258	ARATH
71	Ole e 1_71A2	Pistil-specific extensin-like prot.	Q03211	PELFP	81	Ole e 1_81A1	-	D8TCE6	SEML
71	Ole e 1_71B1	Pistil extensin like protein	Q40549	TOBAC	91	Ole e 1_81A2	-	D8TF48	SEML
71	Ole e 1_71B1	Pistil extensin like protein	Q40552	TOBAC	91	Ole e 1_81B1	-	D8TCE7	SEML
72	Ole e 1_72A1	120 kDa style glycoprotein	Q49988	NICAL	92	Ole e 1_82A1	-	D8TCF0	SEML
72	Ole e 1_72A2	120 kDa pistil extensin-like prot.	Q49728	NiLa	93	Ole e 1_83A1	Pollen ole e 1 allergen	D7LYX8	ARALY
72	Ole e 1_72A3	120 kDa pistil extensin-like prot.	Q49829	NiLa	93	Ole e 1_83A2	At3g05500	Q5FFG5	ARATH
72	Ole e 1_72A4	120 kDa pistil extensin-like prot.	Q49877	NiLa	93	Ole e 1_83B1	-	B9HHU1	POPTR
72	Ole e 1_72A5	120 kDa pistil extensin-like prot.	Q49832	NiLa	93	Ole e 1_83B2	-	B9HSK7	POPTR
72	Ole e 1_72A6	120 kDa pistil extensin-like prot.	Q49833	NICPL	93	Ole e 1_83B3	-	B9SQR0	RICCO
72	Ole e 1_72A7	120 kDa pistil extensin-like prot.	Q49834	TOBAC	93	Ole e 1_83B4	PN40024	D7T4L1	VITVI
73	Ole e 1_73A1	120 kDa pistil extensin-like prot.	Q49830	NiLa	93	Ole e 1_83B5	-	A5C9V2	VITVI
74	Ole e 1_74A1	Pollen ole e 1 allergen	D7MA28	ARALY	94	Ole e 1_84A1	-	A2WL03	ORYSJ
74	Ole e 1_74A2	At4g02270	Q81417	ARATH	94	Ole e 1_84A2	-	Q8LJN2	ORYSJ
75	Ole e 1_75A1	-	C5T5T7	SOYBN	94	Ole e 1_84A3	-	A2WL01	ORYSJ
75	Ole e 1_75A2	Drought resistance protein	E0A235	SOYBN	94	Ole e 1_84A4	-	B9ETU7	ORYSJ
75	Ole e 1_75A3	-	C6T425	SOYBN	94	Ole e 1_84A5	B1189A09.32	Q5VVR2	ORYSJ
75	Ole e 1_75B1	-	B9B9P3	POPTR	94	Ole e 1_84A6	-	A2WL00	ORYSJ
75	Ole e 1_75B2	-	B9B9P2	POPTR	94	Ole e 1_84A7	-	A2WL05	ORYSJ
75	Ole e 1_75C1	-	B9MX40	POPTR	94	Ole e 1_84A8	-	A2WL08	ORYSJ
