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# ‘红阳’猕猴桃全基因组AP2/EREBP转录因子生物信息学分析

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**摘 要**:**【目的】**分析‘红阳’猕猴桃全基因组AP2/EREBP转录因子家族。**【方法】**利用Kiwifruit Genome Database、EMBI、TAIR、SMART、Pfam、MEME、Protparam、SOPM、SWISS-MODEL、SignalP4.1 Sever网站,和ClustalX2、BioEdit、MEGA6.0、MapInspect、MEV软件,分析‘红阳’猕猴桃AP2/EREBP转录因子类型、结构域、系谱进化、蛋白理化性质及高级结构、信号肽分析、基因定位、序列元件和基因表达模式。**【结果】**‘红阳’猕猴桃全基因组中有204条AP2/EREBP转录因子,根据其结构域划分为4个亚家族。进行多序列比对和系谱进化分析,发现2个亚家族各分为6个亚组。生物信息学分析表明,204条蛋白氨基酸序列高级结构与拟南芥AP2/EREBP转录因子相似性较高。其中存在2条分泌型蛋白。基因定位表明,该家族基因在10号染色体无定位;有染色存在串联复制现象。同源拟南芥基因表达模式分析表明,AP2/EREBP转录因子对外界胁迫有显著性表达。**【结论】**利用生物信息学方法获得204条猕猴桃AP2/EREBP家族转录因子,并与拟南芥AP2/EREBP转录因子进行系谱进化、结构域、基因定位和同源表达等分析,结果表明猕猴桃AP2/EREBP转录因子在进化过程中比较保守,并参与了植物发育和胁迫应答调控。

**关键词**:猕猴桃;AP2/EREBP;转录因子;生物信息学分析

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# Genome-wide bioinformatics analysis of AP2/EREBP transcription factor in ‘Hongyang’ kiwifruit

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**Abstract**:【Objective】AP2/EREBP transcription factor family is a plant-specific transcription factor, which plays an important role in plant growth, development and stress response. It contains at least one AP2 binding domain and about 60-70 highly conserved amino acids. The function of the AP2/EREBP transcription factor family of the genome of *Actinidia chinensis* was analyzed with the completion of sequencing of the full genome of ‘Hongyang’ kiwifruit.【Methods】AP2/EREBP family transcription factors were analyzed by bioinformatics. The protein and nucleic acid sequence of AP2/EREBP transcription factor of kiwifruit and Arabidopsis were obtained by Kiwifruit Genome Database and TAIR database. And the domains of the AP2/EREBP transcription were analyzed by SMART, Pfam. The AP2/EREBP transcription factor was used for sequence element analysis. The domain sequence mapping was analyzed by MEME. In order to analyze the evolutionary relationship of 204 AP2/EREBP transcription factors in ‘Hon-

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gyang’ kiwifruit, ClustalX2 and MEGA6.0 were used to sequence the AP2/EREBP transcripts of *Actinidia chinensis* and *Arabidopsis thaliana*, and to carry out the phylogenetic analysis. The Physicochemical properties, secondary structure, tertiary structure, and signal peptide analysis of the AP2/EREBP transcription factor protein sequence of *Actinidia chinensis* were carried out using Protparam, SOPM, SWISS-MODEL and SignalP4.1 Sever. The Kiwifruit AP2/EREBP transcription factor sequence information was obtained from the Kiwifruit Genome Database. The MapInspect tool was used to construct the gene mapping map. The *Arabidopsis thaliana* AP2/EREBP transcription factor local database was constructed using BioEdit software. Blast was used to obtain the *Arabidopsis thaliana* sequence of AP2/EREBP transcription factor, and the *Arabidopsis thaliana* expression data was downloaded from EBI. The MEV tool was used to log in the downloaded data and to make an expression heat-map.【Results】The protein and nucleic acid sequence of AP2/EREBP transcription factor of 204 kiwifruit were obtained from Kiwifruit Genome Database. AP2/EREBP transcription factor was divided into four subfamilies of AP2, RAV, ERF, and DREB by SMART and Pfam. In addition to the AP2 and B3 domains, the AP2/EREBP transcription factor of kiwifruit contained “UQ_CON” “MBOAT” “BAG” “LRR” “Malectin” “RRM” “Mito_carr” “C2” “Copine” “HEAT” and “Vac14_Fab1_bd” domains. Sequence element analysis showed that Motif1 belonged to the AP2 domain, Motif2, and Motif3 belonged to the B3 domain of RAV subfamily. Motif1, Motif2 and Motif3 belonged to the AP2 domain of AP2 and ERF/DREB subfamily. All Motifs would play an important role in the combination of DNA recognition. A total of 204 AP2/EREBP transcription factors of *Actinidia chinensis* and 129 *Arabidopsis* AP2/EREBP transcription factor protein sequences were sequenced. The ERF subfamilies were further divided into B1, B2, B3, B4, B5 and B6. DREB subfamilies were divided into A1, A2, A3, A4, A5 and A6. The phylogenetic analysis showed that the AP2 and RAV subfamily differentiated quite early and greatly. The ERF and DREB subfamily were closely located on the same branch and showed a shorter evolutionary history, which was consistent with the Arabidopsis AP2/EREBP subfamily classification, suggesting that the evolutionary pathways of AP2/EREBP family transcription factor in kiwifruit be similar to that of the *Arabidopsis thaliana*. When the MapInspect tool was used to locate the 204 sequences of kiwifruit, it was found that the 204 sequences distributed on all the 29 chromosomes but number 10. The number of sequences distributed on the chromosomes varied from 1 to 24. Among them, 17 sequences distributed on number 3 and 14 on number14. The locations of 29 sequences still remained unclear. The secondary protein structure, protein tertiary structure and signal peptide of AP2/EREBP transcription factor of kiwifruit were analyzed by Protparam, SOPM, SWISS-MODEL and SignalP4.1 Sever. The results showed that the AP2/EREBP family proteins were rich in acidic amino acids and the theoretical isoelectric points of the most amino acids were within this acidic range. The secondary structure analysis showed that 23 amino acid sequences were composed of α-helix, and the other amino acid sequences were β-sheet and β-turn, which scattered throughout the protein sequence. The tertiary structure prediction was very similar to that of *Arabidopsis thaliana*. Signal peptide analysis showed that only Achn132541 and Achn240471 had signal peptides and the rest proteins did not exist in signal peptide, which belonged to non-secretory protein. The Illumia RNA-Seq data was downloaded from the EBI, under accession numbers GSE80565, GSE72806 and GSE67332. At the same time, the expression data of *Arabidopsis* homologous genes in each organ was downloaded from EMBI. The expression of homologous Arabidopsis gene was analyzed by MEV software. The results showed that these genes were highly induced by low temperature, high temperature, high salt and exogenous ABA treatment. They strongly expressed in flower, fruit, leaf and root.【Conclusion】AP2/EREBP transcription factor was conservervative in

evolutionary process, being involved in plant development and stress response regulation. AP2/EREBP transcription factor could be used to explore other function.

