Genome-scale bioinformatic analysis of MOB-like proteins in tomato[1]

ABSTRACT

Aims: The MOB protein family is an evolutionarily highly conserved protein family that participates in the regulation of cell volume and proliferation. However, its function in tomato growth and development remains unclear. Clarifying the properties, structure and protein interaction network of SlMOB proteins is of great significance for exploring the regulatory mechanism of tomato growth and development.

Study Design: To explore the characteristics and potential functions of the tomato SlMOB protein family, we conducted systematic bioinformatics analyses to predict and characterize the SlMOB proteins in *Solanum lycopersicum*. The results of this study laid a solid foundation for further in-depth exploration of the regulatory role of SlMOB proteins in tomato fruit development and the breeding of high-yield tomato varieties.

Methodology: In this study, bioinformatics methods were used to comprehensively analyze the physicochemical properties, transmembrane structure, subcellular localization, signal peptide, secondary structure, conserved domain, open reading frame, 3D structure, protein interaction relationship and phylogenetic evolution of tomato SlMOB proteins.

Results: The results showed that there were three members of the tomato SlMOB protein family, and all contained 215 amino acids, with no transmembrane regions or signal peptides, and were localized in the cytoplasm and nucleus. The secondary structure was mainly composed of α-helix, and all members contained the conserved Mob1_phocein domain. The 3D models of all SlMOB proteins were constructed with 5twg.1.A as the template, showing high evolutionary conservation. The proteins interacting with SlMOB family members mainly included serine/threonine protein kinase 38-like, serine/threonine protein kinase 39-like and other kinases involved in signal

transduction and cell cycle regulation. Phylogenetic tree analysis revealed that tomato SlMOB proteins had a close evolutionary relationship with Camellia sinensis MOB proteins.

Conclusions: The results of this study clarified the basic characteristics and evolutionary relationships of the tomato SlMOB protein family, enriched the information of the MOB protein family in plants, and provided a theoretical basis for further experimental verification of the function of SlMOB proteins and the molecular breeding of high-yield and high-quality tomatoes.

Keywords：Tomato; MOB protein; Bioinformatics; Hippo signal pathway

1. INTRODUCTION

Tomato (*Solanum lycopersicum*), an annual or perennial herbaceous plant belonging to the genus *Solanum* in the family Solanaceae, is native to Central and South America and widely cultivated as an economic crop worldwide (Biondi et al., 2018). It is not only rich in nutrients but also functionally beneficial for health (Zhang et al., 2023; Collins et al., 2022). China is the world's largest tomato producer, yet there remains a gap in tomato yield per unit compared with the Netherlands (Quinet et al., 2019). The change in fruit size during various stages of tomato fruit development has long attracted human interest, and increasing tomato yield by enlarging fruit size is of great significance in tomato production (Zhang et al., 2019; Bozhinov et al., 2016). Therefore, it is crucial for in-depth exploration of the regulatory factors affecting tomato yield per unit and breeding high-yield and high-quality tomato varieties.

Tomato yield is influenced by fruit size (Thulasiram et al., 2015). The Hippo signaling pathway is a central growth control mechanism in multicellular organisms (Zhong et al., 2024) and a key mediator of organ size regulation (Pan et al., 2022), which can modulate organ size and tissue regeneration through cell proliferation, differentiation and apoptosis (Han et al., 2024; Mei et al., 2022). MOB proteins are core components of the Hippo pathway (Couzens et al., 2017) and regulate organ size by controlling cell proliferation and apoptosis (Lai et al., 2005; Hergovich et al., 2005; Citterio et al., 2005). Studies have shown that the homolog of mammalian Hippo protein in plants is SIK1, which binds to plant MOB1A/B in a manner similar to the phosphorylation of MST1/2 and SAV1, jointly regulating plant growth and development (Zhang et al., 2017). In the plant field, AtMOB1A protein in *Arabidopsis* can regulate the growth and development of seedling cotyledons through auxin mediation (Xiong et al., 2016), and plant Mob1A, like its homologous genes in other multicellular eukaryotes, is involved in coordinating tissue patterning and organ growth (Galla et al., 2011).