75	Ole e 1_75C2	-	B9P957	POPTR	94	Ole e 1_84A9	-	Q8LJM3	ORYSJ
75	Ole e 1_75D1	-	B9G5D2	POPTR	94	Ole e 1_84A10	-	A2WL07	ORYSJ
76	Ole e 1_76A1	-	B9SAV5	RICCO	94	Ole e 1_84A11	-	Q8LJM3	ORYSJ
76	Ole e 1_76B1	Structural constituent cell wall	B9SAV4	RICCO	94	Ole e 1_84A12	-	A2WL04	ORYSJ
77	Ole e 1_77A1	-	B9QSD1	POPTR	94	Ole e 1_84A13	-	Q8LJN3	ORYSJ
77	Ole e 1_77A2	Structural constituent cell wall	B9SAV3	RICCO	94	Ole e 1_84A14	-	A2ZPK9	ORYSJ
77	Ole e 1_77B1	PN40024	D7U2C5	VITVI	94	Ole e 1_84A15	B1189A09.34	Q5VVR3	ORYSJ
77	Ole e 1_77B2	-	A5B1Z7	VITVI	94	Ole e 1_84B1	-	A2WL02	ORYSJ
77	Ole e 1_77C1	PN40024	D7U2C3	VITVI	94	Ole e 1_84C1	-	A2WL12	ORYSJ
77	Ole e 1_77C2	-	A5B1Z5	VITVI	94	Ole e 1_84C2	-	Q8LJM5	ORYSJ
77	Ole e 1_77D1	Pollen ole e 1 allergen	D7LQP2	ARALY	94	Ole e 1_84C3	-	B9ADE9	ORYSJ
77	Ole e 1_77D2	At2g47540	Q22257	ARATH	94	Ole e 1_84C4	-	A2ZPL3	ORYSJ
78	Ole e 1_78A1	-	A5B1Z6	VITVI	94	Ole e 1_84C5	B1189A09.42	Q5VVR2	ORYSJ
78	Ole e 1_78A2	PN40024	D7U2C4	VITVI	94	Ole e 1_84C6	-	A2WL11	ORYSJ
79	Ole e 1_79A1	-	D7KQ21	ARALY	94	Ole e 1_84C7	-	Q8LJM6	ORYSJ
79	Ole e 1_79A2	-	D7KQ24	ARALY	94	Ole e 1_84D1	B1189A09.38	Q5VVR3	ORYSJ
79	Ole e 1_79A3	Proline-rich protein 1	Q9FZ35	ARATH	94	Ole e 1_84E1	-	B9ETU8	ORYSJ
79	Ole e 1_79A4	Proline-rich protein 1	Q9M7P1	ARATH	94	Ole e 1_84F1	-	A2ZPL6	ORYSJ
79	Ole e 1_79A5	Proline-rich protein	Q9LZJ7	ARATH	94	Ole e 1_84F2	B1189A09.45	Q5VVR2	ORYSJ
79	Ole e 1_79A6	Proline-rich protein 3	Q9M7N9	ARATH	94	Ole e 1_84G1	-	A2WL13	ORYSJ
79	Ole e 1_79A7	-	D7LT86	ARALY	94	Ole e 1_84G2	Sb03g005060	C5XPF8	SORBI
80	Ole e 1_80A1	-	D7LGP0	ARALY	95	Ole e 1_85A1	-	D8SHH8	SEML