**Key words**: *Actinidia chinensis*; AP2/EREBP; Transcription factors; Bioinformatics

植物体内存在大量转录因子,在植物生长发育、生理生化反应的信号转导和对外界环境的响应中发挥重要作用。拟南芥作为一个模式植物,其基因组中编码转录因子的序列占全基因组的5%,共编码了1 500个转录因子,其中45%是植物所特有的[1]。转录因子根据其DNA结构域的不同,被划分为bZIP、MYB、AP2/EREBP、WRKY和NAC等几个大家族[2]。AP2/EREBP家族转录因子是植物所特有的一类转录因子,AP2/EREBP结合域最初是在拟南芥APETALA2和烟草EREBP中得到确认的[3-4]。其主要特征是至少含有1个AP2结合域,包含60~70个氨基酸,且高度保守[5]。根据AP2/EREBP转录因子家族所含AP2结构域数量的不同,将AP2/EREBP转录因子家族分为AP2亚族,含有2个AP2结构域;RAV亚族,含有1个AP2和B3结构域;EREBP亚族,含1个AP2结构域[6-7]。Sakuma等[8]将拟南芥的145个AP2基因做进一步分类,将EREBP亚族根据其保守氨基酸序列的不同分为ERF、DREB和其他类基因。研究证实AP2基因编码的AP2/EREBP家族转录因子与植物的干旱[9]、低温[10]、高盐[11]、病害[8]和开花[12]密切联系,在决定种子的大小、质量、种子发育、种子发芽、花发育、果实发育以及维持分生组织分生能力、在油类和蛋白的积累过程中也发挥重要的作用[13-18]。例如,研究证明花器官发育模型为ABC型[19],拟南芥A功能基因APETALA2(AP2)抑制C功能基因AGAMOUS(AG)在外轮花器官中的表达,对萼片和花瓣的器官特征起决定作用。对拟南芥ap2突变体和ant突变体的研究表明,AP2基因影响花的形态建成,与ABC模型论述相符[20]。此外,一些AP2/EREBP家族基因的表达受MicroRNA172(miR172)的调控。如miR172水平提高,负调控AP2蛋白的表达,致使花器官特性缺失[21]。同时,芸薹属和雏豆AP2/EREBP家族基因在转基因植物中的超表达,使转基因植物具有较强的抗逆性和优良表型性状,表明AP2/EREBP家族转录因子同时参与了植物发育和胁迫途径[22-23]。

猕猴桃(*Actinidia chinensis*)是猕猴桃科(Actinidiaceae)、猕猴桃属(*Actinidia*)植物,是一种重要的果树资源。随着分子生物学与生物信息学的快速发展,对植物全基因组数据中功能基因的挖掘、定位等已成为研究的热点。笔者通过生物信息学分析方法研究猕猴桃AP2/EREBP基因家族分类及系统发生规律,进而推测其功能与猕猴桃生长发育、抗病性和胁迫应答之间的关系,为以后该基因的克隆与表达分析,尤其是为猕猴桃遗传改良育种提供理论依据。

## 1 材料和方法

### 1.1 材料来源

'红阳'猕猴桃全基因组AP2/EREBP转录因子信息下载于Fei Bioinformatics Lab(http://bioinfo.bti.cornell.edu/)。拟南芥全基因组AP2/EREBP转录因子信息从TAIR(http://www.arabidopsis.org/)中下载。

### 1.2 方法

1.2.1 '红阳'猕猴桃AP2/EREBP转录因子的鉴定及分类 利用Huang等[24]2013年发表于猕猴桃基因组数据库中'红阳'猕猴桃全基因组所有AP2/EREBP转录因子ID号,并在Kiwifruit Genome Database[25]获得对应蛋白序列和核酸序列。利用SMART(http://smart.embl- heidelberg.de/)和Pfam(http://pfam.xfam.org/)鉴定AP2/EREBP转录因子结构,确定有无AP2结构域,再根据结构特点,将AP2/EREBP转录因子进行初步筛选及分类。

1.2.2 '红阳'猕猴桃AP2/EREBP转录因子保守结构域及序列元件分析 利用在线软件SMART(http://smart.embl- heidelberg.de/)、Pfam(http://pfam.xfam.org/)和MEME(http://meme.sdsc.edu/meme/ meme-intro.html),对'红阳'猕猴桃AP2/EREBP转录因子蛋白保守域和结构元件进行分析。

1.2.3 '红阳'猕猴桃AP2/EREBP转录因子系谱发生树分析 利用ClustalX2软件将候选蛋白与拟南芥AP2/EREBP家族蛋白进行多序列比对,进化树绘制使用MEGA 6.0软件完成,采用NJ(neighbor-joining)方法,选择Bootstrap method、pairwise deletion,重复设置为1 000。

1.2.4 '红阳'猕猴桃全基因组AP2/EREBP转录因子基因定位 使用MapInspect工具对'红阳'猕猴桃

全基因组AP2/EREBP转录因子进行基因定位，并制做定位图。其中“ChrN”（N为染色体编号，1~29）表示序列所定位的染色体号，“Unknow”表示无法定位到已知染色体上。

1.2.5 ‘红阳’猕猴桃AP2/EREBP蛋白质理化性质、高级结构和信号肽分析　利用在线软件Protparam（http://us.expasy.org/tools/protparam.html）、SWISS-MODEL（https://swissmodel.expasy.org/interactive）、SOPM（https://npsa- prabi.ibcp.fr/cgi- bin/npsa_automat.pl?page=/NPSA/npsa_sopm.html）和SignalP4.1 Sever（http://www.cbs.dtu.dk/services/SignalP/）分别对‘红阳’猕猴桃AP2/EREBP转录因子的蛋白理化性质、高级结构和信号肽进行预测分析。

1.2.6 ‘红阳’猕猴桃AP2/EREBP转录因子的同源表达分析　从NCBI提供的GEO（http://www.ncbi.nlm.nih.gov/gds）数据库中下载拟南芥Illumina RNA-Seq数据，登录号为GSE80565、GSE72806和GSE67332，用‘红阳’猕猴桃AP2/EREBP蛋白序列为探针，使用BioEdit程序搜索拟南芥全基因组数据，获得同源拟南芥基因，然后提取同源拟南芥AP2/EREBP基因在各种非生物胁迫下的RNA-Seq数据，同时从EMBI数据库（http://www.ebi.ac.uk/）中下载同源拟南芥不同组织的表达数据，通过MEV软件对数据进行log2转换，制作电子表达热图（heatmap）。