In tomato, *Lc* is encoded by the homologous gene *Wuschel* (*WUS*), and *Fas* is encoded by the homologous gene *Clavata3* (*CLV3*). Both *Lc* and *Fas* control the number of ovary locules, thereby promoting the enlargement of tomato fruit size (Vishwakarma et al., 2007; Premachandra et al., 1986; Chu et al.,2019). As MOB proteins are known to regulate cell proliferation, and fruit expansion is the result of cell division and cell expansion, analyzing the physicochemical properties, transmembrane domains, conserved domains, and signal peptides of SlMOB proteins will lay a foundation for further studying on the regulation role of SlMOB proteins the growth and development of tomato fruits, as well as its subsequent impact on tomato fruit weight and size.

2. MATERIALS AND METHODS

2.1 Target Sequences

The MOB protein sequences of tomato and other species were obtained from the NCBI website (http://www.ncbi.nlm.nih.gov/).

2.2 Bioinformatics Analysis Tools

Predictive analysis was mainly conducted on the physicochemical properties, transmembrane structure, subcellular localization, signal peptide, secondary structure, conserved domain, open reading frame, 3D structure, protein interaction relationship and phylogenetic evolution of tomato SlMOB proteins. The specific bioinformatics analysis contents and tools were listed in Table 1.

Table 1. Tools for bioinformatics analysis

Analysis items	Software name	Website of bioinformatics analysis tool
Physicochemical properties	ProtParam	http://web.expasy.org/protparam/
Secondary structure	SOPMA	https://npsa-prabi.ibcp.fr/cgi-bin/secpred_sopma.pl
Transmembrane region	TMHMM	http://www.cbs.dtu.dk/services/TMHMM/
Subcellular localization	Plant−mPLoc	http:/ /www.csbio.sjtu.edu.cn /bioinf /plant -multi /
Signal peptide	SignalP 4.1	http://www.cbs.dtu.dk/services/SignalP/
Conserved domain	NCBI	http://www.ncbi.nlm.nih.gov/pmc/
Open reading frame	ORFFINDER	https://www.genome.jp/kegg/pathway.html
Protein interaction	STRING	http://string-db.org/
3D structure prediction	Swiss−Model	https://swissmodel.expasy.org/

3. RESULTS AND ANALYSIS

Through NCBI search, 3 tomato SlMOB proteins were obtained, named SlMOB1A1 (XP_025887771.1), SlMOB1A2 (XP_004253087.1), and SlMOB1A3 (XP_004245954.1) respectively. Meanwhile, SlMOB protein sequences of other species were retrieved, including MOB.1 (XP_028113453.1) and MOB.2 (XP_028102438.1) in *Camellia sinensis*, MOB

(XP_015627873.1) in *Oryza sativa*, MOB (XP_427212.4) in *Gallus gallus*, and MOB (NP_001304039.1) in *Homo sapiens*.

3.1 Physicochemical Property Analysis

Online analysis via ProtParam (Table 2) showed that the three members of the tomato SlMOB protein family all contain 215 amino acids, with roughly similar proportions of various amino acids (Fig.1), and their molecular weights are all close to 24.7 kDa. Isoelectric point analysis revealed that the isoelectric points of the tomato SlMOB protein family ranged from 7.05 to 8.35, indicating these members might be rich in basic amino acids and mainly existed as cations in tomato. Proteins with an instability index less than 40 were stable, among which 2 were stable proteins and 1 was unstable. The average hydropathicity index of the amino acid sequences was all less than 0, belonging to hydrophilic proteins.