85	Ole e 1_85B1	-	D8T5S3	SEML	97	Ole e 1_97A3	Sb02g042740	C5XJ00	SORBI
86	Ole e 1_86A1	-	D8SHH9	SEML	98	Ole e 1_98A1	-	A2XGJ7	ORYSJ
87	Ole e 1_87A1	-	D8T5S4	SEML	98	Ole e 1_98A2	-	Q10LN4	ORYSJ
88	Ole e 1_88A1	-	D8R4E3	SEML	98	Ole e 1_98B1	-	A2XGJ8	ORYSJ
88	Ole e 1_88A2	-	D8RK67	SEML	98	Ole e 1_98B2	Os03g0342100	Q10LN2	ORYSJ
89	Ole e 1_89A1	Pollen ole e 1 allergen	D7LW64	ARALY	98	Ole e 1_98C1	Sb01g035830	C5XJ02	SORBI
89	Ole e 1_89A2	-	Q3EBA2	ARATH	99	Ole e 1_99A1	-	B6UHT3	MAIZE
89	Ole e 1_89B1	-	B9MTK3	POPTR	100	Ole e 1_100A1	-	A2WUN2	ORYSJ
89	Ole e 1_89B2	-	B9S0B7	RICCO	100	Ole e 1_100A2	Os01g0725900	Q8S1S8	ORYSJ
89	Ole e 1_89C1	-	C6T3U0	SOYBN	100	Ole e 1_100A3	-	A2ZXF1	ORYSJ
90	Ole e 1_90A1	PN40024	D7TUV6	VITVI	100	Ole e 1_100A4	Sb03g033350	C5XIF5	SORBI
90	Ole e 1_90A2	PN40024	D7TUX1	VITVI	100	Ole e 1_100B1	Sb03g033360	C5XIFE	SORBI
91	Ole e 1_91A1	-	A2Z9X7	ORYSJ	100	Ole e 1_100C1	QJ1131_E09.17	Q75K53	ORYSJ
91	Ole e 1_91A2	Os10g0546100	Q9AV31	ORYSJ	100	Ole e 1_100C2	-	B9FH39	ORYSJ
91	Ole e 1_91B1	Sb01g030090	C5WTH1	SORBI	100	Ole e 1_100C3	-	A2Y6T6	ORYSJ
92	Ole e 1_92A1	-	D7LH66	ARALY	100	Ole e 1_100C4	Os05g0531400 protein	Q0DGH6	ORYSJ
92	Ole e 1_92A2	At2g41400	Q6DBF8	ARATH	100	Ole e 1_100D1	Sb03g026510	C5YUF6	SORBI
92	Ole e 1_92A3	RAFL22-93-A12	Q67ZJ1	ARATH	100	Ole e 1_100D2	Arabinogalactan protein	B6SLV3	MAIZE
92	Ole e 1_92B1	At2g41400	Q9ZVC0	ARATH	101	Ole e 1_101A1	-	A2Y6T4	ORYSJ
92	Ole e 1_92B1	At2g41390	Q9ZVC4	ARATH	101	Ole e 1_101A2	Os05g0531200 protein	Q75K55	ORYSJ
93	Ole e 1_93A1	At5g05070	Q9FF72	ARATH	101	Ole e 1_101B1	Pistil-specific extensin-like protein	B6UHM8	MAIZE
94	Ole e 1_94A1	-	D7KW90	ARALY	101	Ole e 1_101B2	-	B4FGH8	MAIZE
95	Ole e 1_95A1	At3g16660	Q8GYB6	ARATH	101	Ole e 1_101B3	Sb08g026500	C5Z1H9	SORBI
95	Ole e 1_95A2	MGL6	Q9LUR8	ARATH	102	Ole e 1_102A1	-	A2WUN3	ORYSJ
95	Ole e 1_95A3	-	D7L657	ARALY	102	Ole e 1_102A2	Os01g0726100 protein	Q8S1S4	ORYSJ
95	Ole e 1_95B1	-	D7L658	ARALY	102	Ole e 1_102B1	Sb03g033370	C5XIF7	SORBI
95	Ole e 1_95B2	AT3g16670/MGL6_12	Q9LUR5	ARATH	102	Ole e 1_102B2	Pistil-specific extensin-like prot.	B6UHE3	MAIZE
95	Ole e 1_95C1	-	B9HXT5	POPTR	103	Ole e 1_103A1	-	D8RZL9	SEML
95	Ole e 1_95C2	PN40024	D7SYD8	VITVI	104	Ole e 1_104A1	-	B4FMQ8	MAIZE
95	Ole e 1_95C3	Phyllolipin	B9RT72	RICCO	105	Ole e 1_105A1	-	D8RCI2	SEML
95	Ole e 1_95D1	-	C6TK85	SOYBN	106	Ole e 1_106A1	-	D8T995	SEML
95	Ole e 1_95E1	Phyllolipin	Q56S59	PHYLL	107	Ole e 1_107A1	-	A9SC13	PHYPA
95	Ole e 1_95F1	Phyllolipin	Q1PCF2	TOBAC	108	Ole e 1_108A1	-	D8QY67	SEML
96	Ole e 1_96A1	-	B9APE1	ORYSJ	109	Ole e 1_109A1	-	D8S5V6	SEML
96	Ole e 1_96A2	-	B9F8E1	ORYSJ					
96	Ole e 1_96B1	-	A2YPV4	ORYSJ					
96	Ole e 1_96B2	Os07g0674400 protein	Q6ZDW8	ORYSJ					
96	Ole e 1_96B3	Sb02g042730	C5XJ09	SORBI					
96	Ole e 1_96B4	-	B4FF59	MAIZE					
96	Ole e 1_96B5	Sb01g035810	C5XJ00	SORBI					
97	Ole e 1_97A1	-	A2YPV5	ORYSJ					
97	Ole e 1_97A2	Os07g0674500	Q6ZDW7	ORYSJ					