## 2　结果与分析

### 2.1 ‘红阳’猕猴桃AP2/EREBP家族转录因子鉴定及分类

根据前人的分类方法[6-8]，笔者利用Pfam和SMART网站鉴定分析，获得204条AP2/EREBP转录因子，按含结构域的不同，将AP2/EREBP家族初步分为AP2、RAV、ERF和DREB亚家族。与拟南芥全基因组AP2/EREBP转录因子进行比对，将ERF、DREB亚家族进一步分别分为B1~B6和A1~A6六个亚组。

### 2.2 ‘红阳’猕猴桃AP2/EREBP蛋白中的保守结构域分析

对‘红阳’猕猴桃全基因组204条AP2/EREBP蛋白进行结构域分析，发现AP2/EREBP转录因子除了具有AP2和B3结构域外，部分AP2/EREBP转录因子还包含了UQ_CON、MBOAT、BAG、LRR、Malectin、RRM、Mito_carr、C2、Copine、HEAT、Vac14_Fab1_bd等结构域。其中，‘红阳’猕猴桃的Achn181331蛋白检测出LRR、Malectin结构域；Achn366301、Achn350331蛋白检测含有线粒体载体蛋白Mito_carr结构域；Achn303171和Achn191231蛋白检测含有UQ_CON（ubiquitin-conjugating enzyme）结构域；Achn271311含有C2、Copine结构域；Achn239411含有HEAT、Vac14_Fab1_bd结构域；Achn169731含有RRM（RNA recognition motif）结构域；Achn023491蛋白检测含有核糖体蛋白S17（ribosomal protein S17）；Achn132541含有MBOAT、BAG结构域。由此推测可能是‘红阳’猕猴桃AP2/EREBP转录因子具有更加广泛的生物学功能。

### 2.3 ‘红阳’猕猴桃AP2/EREBP蛋白序列元件分析

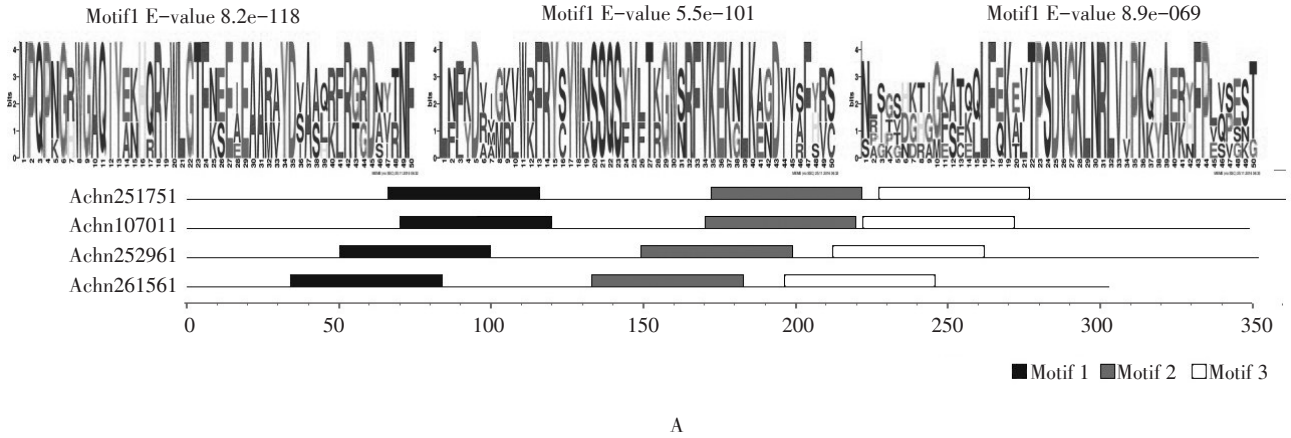
使用MEME软件对204条蛋白进行序列元件分析，默认设置发现3个序列元件（图1）。RAV亚家族Motif1属于AP2结构域，Motif2和Motif3属于B3结构域；AP2和ERF/DREB亚家族Motif1、Motif2和Motif3属于AP2结构域，均在DNA识别结合过程中发挥重要作用。

### 2.4 ‘红阳’猕猴桃AP2/EREBP转录因子系谱进化分析

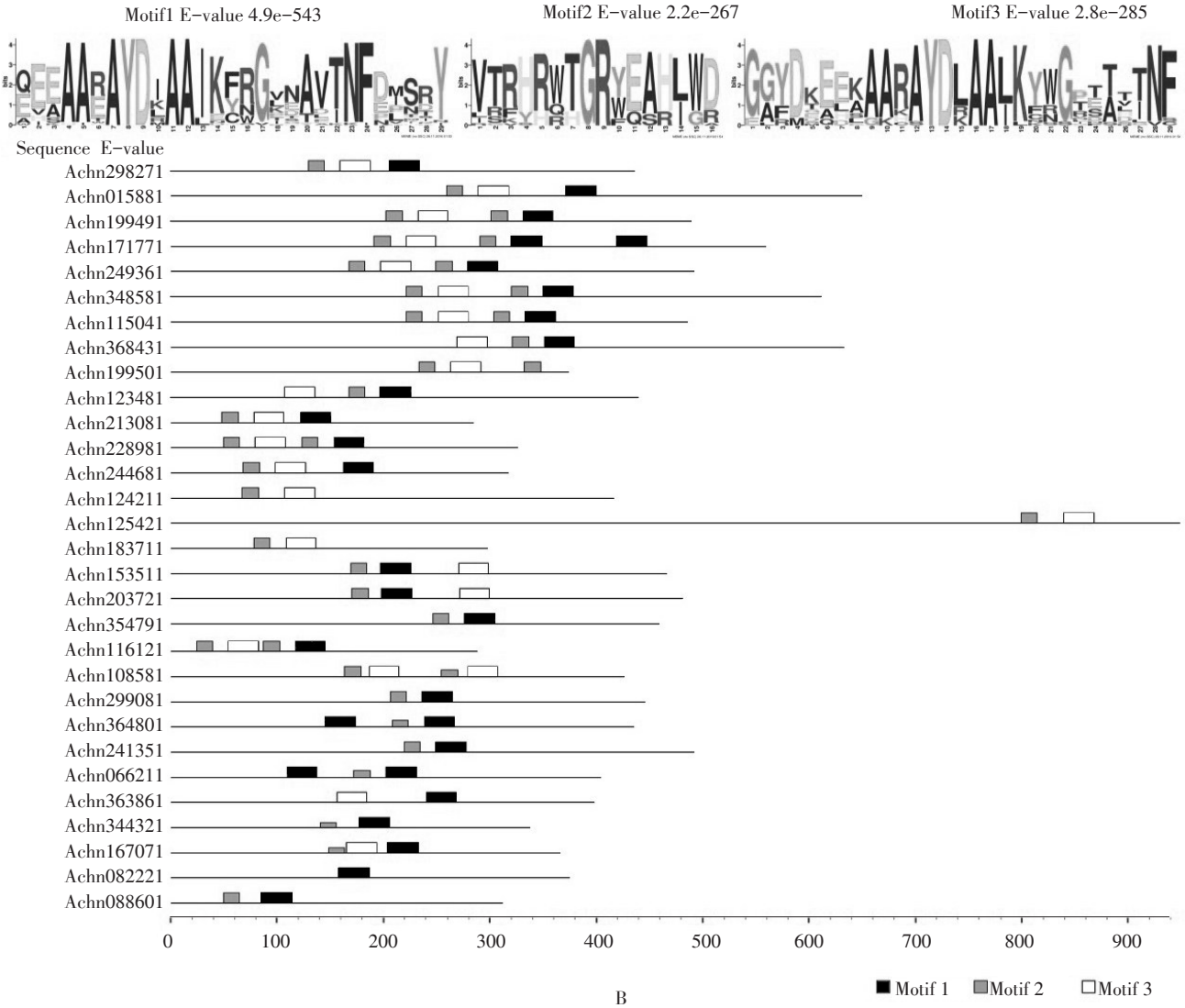
为了考察猕猴桃AP2/EREBP转录因子的系谱发生关系，在多序列联配的基础上，以NJ法构建AP2/EREBP转录因子的系谱发生树。为了更好地对猕猴桃AP2/EREBP转录因子家族进行分类，把猕猴桃204条序列与拟南芥129条AP2/EREBP家族序列作系谱发生树，结果显示，AP2、RAV亚家族分支非常明显，表明其在很早的时候就发生了分化，基因序列发生较大分化；而ERF和DREB亚族在同一分支上且分支较近，表明进化历史较短（图2）。这与拟南芥AP2/EREBP各亚族分类基本吻合，表明猕猴桃与拟南芥AP2/EREBP家族转录因子进化路径相似。