Table 2. Prediction of physical and chemical properties for SlMOB protein in tomato

Name	Molecular weight	Asp+Gu	Arg+Ls	GGRAY	PI	Instability index	Aliphatic index
SlMOB1A1	24746.41	23	25	-0.3	8.35	45.72	82.09
SlMOB1A2	24735.41	25	25	-0.316	7.05	39.59	84.79
SlMOB1A3	24747.51	25	26	-0.303	7.74	39.73	85.26

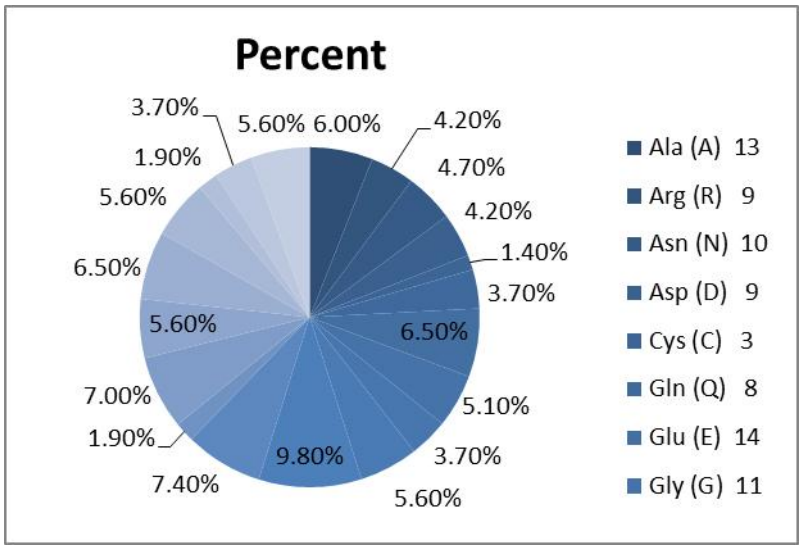

Fig. 1. The percentage of various amino acids in SlMOB1A1

Note: Due to the close number and percentage of amino acids among members of the SlMOB family, only the detailed data of SlMOB1A1 was presented in this study.

3.2 Transmembrane Structure Analysis

Transmembrane structure prediction of the three SlMOB proteins using the online software

TMHMM showed no transmembrane regions (Table 3). The number of predicted transmembrane helices was 0 for all, verifying the absence of transmembrane domains in SlMOB proteins, while the total prob of N-in was all greater than 0.02, indicating that SlMOB proteins were most likely localized on the cytoplasmic side of the membrane.

Table 3. Prediction of transmembrane structure of SlMOB protein in tomato

Name	Gene ID	Transmembrane region	AAs in TMHs	First 60 Aas	N-in
SlMOB1A1	101254611	None	0.00251	0.00011	0.04368
SlMOB1A2	101264305	None	0.00059	0.00005	0.02133
SlMOB1A3	101260752	None	0.00043	0.00005	0.02128

3.3 Prediction of Subcellular Localization

Analysis of subcellular localization indicated that all members of the SlMOB protein family were localized in the cytoplasm and nucleus (Table 4), suggesting that this protein family mainly functions in the nucleus and cytoplasm, which was consistent with the previous prediction that the protein had no transmembrane domain.

Table 4. Subcellular localization and signal peptide prediction of SlMOB protein in tomato

Name	Gene ID	Subcellular localization	Signal peptide
SlMOB1A1	101254611	Cytoplasm, Nucleus	None
SlMOB1A2	101264305	Cytoplasm, Nucleus	None
SlMOB1A3	101260752	Cytoplasm, Nucleus	None

3.4 Prediction Analysis of Signal Peptide

A signal peptide is a short peptide chain (5-30 amino acids in length) that guides newly synthesized proteins to the secretory pathway, usually locate at the N-terminus of secretory proteins. Signal peptide prediction of the three SlMOB proteins using the online tool SignalP (Fig,2) showed that none of these three SlMOB proteins had signal peptides.