Table 1. (continued). The Ole e 1 protein superfamily: new and unified nomenclature.

3.2 Phylogenetic analysis of the extended Ole e 1 protein families

A member of each retrieved full-length Ole e 1 sequences family was aligned to determine phylogenetic relationships within the Ole e 1 extended family. A phylogenetic tree of the Ole e 1 extended sequences is depicted in Figure 1.

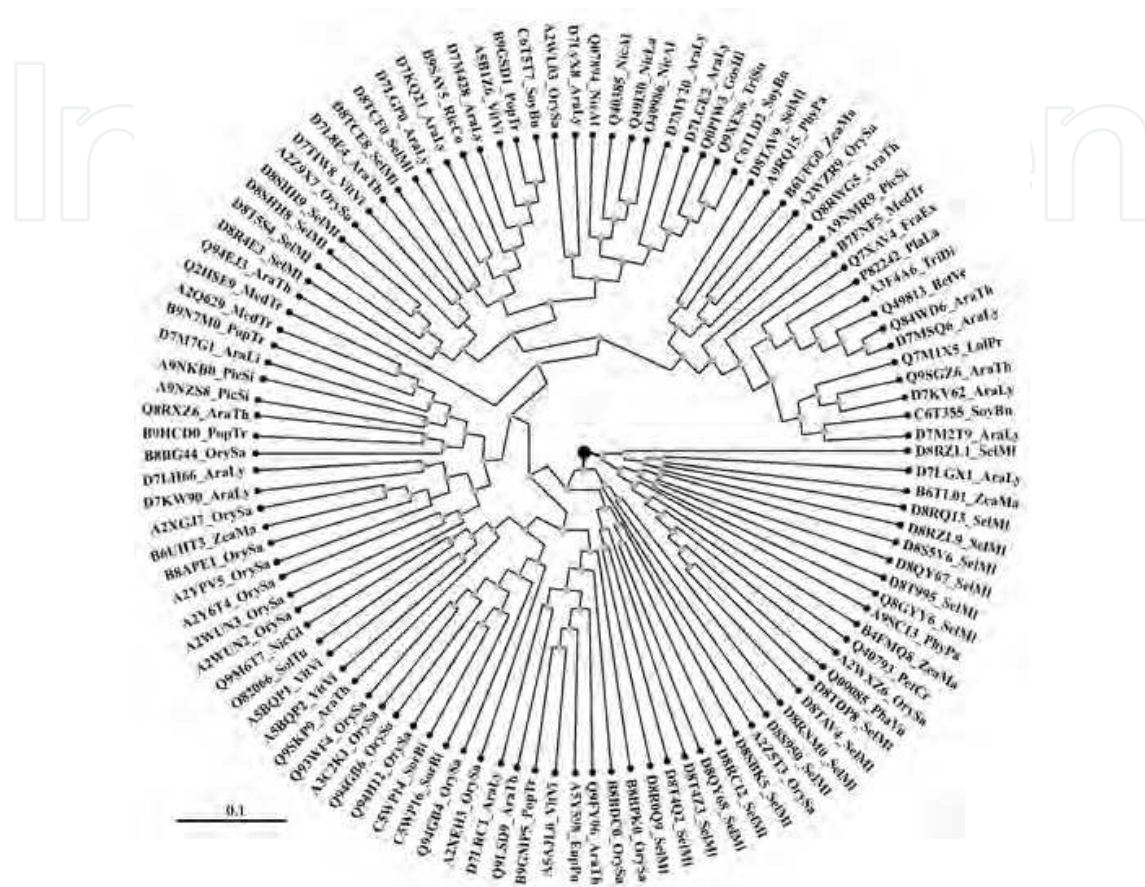


Fig. 1. Phylogenetic analysis of plant Ole e 1 proteins. Neighbour-Joining (NJ) method was used to perform a phylogenetic analysis of Ole e 1 proteins from 109 families. One representative sequence of each family was used, based in its higher consensus ability. Plant species analyzed included *Arabidopsis*, poplar, rice, spikemoss, tobacco, maize, potato, grape, *Sorghum*, kidney bean, barrel medic, *Pinus*, poinsettia, perennial ryegrass, soybean, white birch, ash, *Platanus*, *Physcomitrella*, cotton, subterranean clover, Persian tobacco and castor bean.

The phylogenetic tree shows that the 109 Ole e 1 extended families, although highly divergent, are split into two clades. The smaller clade was integrated by a few species like *Selaginella moellendorffii*, *Arabidopsis* and maize among others. The second clade included the majority of the Ole e 1 family proteins, clustering together almost all the biological functions (Figure 1). Numerous branches aroused from this clade.