### 2.5 ‘红阳’猕猴桃全基因组AP2/EREBP转录因子基因组定位

基因定位是指确定基因在连锁群上的分布位置。基因定位有助于了解基因的作用与功能及其之间的相互作用关系。使用MapInspect工具对猕猴桃204条序列进行基因定位发现，在猕猴桃29条染色体上，只有第10号染色体没有分布，其余染色体的基因分布数量从1到24不等，以第3号和第14号上分布最多，分别为17和14个（图3）。有29条序列无




A




B

A. RAV 亚家族；B. AP2 亚家族；C. ERF/DREB 亚家族。

A. RAV subfamily; B. AP2 subfamily; C. ERF/DREB subfamily.

**图 1 AP2/EREBP 转录因子 AP2 结构域序列 Logo 及蛋白保守基序**

**Fig. 1 AP2/EREBP transcription factor AP2 domain sequence Logo and protein conserved motif**

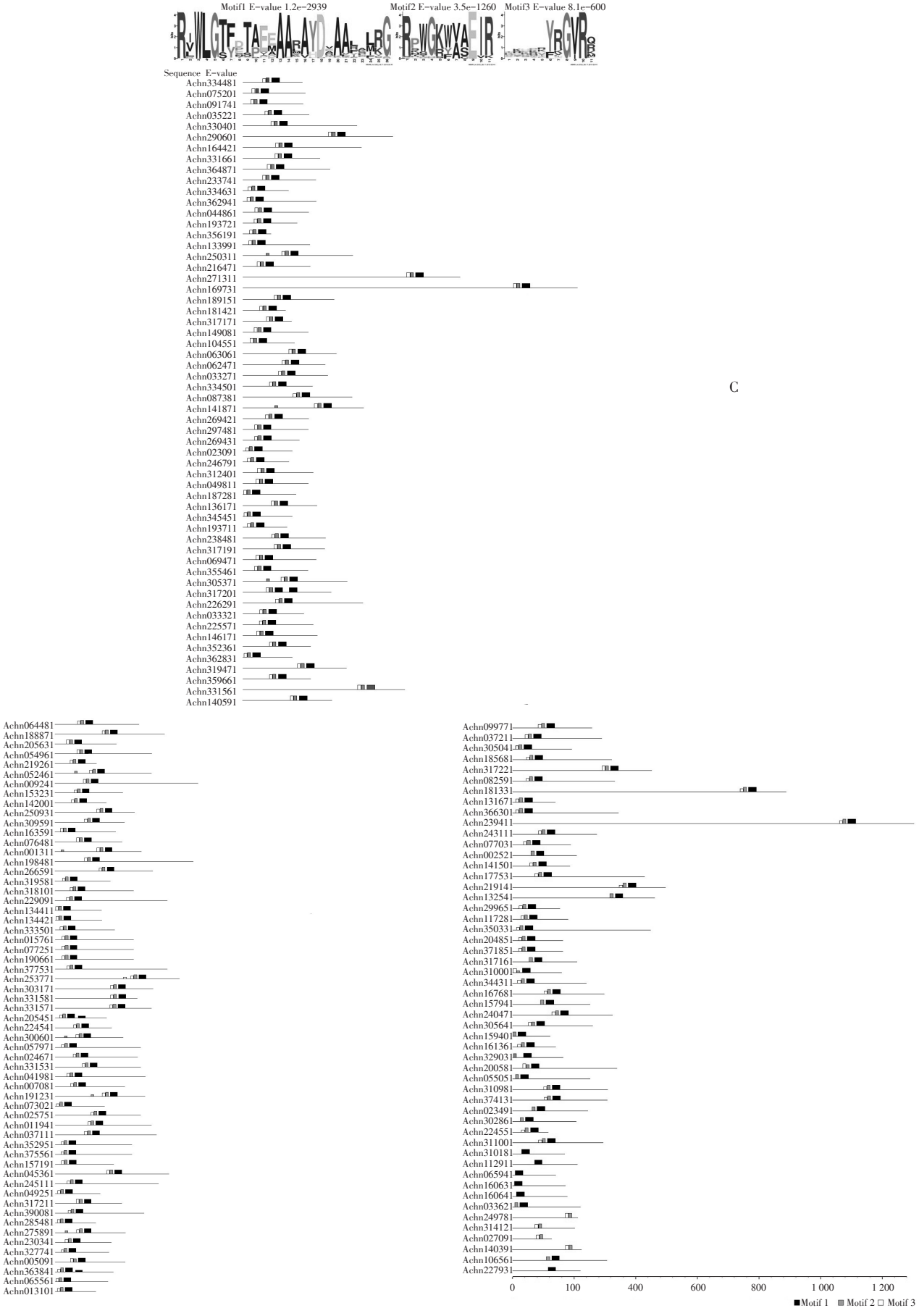



**图1（续）　Fig. 1（continued）**

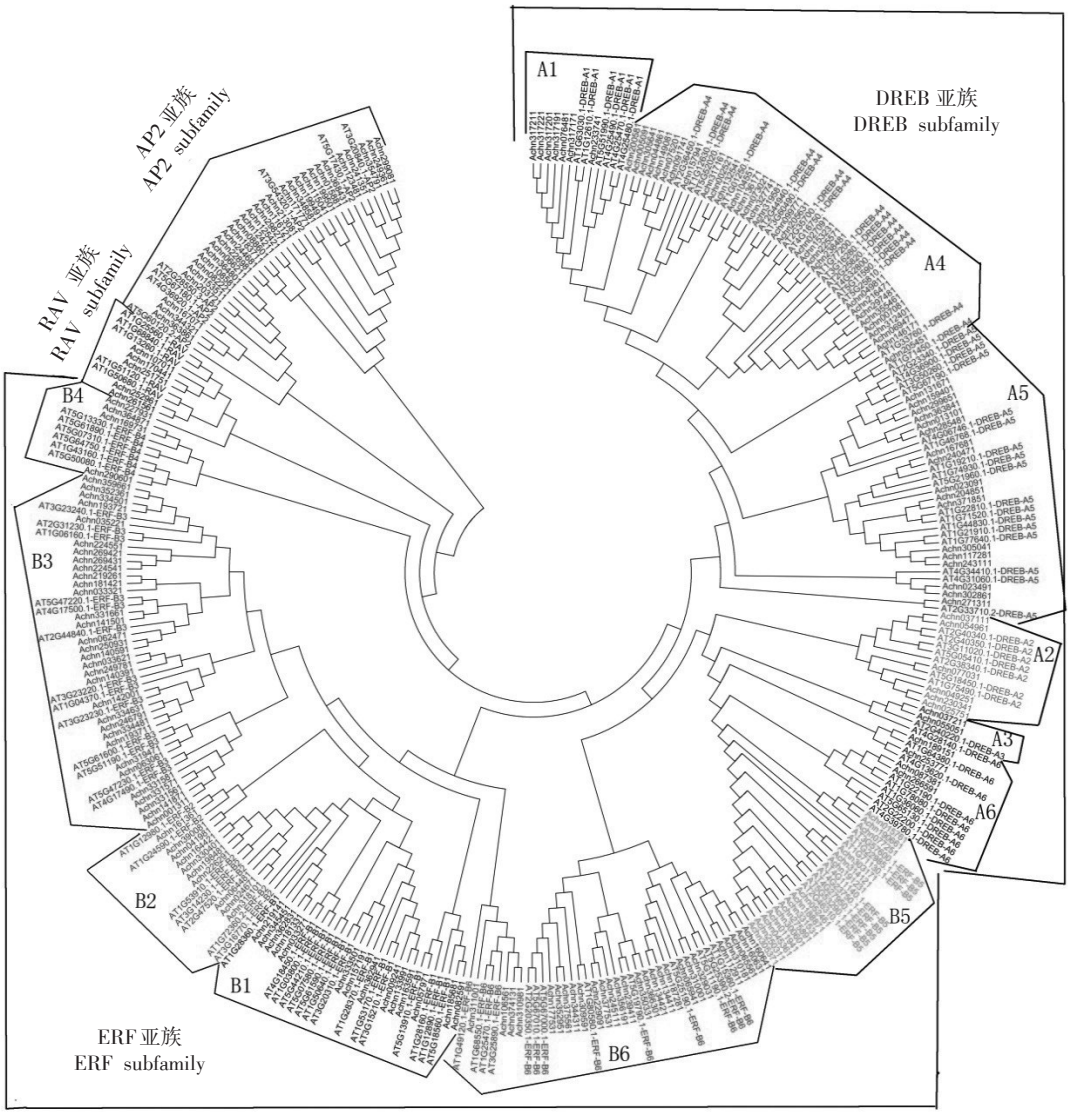