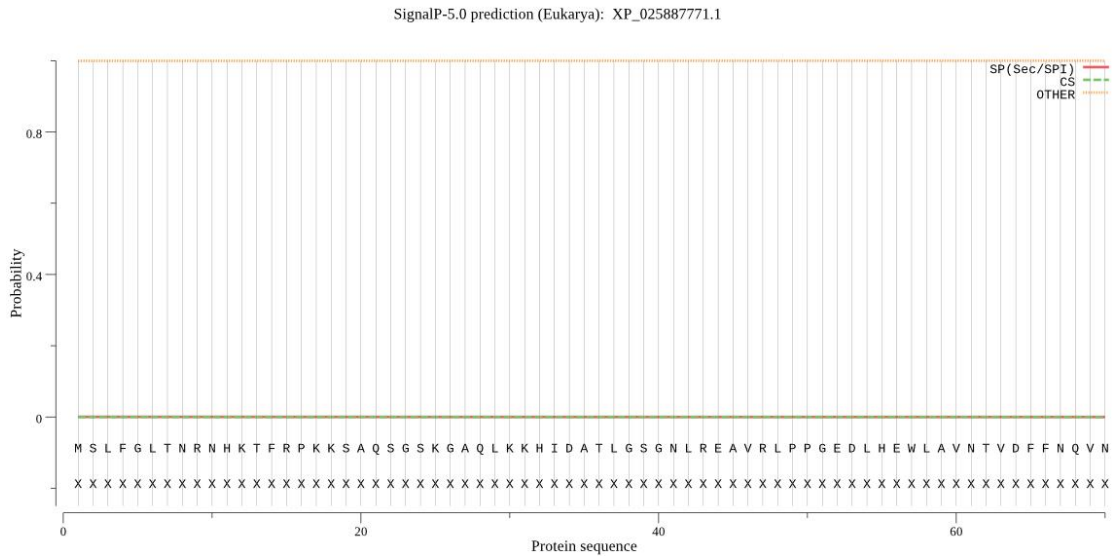

Fig. 2. Signal peptide prediction of SlMOB1A1 by SignalP 5.0 database

Note: SlMOB1A1 had no signal peptide. Since the signal peptide prediction results for the SlMOB family were consistent, only the prediction map of SlMOB1A1 was presented in this study.

3.5 Secondary Structure Analysis

Online analysis of α-helix, β-turn, random coil and extended strand in the tomato SlMOB protein sequences using the protein secondary structure prediction software SOPMA (Table 5) showed that all members of the tomato SlMOB protein family contained these structural elements, but there were no significant differences in the proportions of each part. The secondary structure of SlMOB proteins was mainly composed of α-helices, accounting for more than 50%, followed by random coils and extended strands, while β-turns accounted for the lowest proportion (all below 4.65%).

Table 5. Secondary structure prediction of SlMOB protein in tomato

Secondary structure	Alpha helix	Extended strand	Beta turn	Random coil
SlMOB1A1	114(53.02%)	17(7.91%)	9(4.19%)	75(34.88%）
SlMOB1A2	109(50.70%)	18(8.37%)	10(4.65%)	78(36.28%)
SlMOB1A3	115(53.49%)	13(6.05%)	8(3.72%)	79(36.74%)

3.6 Conserved Domain Analysis

By analyzing the conserved domains of the SlMOB protein family in tomato through the NCBI Conserved Domain Search online analysis software and the smart database (Table 6), it was found that all members of the SlMOB protein family in tomato contained a conserved domain, namely the Mob1 phocein domain (Fig.3). Proteins containing this domain often participated in the formation of the spindle and the regulation of the mitotic centromeres during cell mitosis, influencing cell division and proliferation, and thereby regulating the size of organs. It could be

inferred from this that the SlMOB protein contained in tomato might play an important role in regulating the size of tomato fruits.