3.3 Ole e 1 protein superfamilies: Structural and conformational variability

The crystallographic structural coordinates of relatively few proteins of the Ole e 1 family have been deposited in the Protein Database (PDB) up to date. To our knowledge, detailed comparative studies of the structural and conformational features of members of the Ole e 1

extended protein families have not been performed in higher plants. Using computational modelling analysis, we have determined and modelled the molecular-structural features of selected members of the Ole e 1 extended families. A first overview of the generated models (Figure 2) indicated a relatively high level of similitude.

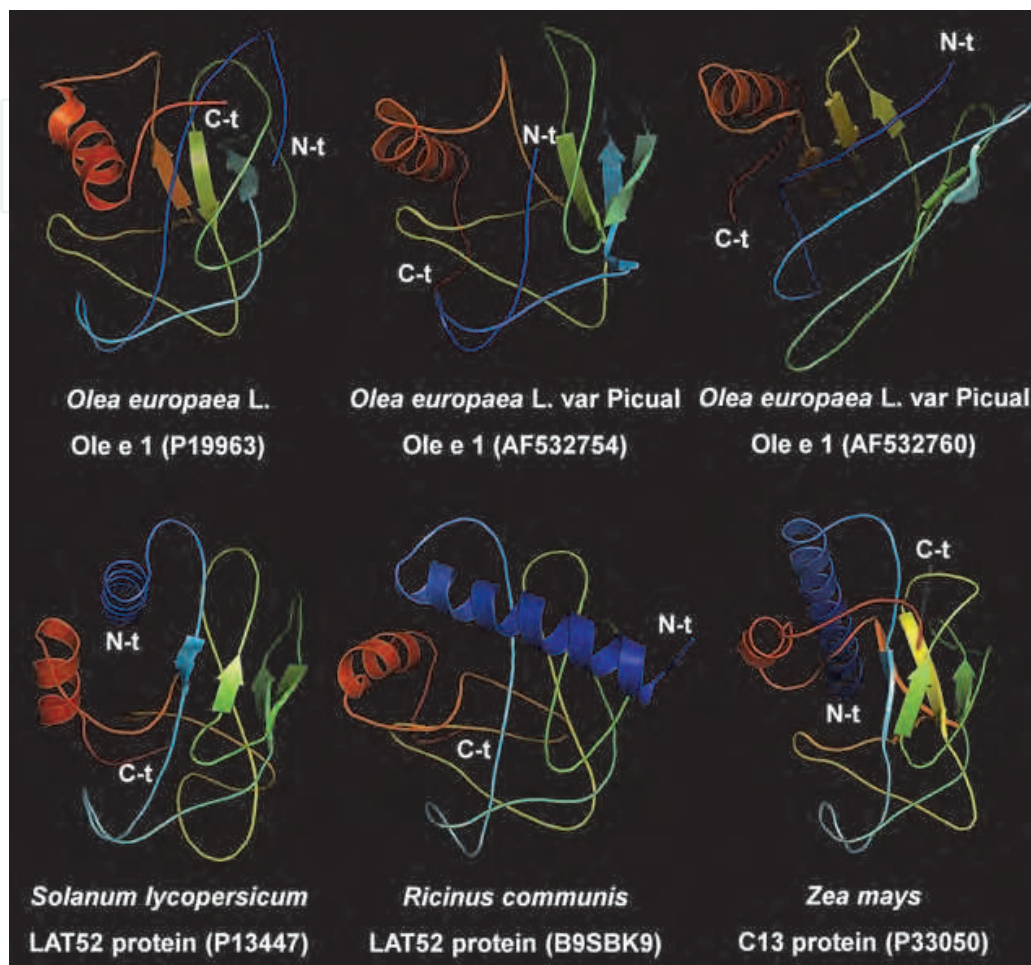


Fig. 2. Three-dimensional structure analysis of selected members of Ole e 1 family proteins. The model proteins are depicted as cartoon diagrams. The secondary elements of the crystallographic structures are rainbow coloured, with N-terminus in blue, and C-terminus in red.