**图 2 猕猴桃与拟南芥 AP2/EREBP 家族转录因子系统发生树**

**Fig. 2 Phylogenetic tree of kiwifruit and Arabidopsis AP2/EREBP family transcription factors**

法定位到已知染色体上(表1),以Unknow表示。

### 2.6 '红阳'猕猴桃AP2/EREBP蛋白质理化性质、高级结构和信号肽分析

2.6.1 蛋白质理化性质分析 AP2/EREBP家族转录因子编码蛋白理化性质分析(表1)表明,各亚族之间蛋白质理化性质存在一定差异。猕猴桃204条AP2/EREBP家族转录因子蛋白的总平均亲水性GRAVY均为负值,表明AP2/EREBP家族蛋白均为亲水性蛋白。其中ERF亚家族以B3亚族Achn334631亲水性最大,为-1.165;DREB亚家族以A5亚族Achn285481亲水性最大,为-1.106。猕猴桃AP2/EREBP家族氨基酸理论等电点大多数在酸性范围内,表明该家族蛋白富含酸性氨基酸。在4个亚族中,RAV亚族理化性质差异最小。

2.6.2 蛋白质高级结构分析 蛋白质的高级结构决定其生物功能。对204条蛋白二级结构预测分析表明,有23条氨基酸序列以α-螺旋为主要组成成分,其余则以无规则卷曲为主要组成成分,β-折叠与β-转角散布于整个蛋白序列中。

选取每个亚家族具有代表性的序列进行三级结构预测。RAV亚家族以Achn170441为代表,AP2和EREBP亚族含1个AP2结构域,以Achn203721为代表进行预测,结果表明猕猴桃AP2/EREBP家族三级结构预测与拟南芥十分相似(图4)。