Table 6. Functional structure prediction of SlMOB protein in tomato

Name	Gene ID	Conserved domain	Start	End	E-value
SlMOB1A1	101254611	Mob1_phocein	32	205	1.69E-110
SlMOB1A2	101264305	Mob1_phocein	31	204	1.46E-114
SlMOB1A3	101260752	Mob1_phocein	31	204	4.49E-115

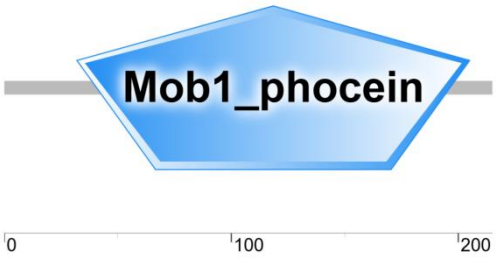

Fig. 3. Functional structure prediction of SlMOB1A1 by smart database

Note: Since the functional structure prediction results of the SlMOB family were consistent, only the prediction diagram of SlMOB1A1 was presented in this study.

3.7 Prediction of Open Reading Box

An open reading frame (ORF) is a normal nucleotide sequence of structural genes. The reading frame from the start codon to the stop codon can encode a complete polypeptide chain, and there is no stop codon in between that will interrupt translation. The number of open reading frames in the *SlMOB* family of tomato was analyzed through the NCBI database online tool ORFFINDER. In terms of quantity, the largest number of open reading frames was *SlMOB1A3* with 53, and the one with the fewest was *SlMOB1A1* with 31 (Table 7).

Table 7. Open reading frame numbers of *SlMOB* in tomato

Name	Gene ID	Number of aa	Molecular weight	Formula	ORF
SlMOB1A1	101254611	215	24746.41	$C_{1133}H_{1730}N_{296}O_{314}S_7$	31
SlMOB1A2	101264305	215	24735.41	$C_{1134}H_{1737}N_{295}O_{315}S_6$	39
SlMOB1A3	101260752	215	24747.51	$C_{1137}H_{1745}N_{295}O_{313}S_6$	53

3.8 3D Structure Prediction of Tomato SlMOB Protein

The 3D structure of the SlMOB family in tomatoes was predicted using the Swiss-Model database (Fig.4 A-D). The results indicated that the model closest to the SlMOB protein was 5twg.1.A, with a similarity of more than 64%, and 5twg.1.A was the configuration of the human SlMOB protein. It suggests a high degree of homology between tomato SlMOB proteins and human MOB proteins.