However, a more detailed analysis allowed identifying certain differences in the generated models, particularly consisting in 2D structural features. These differences can be distinguished even between very close proteins like P19963, AF532754 and AF532760 (Ole e 1_{57A9}, Ole e 1_{57A25} and Ole e 1_{57A23} with the new nomenclature), corresponding to the olive pollen major allergen cloned from different varietal sources or even to different clones of the same cultivar (Figure 2). The differences become higher when models of the same protein obtained from different plant species are compared. This is the case of P13447 and B9SBK9 (Ole e 1_{52L1} and Ole e 1_{52J1}), which correspond to the LAT52 gene product in tomato and *Ricinus*, respectively (Figure 2). Divergences are even more obvious between the models indicated above and that of a P33050 (Ole e 1_{48H6}), a different member of the Ole e 1 superfamily corresponding to a pollen protein from maize (C13 protein) (Figure 2).

4. Discussion

Research as regard to the proteins of the Ole e 1 family has been carried out steadily since its definition. At present, many genes from the allergen Ole e 1 family of proteins have been characterized, and data are available concerning the sequence, structure, expression and biological function (e.g. extensin-like proteins constituting part of the cell wall). However, and as depicted in this chapter, the precise identification of more than half members of this family remains uncompleted. Up to now, Ole e 1 and Ole e 1-like genes are deposited into the databases, many of them with repetitive or arbitrary naming system by authors. This nomenclature includes a variety of generic names, such as Ole e 1 major olive pollen allergen, putative Ole e 1-like protein, anther-specific Ole e 1-like protein, and others depending of the protein location in the chromosome, e.g. At3g26960, Os09g0508200, or simply giving a random name e.g. P1 clone: MOJ10. For those members of the Ole e 1 family which have been recognized like allergens, a more sustainable and precise nomenclature has been built, by following the recommendations of the International Union of Immunological Societies (IUIS) (<http://www.allergen.org/>). However, these allergenic proteins only represent a part of the members of the Ole e 1 family, and this nomenclature still does not display the relationships among these proteins. In several cases, it is still common for researchers to use different names for the same allergen. Allergen biochemistry is now entering a new time of structural biology and proteomics that will require sophisticated tools for data processing and bioinformatics, and might require further definition of the nomenclature. Increasingly, the wealth of structural information is enabling the biologic function of allergens to be established and the assignment of allergen function to diverse protein families. Therefore, the arbitrary nomenclature currently in use is not sustainable for adequate comparative mega-functional genomics studies, especially as the number of Ole e 1 genes has increased steadily and will continue with this upward trend with the completion of the sequencing projects corresponding to more plant genomes.

The implementation of modifications in the nomenclature as proposed here may assist further developments of allergy understanding and new clinical approaches. As an example, nomenclature and structural biology have been proposed to play a crucial role in defining allergens for research studies and for the development of new clinical products [Chapman et al. 2007]. Sequence comparisons and assignments to protein families provide a molecular basis for clinical cross-reactions between food, pollen, and latex allergens that give rise to oral allergy syndromes [Wagner et al. 2002, Scheiner et al. 2004, van Ree 2004]. For food and pollen allergens, intrinsic protein structure probably plays an important role in determining allergenicity by conferring, for example, heat stability or resistance to digestion in the digestive tract, e.g. storage proteins from seed/nuts or legumes [Orruño and Morgan 2011]. Interestingly, analysis of databases, e.g. pFAM shows that there are currently more than 120 molecular architectures that are responsible for eliciting IgE responses. It will be important to link nomenclature with classification of allergens into protein families and subfamilies to provide complete definition of allergens and their structure-functional relationships as part of a comprehensive bioinformatics database. The practical consequences of this approach are seen most clearly with genetically modified foods, in which sequence comparisons can be used for safety assessment of genetically modified organisms [Goodman and Tetteh 2011].

The success of our new and unified nomenclature lies in its simplicity, with genetic basis and structural-functional characterizations of the proteins, regardless of the species origin,

with the possibility to further nomenclature expansion, to include as-yet-unidentified protein allergens from different sources or species: mites, insects, pollens, molds and foods. It might be also possible to include in the system engineered protein molecules, such as hypoallergens, or others being described as non-protein allergens. Allergens entered into the nomenclature could be used to develop allergen-specific diagnostics and to formulate recombinant allergen vaccines that will benefit patients [Chapman et al. 2000, Ferreira et al. 2004, Jutel et al. 2005, Sastre 2010].