2.6.3 信号肽预测 信号肽预测分析结果(图5)表明,猕猴桃204条AP2/EREBP蛋白,只有

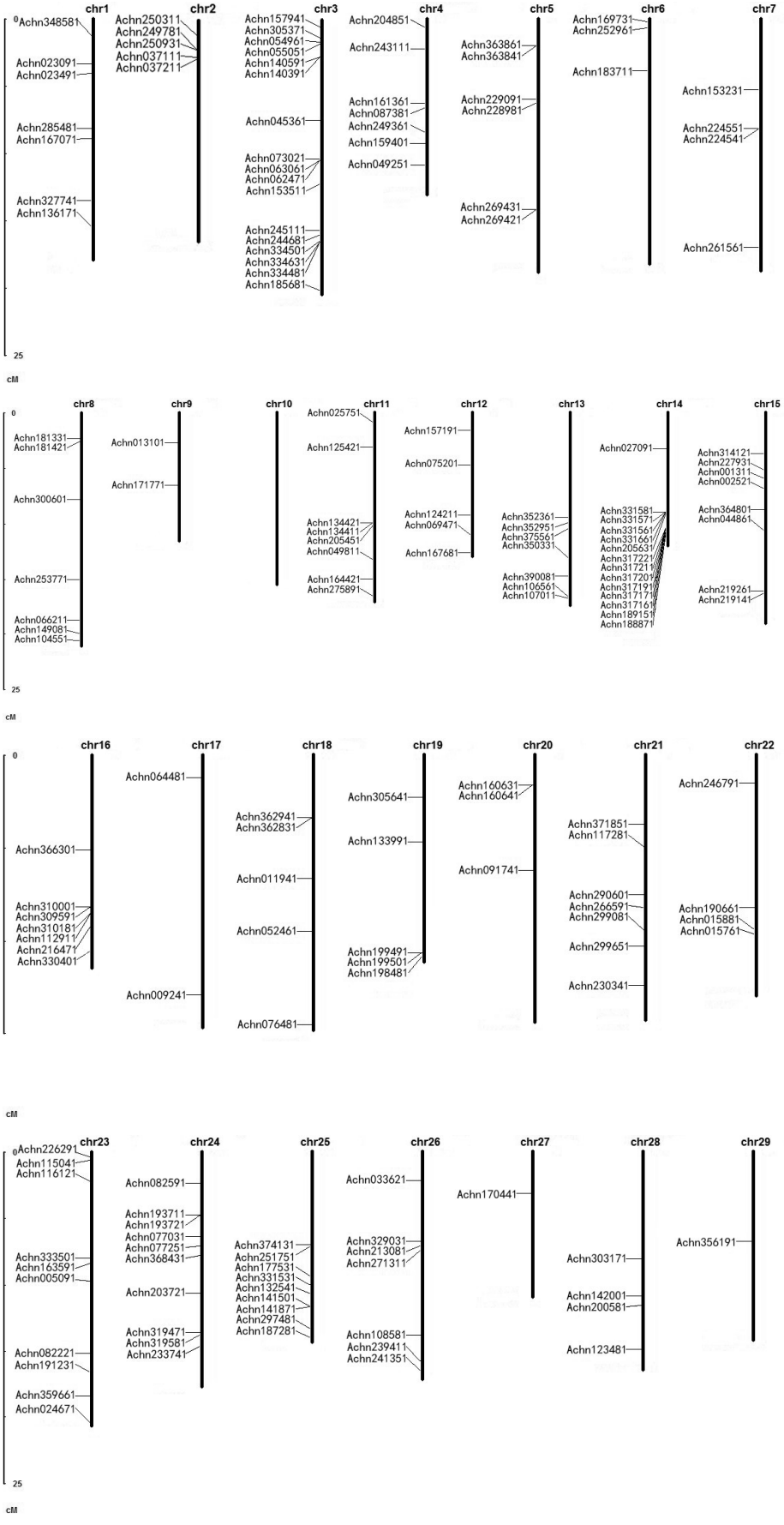



**图 3　猕猴桃 AP2/EREBP 基因定位**

**Fig. 3　AP2/EREBP gene localization of kiwifruit**

**表 1 猕猴桃 AP2/EREBP 基因定位及蛋白的理化性质**

**Table 1 Kiwifruit AP2/EREBP gene localization and protein physical and chemical properties**

| 亚族 Subfamily | 编号 Numbering | 染色体:位置 Chromosome: Location | 蛋白长度 Protien length/aa | 分子质量 Molecular mass/ku | 等电点 Isoelectric point | 总平均亲水性 GRAVY |
|---|---|---|---|---|---|---|
| RAV | Achn170441 | Chr27:3096850-3097932 | 360 | 39 770.00 | 9.36 | -0.510 |
| | Achn251751 | Chr25:7098369-7099451 | 360 | 39 852.31 | 9.47 | -0.506 |
| | Achn107011 | Chr13:16732064-16736605 | 348 | 38 975.75 | 9.17 | -0.672 |
| | Achn252961 | Chr6:674409-675464 | 351 | 40 059.41 | 8.36 | -0.576 |
| | Achn261561 | Chr7:17003571-17004479 | 302 | 34 460.20 | 8.46 | -0.409 |
| AP2 | Achn108581 | Chr26:13795211-13798521 | 425 | 47 036.96 | 6.33 | -0.724 |
| | Achn203721 | Chr24:10640531-10644563 | 480 | 52 529.53 | 8.38 | -0.567 |
| | Achn364801 | Chr15:8733865-8737420 | 435 | 48 239.18 | 6.37 | -0.692 |
| | Achn153511 | Chr3:12262577-12266338 | 465 | 5 123.17 | 8.07 | -0.578 |
| | Achn199491 | Chr19:10617631-10622495 | 489 | 54 551.05 | 6.13 | -0.845 |
| | Achn171771 | Chr9:6522831-6529291 | 559 | 61 399.12 | 6.00 | -0.560 |
| | Achn348581 | Chr1:1214458-1227317 | 595 | 65 768.66 | 6.17 | -0.672 |
| | Achn199501 | Chr19:10623743-10627601 | 373 | 42 149.54 | 8.06 | -0.919 |
| | Achn015881 | Chr22:9350458-9356038 | 649 | 71 462.34 | 5.93 | -0.739 |
| | Achn116121 | Chr23:2211035-2215550 | 288 | 32 575.83 | 7.77 | -0.957 |
| | Achn124211 | Chr12:9204965-9209467 | 416 | 46 133.67 | 8.87 | -0.752 |
| | Achn066211 | Chr8:18747751-18751086 | 404 | 44 012.23 | 5.43 | -0.541 |
| | Achn363861 | Chr5:1989035-1992443 | 398 | 43 916.94 | 5.04 | -0.696 |
| | Achn167071 | Chr1:8884342-8886995 | 365 | 39 169.70 | 5.70 | -0.741 |
| | Achn249361 | Chr4:8444610-8447599 | 491 | 54 530.47 | 6.37 | -0.700 |
| | Achn115041 | Chr23:610138-615527 | 485 | 54 201.99 | 6.04 | -0.747 |
| | Achn368431 | Chr24:7785336-7790877 | 632 | 69 623.42 | 5.35 | -0.690 |
| | Achn228981 | Chr5:6270334-6272132 | 326 | 37 320.53 | 6.81 | -0.863 |
| | Achn244681 | Chr3:16015692-16018128 | 317 | 36 122.34 | 5.76 | -0.678 |
| | Achn123481 | Chr28:14874424-14881229 | 438 | 48 183.04 | 5.34 | -0.574 |
| | Achn298271 | Unknow:78256159-78262467 | 435 | 46 783.69 | 6.40 | -0.517 |
| | Achn213081 | Chr26:7056749-7061362 | 284 | 31 531.00 | 6.07 | -0.876 |