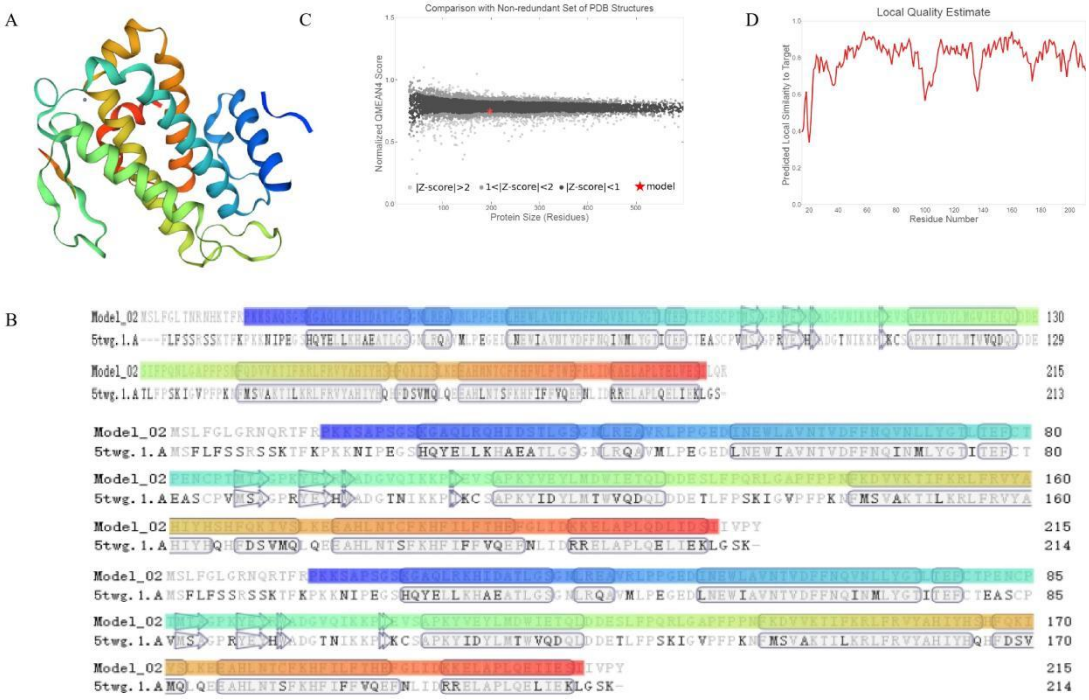

Fig. 4. Crystal structure of 5twg.1 and similarity analysis between SlMOB1A1 protein sequence and 5twg.1

Note: A, Crystal structure of 5twg.1. B, Similarity comparison between the protein sequence of SlMOB1A1 and 5twg.1. C and D, Similarity analysis of SlMOB1A1 and 5twg.1.

3.9 Interacting Proteins Prediction of the SlMOB Family in Tomato

The STRING database was used to predict the proteins that might interact with the SlMOB protein family. The results showed that there were many kinases associated with the SlMOB protein (Table 8). Including serine/threonine protein kinase 38-like (serine/threonine protein kinase 38-like), serine/Threonine protein kinase 39-like (serine/threonine protein kinase 39-like, serine/threonine protein kinase tricorner, serine/threonine protein phosphatase, serine/threonine-protein kinase sid1 (Fig.5). These kinases promote the phosphorylation of substrate proteins, thereby regulating substrate activity and downstream signaling molecules, and triggering a series of cellular responses, mainly playing a regulatory role in DNA replication and mitosis. It affects life activities such as DNA replication, transcription and intracellular signal transduction. It also plays a certain role in the transcription and regulation of genes, including regulating the binding of transcription factors to DNA and adjusting the activation activity of transcription factors(Rajpurohit et al., 2022).

Table 8. Protein prediction associated with SlMOB

Name	Interacting protein name	Interacting protein type	Interacting protein domain
SlMOB1A1	Solyc05g055610.2.1	serine/threonine-protein kinase 38-like	TYW3、Kelch_5、Kelch_1、Met_10
	Solyc12g088820.1.1,	serine/threonine-protein kinase 38-like	S_TKc、S_TH_X
	Solyc12g009010.1.1	serine/threonine-protein kinase 39-like	S_TKc、S_TH_X
	Solyc09g090200.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc12g044800.1.1	serine/threonine protein phosphatase	WD40
	Solyc07g062940.2.1	serine/threonine-protein kinase sid1	S_TKc
	Solyc09g066460.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc08g062670.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc06g008330.1.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
SlMOB1A2	Solyc04g078870.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc05g055610.2.1	serine/threonine-protein kinase 38-like	TYW3、Kelch_5、Kelch_1、Met_10
	Solyc12g088820.1.1,	serine/threonine-protein kinase 38-like	S_TKc、S_TH_X
	Solyc12g009010.1.1	serine/threonine-protein kinase 39-like	S_TKc、S_TH_X
	Solyc09g090200.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc12g044800.1.1	serine/threonine protein phosphatase	WD40
	Solyc07g062940.2.1	serine/threonine-protein kinase sid1	S_TKc
	Solyc09g066460.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc08g062670.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc06g008330.1.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
SlMOB1A3	Solyc04g078870.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc05g055610.2.1	serine/threonine-protein kinase 38-like	TYW3、Kelch_5、Kelch_1、Met_10
	Solyc12g088820.1.1,	serine/threonine-protein kinase 38-like	S_TKc、S_TH_X
	Solyc12g009010.1.1	serine/threonine-protein kinase 39-like	S_TKc、S_TH_X
	Solyc09g090200.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc12g044800.1.1	serine/threonine protein phosphatase	WD40
	Solyc07g062940.2.1	serine/threonine-protein kinase sid1	S_TKc
	Solyc09g066460.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc08g062670.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc06g008330.1.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X
	Solyc04g078870.2.1	serine/threonine-protein kinase tricorner	S_TKc、S_TH_X