The proposed system may also assist to clarify the importance of allergen polymorphism. Allergens often display numerous variants. These are proteins with typically greater than 90% sequence identity, but with enough differences in their amino acid sequences to make worth individual structural and or functional characterization and identification. This polymorphism has been deeply analyzed in mites, as their allergens present an extensive number of isoforms: 23 for Der p 1 and 13 for Der p 2 [Smith et al. 2001, Smith et al. 2001]. Furthermore, these polymorphisms might affect T-cell responses or alter antibody-binding sites. These differences can be structurally characterized to distinguish isoforms in a well-defined nomenclature system, by mean of structural-functional differentiation, helping to design allergen formulations for immunotherapy [Jutel et al. 2005, Piboonpocanun et al. 2006]. In the case of pollen allergens, Ole e 1 from olive pollen is a clear example of extreme polymorphism, both in its peptide and in its carbohydrate moieties, as demonstrated by peptide mapping and N-glycopeptide analysis [Castro et al. 2010]. Olive cultivar origin is a major cause of polymorphism for Ole e 1 pollen allergen [Hamman-Khalifa et al. 2008, Castro et al. 2010]. The olive tree has an extremely wide germplasm, with over 1200 varieties cultivated over the world [Bartolini et al. 1994]. Therefore, the number of Ole e 1 isoforms yet to be characterized in olive pollen is expected to be enormous. A similar situation is also likely to occur in many other plant species.

Overall, our developed unified nomenclature system is helpful in a quick functional prediction of any newly cloned Ole e 1 gene(s), because from the nomenclature point of view, the newly sequenced gene(s) will always be characterized/named with sequence similarity with previously characterized Ole e 1 genes/proteins, as well as a protein structure-functional characterization and comparison. The changes that have been introduced reflect into which extended family or subfamily a certain Ole e 1 protein belongs. Accordingly, the new nomenclature will have no significant impact on already published data with old/arbitrary naming system. However, we urge scientists working on Ole e 1's to adopt this new and easy nomenclature system. In this regard, we have made an effort to preserve the user friendly linkage between the old and the new designations, which we hope will help researchers to adapt the new names. As the revised nomenclature should facilitate communication and understanding within the community interested in Ole e 1 allergen proteins, we advocate that this new naming system be used in all future studies.

The classification model used here has been developed under the basis of a previously designed gene nomenclature model for male fertility restorer (RF) proteins in higher plants [Kotchoni et al. 2010]. The increasing numbers of RF genes described in the literature represented an ongoing challenge in their clear identification and logical classification which was solved using the proposed nomenclature. Undoubtedly, similar approaches could be applied to numerous protein families involving relevant levels of nomenclature heterogeneity, many of them registered in specialized databases like pFam. In the case of allergens, other numerous protein families like profilins (Ole e 2 in the case of olive pollen)

prolamins, cupins, Bet v 1-related proteins etc., which are currently included in the AllFam database [Radauer et al. 2008] (<http://www.meduniwien.ac.at/allergens/allfam/>) could benefit of the use of similar approaches.

5. Conclusion

We propose for first time a unified naming system for Ole e 1-like genes and pseudogenes across all plant species, which accommodates the numerous sequences already deposited in several databases, offering the needed flexibility to incorporate additional Ole e 1-like proteins as they become available. Additionally, we provide an analysis of the phylogenetic relationships displayed by the members of the Ole e 1-like family and use computational protein modelling to determine structural features of selected members of this family. These data are of particular relevance for the understanding of their biological activity and allergenic cross-reactivity.

6. Acknowledgment

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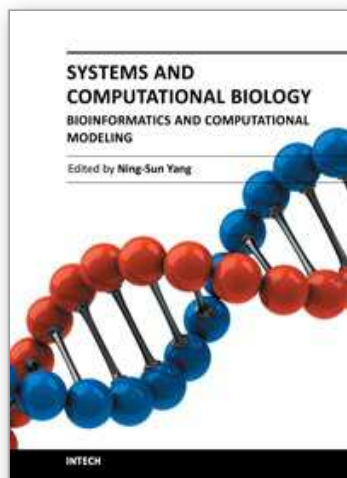
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