| | Achn299081 | Chr21:9398765-9402017 | 445 | 49 355.64 | 5.86 | -0.656 |
| | Achn354791 | Unknow:97192067-97195169 | 458 | 50 646.08 | 6.10 | -0.660 |
| | Achn241351 | Chr26:16487908-16493059 | 491 | 53 439.92 | 5.74 | -0.580 |
| | Achn088601 | Unknow:31381196-31383424 | 311 | 35 437.74 | 9.55 | -0.884 |
| | Achn183711 | Chr6:3839609-3841821 | 297 | 33 587.50 | 8.46 | -0.897 |
| | Achn125421 | Chr11:3073688-3094507 | 948 | 107 186.06 | 9.04 | -0.375 |
| | Achn344321 | Unknow:93947079-93951042 | 337 | 36 714.01 | 6.08 | -0.830 |
| | Achn082221 | Chr23:15172547-15176039 | 374 | 41 070.84 | 5.11 | -0.670 |
| ERF-B1 | Achn219141 | Chr15:16284261-16306115 | 496 | 53 912.82 | 579 | -0.404 |
| | Achn345451 | Unknow:4187779-4188252 | 157 | 17 121.38 | 8.82 | -0.429 |
| | Achn362831 | Chr18:3383161-3383634 | 157 | 17 231.52 | 9.30 | -0.492 |
| | Achn181331 | Chr8:2329439-2347371 | 887 | 96 953.82 | 8.50 | -0.270 |
| | Achn033271 | Unknow:121492328-121493143 | 271 | 30 613.03 | 4.91 | -0.751 |
| | Achn333501 | Chr23:7988531-7989163 | 210 | 23 053.82 | 8.72 | -0.671 |
| | Achn157191 | Chr12:1565071-1565691 | 206 | 22 247.03 | 8.40 | -0.442 |
| | Achn362941 | Chr18:3360584-3361285 | 233 | 25 570.85 | 9.43 | -0.497 |
| | Achn009241 | Chr17:12919428-12935295 | 505 | 55 744.05 | 8.20 | -0.400 |
| | Achn133991 | Chr19:4659632-4660273 | 213 | 23 151.94 | 9.71 | -0.488 |
| | Achn163591 | Chr23:8406580-8407227 | 215 | 23 113.92 | 9.79 | -0.493 |
| | Achn057971 | Unknow:132830585-132831490 | 301 | 33 483.44 | 5.94 | -0.843 |
| | Achn185681 | Chr3:20166345-20167313 | 322 | 35 505.83 | 5.73 | -0.798 |
| | Achn082591 | Chr24:2344769-2345764 | 331 | 36 370.49 | 5.32 | -0.880 |
| ERF-B2 | Achn161361 | Chr4:6237722-6238138 | 138 | 15 521.36 | 5.69 | -0.512 |
| | Achn390081 | Chr13:14725292-14726269 | 313 | 34 750.94 | 6.32 | -0.583 |
| | Achn041981 | Unknow:127095666-127096622 | 318 | 35 065.10 | 6.96 | -0.599 |
| | Achn164421 | Chr11:14958412-14960586 | 378 | 42 517.95 | 5.00 | -0.876 |
| | Achn330401 | Chr16:10565608-10567785 | 364 | 40 801.34 | 5.01 | -0.754 |
| | Achn198481 | Chr19:10849723-10854569 | 489 | 54 669.70 | 4.91 | -0.606 |
| | Achn226291 | Chr23:377312-379543 | 382 | 42 810.22 | 5.26 | -0.841 |
| | Achn318101 | Unknow:84837842-84838763 | 278 | 31 099.55 | 5.54 | -0.782 |
| | Achn064481 | Chr17:1204516-1205444 | 295 | 33 678.03 | 6.27 | -0.700 |
| | Achn024671 | Chr23:20319426-20320353 | 291 | 32 756.64 | 5.25 | -0.714 |