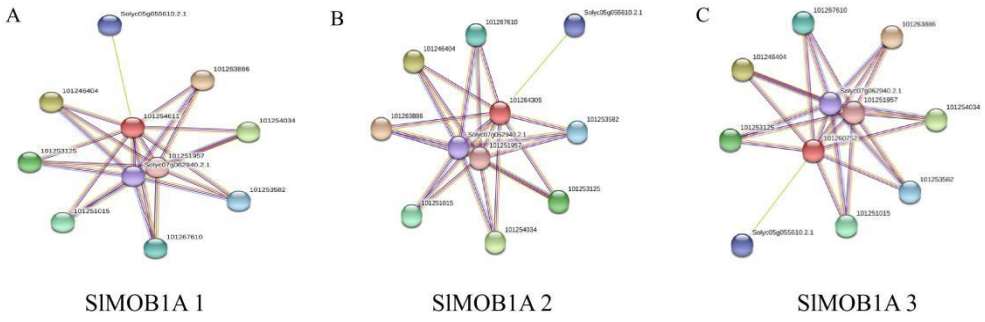

Fig. 5. The related proteins prediction of SlMOB in tomato by STRING database

3.10 Construction of the Evolutionary Tree of Tomato SlMOB Protein Family

In this study, MEGA7.0 software was used to examine tomato (*Solanum lycopersicum*), rice (*Oryza sativa*), tea tree (*Camellia sinensis*), chicken (*Gallus gallus*) and *Homo sapiens* (Homo) The phylogenetic tree of the SlMOB protein sequence (sapiens) was constructed, and the results showed that the SlMOB protein was highly conserved in evolution. In tomato, the sequence similarity between SlMOB1A2 and SlMOB1A3 was relatively close, while that between SlMOB1A1 was relatively far (Fig.6).

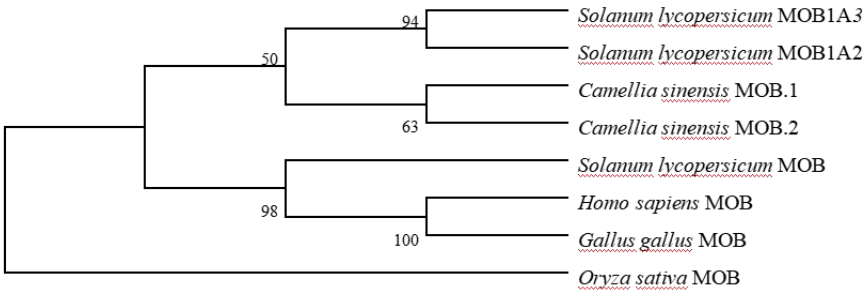

Fig. 6. Construction of the evolutionary tree of SlMOB protein family in *Solanum lycopersicum*, *Camellia sinensis*, *Oryza sativa*, *Gallus gallus* and *Homo sapiens*

4. DISCUSSION

The Hippo signaling pathway, composed of a series of conserved kinases, mainly regulates organ size by modulating cell proliferation and apoptosis. In mammals, the upstream membrane protein receptors of the Hippo signaling pathway act as sensors for extracellular growth-inhibitory signals. Once these signals are detected, they activate a series of kinase cascade phosphorylation reactions, ultimately phosphorylating the downstream effectors YAP and TAZ. Cytoskeletal proteins then bind to the phosphorylated YAP and TAZ, retaining them in the cytoplasm and reducing their nuclear activity, thereby achieving the regulation of organ size and volume (Carlos et al., 2020).

MOB proteins are core components of the Hippo pathway and form a large protein family in eukaryotes. Studies have shown that tissue hyperplasia caused by *SAV1* mutation, *WTS* mutation, and Hippo mutation exhibits similar phenotypes to abnormal cell proliferation induced by MOB mutations. Meanwhile, MOB proteins interact with the nuclear Dbf2-related (NDR) protein kinase

family. MOB1 and 2 interact with NDR by relieving the autoinhibitory effect of the autoregulatory base sequence in the NDR catalytic domain, thereby regulating cell morphology and the cell cycle. In the nervous system, MOB proteins can serve as important substrate proteins for serine/threonine protein kinase (GSK3β), binding to GSK3β to promote axon elongation. In plants, knockout of the *Arabidopsis thaliana AtMOB1A* gene results in shrinkage of the primary root stem cell niche, severe defects in columella tissue patterning, reduced meristem size, and increased sensitivity of root growth to abscisic acid (ABA). In contrast, knockout of *Mob1B* does not cause any significant changes during plant development. Thus, similar to its homologous genes in other multicellular eukaryotes, plant Mob1A is involved in the coordination of tissue patterning and organ growth (Berenice et al., 2020).

Tomato is a widely cultivated cash crop worldwide, and its export volume is mainly affected by fruit size. Therefore, bioinformatics analysis of tomato SlMOB proteins was performed to predict their physicochemical properties, transmembrane domains, subcellular localization, signal peptides, secondary structures, conserved domains, open reading frames, 3D structures and evolutionary relationships. This analysis enhances our understanding of the functions of tomato SlMOB proteins and holds significant implications for subsequent studies on the possible regulation of tomato fruit size by SlMOB proteins, thereby improving yield.

Through bioinformatics analysis of the tomato SlMOB protein family, it was found that the three members shared high similarity. In terms of physicochemical properties, the molecular weight, isoelectric point, number of amino acids and aliphatic index of SlMOB proteins were highly similar, with roughly the same amino acid composition ratio in each protein. All members lacked transmembrane domains and signal peptides, which were consistent with the subcellular localization analysis showing their presence in the cytoplasm and nucleus. In the secondary structure, the proportion of α-helices exceeded 50% in all members, followed by random coils. The only conserved domain was the Mob1_phocein domain. Furthermore, all 3D models were predicted using 5twg.1.A as the template, with a similarity as high as 64%. The interacting proteins of each member were almost identical. Given that tomato fruit size plays a decisive role in yield, the bioinformatics analysis of the tomato SlMOB protein family is of great significance for subsequent research on the possible regulation of tomato fruit size by SlMOB proteins and the improvement of tomato yield. In future research, we will further validate the function of *SlMOB* genes using physiological, biochemical and molecular biology methods based on cloned genes, and investigate the role of the SlMOB family using overexpression and silencing techniques to clarify the function.

5. CONCLUSIONS

Through bioinformatics analysis of the SlMOB protein family in tomato, it was found that the three members of the tomato SlMOB protein family shared high similarity. The molecular weight, isoelectric point, number of amino acids and aliphatic index of SlMOB proteins were highly similar, and the amino acid composition ratio in each protein was roughly the same. All members lacked transmembrane domains and signal peptides, and their subcellular localization was in the cytoplasm and nucleus. In the secondary structure, the proportion of α-helices exceeded 50% in all members. The conserved domain was limited to the Mob1_phocein domain. Moreover, the prediction of all 3D models adopted 5twg.1.A as the template, with a similarity as high as 64%.

The interacting proteins of each member were almost identical. Through phylogenetic tree construction, it was revealed that the tomato SlMOB protein family had a close evolutionary relationship with the MOB protein family of *Camellia sinensis*.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

All authors have declared that no competing interests exist, and that no artificial intelligence (AI) technologies were used in the process of writing this paper.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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