表1（续）　Table 1（continued）

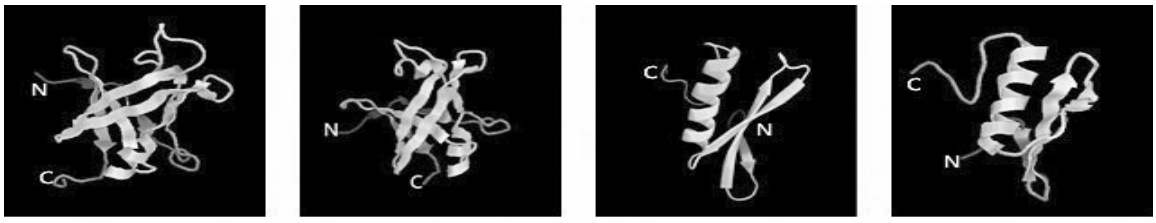
| 亚族 Subfamily | 编号 Numbering | 染色体:位置 Chromosome: Location | 蛋白长度 Protien length/aa | 分子质量 Molecular mass/ku | 等电点 Isoelectric point | 总平均亲水性 GRAVY |
|---|---|---|---|---|---|---|
| ERF-B3 | Achn359661 | Chr23:18417901-18418551 | 216 | 24 266.13 | 5.20 | -0.599 |
| | Achn352361 | Chr13:9414811-9415461 | 216 | 24 483.41 | 5.30 | -0.632 |
| | Achn334501 | Chr3:16517637-16518305 | 222 | 24 907.69 | 4.98 | -0.622 |
| | Achn193721 | Chr24:4768721-4769242 | 173 | 19 351.90 | 8.56 | -0.525 |
| | Achn035221 | Unknow:124384438-124385073 | 211 | 23 512.33 | 4.66 | -0.400 |
| | Achn224551 | Chr7:8142204-8142554 | 116 | 13 875.90 | 10.79 | -0.924 |
| | Achn269421 | Chr5:14150055-14154979 | 210 | 24 090.73 | 9.39 | -0.689 |
| | Achn269431 | Chr5:14143793-14144335 | 180 | 20 484.23 | 9.16 | -0.806 |
| | Achn224541 | Chr7:8153986-8154585 | 199 | 22 581.68 | 7.70 | -0.625 |
| | Achn219261 | Chr15:16037719-16038162 | 147 | 16 426.55 | 8.79 | -0.493 |
| | Achn181421 | Chr8:2592636-2593046 | 136 | 15 041.98 | 9.39 | -0.367 |
| | Achn033321 | Unknow:121489446-121490030 | 194 | 21 539.69 | 9.27 | -0.927 |
| | Achn331661 | Chr14:8965550-8971035 | 246 | 26 664.03 | 5.19 | -0.343 |
| | Achn141501 | Chr25:11645846-11646532 | 186 | 2 911.83 | 10.83 | -0.745 |
| | Achn062471 | Chr3:10509804-10513429 | 262 | 28 950.54 | 6.36 | -0.531 |
| | Achn250931 | Chr2:1993278-1994123 | 281 | 31 156.11 | 6.34 | -0.496 |
| | Achn140591 | Chr3:2809629-2810483 | 284 | 31 656.84 | 6.55 | -0.527 |
| | Achn033621 | Chr26:2137890-2138555 | 221 | 25 522.46 | 4.55 | -0.570 |
| | Achn249781 | Chr2:1979264-1979899 | 211 | 23 121.33 | 4.52 | -0.525 |
| | Achn140391 | Chr3:2820583-2821254 | 223 | 24 600.32 | 4.64 | -0.403 |
| | Achn142001 | Chr28:10850818-10852724 | 181 | 20 754.36 | 8.87 | -0.915 |
| | Achn334631 | Chr3:16540378-16540818 | 146 | 16 793.67 | 5.43 | -1.165 |
| | Achn246791 | Chr22:1511298-1511741 | 147 | 17 064.98 | 6.12 | -1.043 |
| | Achn334481 | Chr3:16546399-16550060 | 190 | 21 405.10 | 9.60 | -0.847 |
| | Achn193711 | Chr24:4743505-4743930 | 141 | 15 944.71 | 7.87 | -1.014 |
| | Achn319471 | Chr24:13590051-13591043 | 330 | 36 262.94 | 5.69 | -0.408 |
| | Achn063061 | Chr3:10501030-10502326 | 298 | 33 539.78 | 9.32 | -0.707 |
| | Achn331581 | Chr14:8926189-8927058 | 289 | 32 873.88 | 8.24 | -0.648 |
| | Achn331571 | Chr14:8931108-8932130 | 340 | 38 100.63 | 5.70 | -0.454 |
| | Achn331561 | Chr14:8944863-8961934 | 516 | 58 618.92 | 5.93 | -0.497 |
| | Achn141871 | Chr25:11653723-11658729 | 385 | 43 132.03 | 7.11 | -0.428 |
| | Achn001311 | Chr15:5848178-5849095 | 305 | 33 753.91 | 5.11 | -0.485 |
| ERF-B4 | Achn227931 | Chr15:5117009-5125763 | 219 | 25 477.02 | 9.84 | -0.916 |
| | Achn364871 | Unknow:101474039-101476903 | 278 | 31 086.50 | 5.92 | -0.839 |
| | Achn169731 | Chr6:184584-204184 | 1066 | 118 923.33 | 5.85 | -0.690 |
| | Achn290601 | Chr21:7514844-7524912 | 478 | 52 735.27 | 8.39 | -0.736 |
| ERF-B5 | Achn331531 | Chr25:10001915-10002823 | 302 | 33 440.31 | 6.12 | -0.583 |
| | Achn188871 | Chr14:10993756-11003439 | 387 | 43 152.03 | 5.48 | -0.621 |
| | Achn305371 | Chr3:1407555-1408556 | 333 | 36 937.45 | 5.37 | -0.582 |
| | Achn303171 | Chr28:8033161-8044976 | 345 | 38 628.50 | 6.92 | -0.583 |
| | Achn191231 | Chr23:16553547-16559852 | 317 | 36 354.95 | 8.40 | -0.740 |
| | Achn250311 | Chr2:997581-998630 | 349 | 38 822.51 | 5.44 | -0.585 |
| | Achn052461 | Chr18:9479346-9480371 | 341 | 38 053.31 | 5.11 | -0.659 |
| | Achn011941 | Chr18:6645247-6651989 | 339 | 37 516.14 | 5.40 | -0.548 |
| | Achn314121 | Chr15:3674682-3675353 | 201 | 22 665.14 | 5.41 | -0.756 |
| | Achn015761 | Chr22:9608689-9609522 | 277 | 31 517.50 | 6.21 | -0.703 |
| | Achn190661 | Chr22:8206869-8207702 | 277 | 31 517.50 | 6.21 | -0.703 |
| | Achn077251 | Chr24:7084637-7085470 | 277 | 31 708.66 | 6.68 | -0.768 |
| | Achn300601 | Chr8:7805845-7806561 | 238 | 27 216.57 | 5.24 | -0.540 |
| | Achn275891 | Chr11:16521063-16521809 | 248 | 27 894.55 | 6.18 | -0.497 |
| | Achn045361 | Chr3:7512849-7516034 | 402 | 45 276.44 | 5.33 | -0.714 |
| ERF-B6 | Achn309591 | Chr16:8189771-8190511 | 246 | 27 095.18 | 10.25 | -0.389 |
| | Achn344311 | Unknow:94551212-94553604 | 239 | 26 739.37 | 8.84 | -0.477 |
| | Achn229091 | Chr5:5938553-5939743 | 396 | 44 142.57 | 4.42 | -0.668 |
| | Achn177531 | Chr25:9372180-9378545 | 428 | 47 680.97 | 6.70 | -0.639 |
| | Achn375561 | Chr13:10444568-10445380 | 270 | 29 450.71 | 8.52 | -0.529 |
| | Achn239411 | Chr26:15773497-15791195 | 1303 | 145 591.17 | 5.16 | -0.206 |
| | Achn352951 | Chr13:9927338-9928150 | 270 | 29 450.71 | 8.52 | -0.529 |
| | Achn160641 | Chr20:1608044-1610869 | 178 | 19 867.58 | 6.38 | -0.540 |
| | Achn112911 | Chr16:8554581-8558578 | 210 | 23 358.67 | 7.57 | -0.490 |
| | Achn310181 | Chr16:8535361-8540715 | 169 | 18 651.45 | 7.57 | -0.400 |

表1(续) Table 1(continued)

| 亚族 Subfamily | 编号 Numbering | 染色体:位置 Chromosome: Location | 蛋白长度 Protien length/aa | 分子质量 Molecular mass/ku | 等电点 Isoelectric point | 总平均亲水性 GRAVY |
|---|---|---|---|---|---|---|
| | Achn377531 | Unknow:105421333-105422523 | 396 | 44 019.35 | 4.5 | -0.700 |
| | Achn366301 | Chr16:5111935-5114876 | 343 | 38 179.76 | 6.04 | -0.518 |
| | Achn350331 | Chr13:13062338-13075054 | 448 | 49 924.48 | 7.59 | -0.421 |
| | Achn356191 | Chr29:6735891-6736163 | 90 | 10 182.54 | 9.84 | -0.578 |
| | Achn310981 | Unknow:16102542-16103471 | 309 | 34 566.59 | 4.67 | -0.739 |
| | Achn374131 | Chr25:6979801-6980724 | 307 | 34 671.43 | 4.68 | -0.842 |
| | Achn311001 | Unknow:16086077-16086958 | 293 | 32 480.54 | 5.73 | -0.716 |
| | Achn160631 | Chr20:1604737-1606964 | 171 | 18 956.59 | 6.36 | -0.440 |
| | Achn310001 | Chr16:8151201-8151778 | 159 | 18 121.32 | 8.37 | -0.772 |
| | Achn329031 | Chr26:6729304-6729880 | 163 | 18 629.96 | 8.69 | -0.715 |
| | Achn065561 | Unknow:26260032-26261256 | 186 | 21 053.00 | 8.68 | -0.630 |
| | Achn065941 | Unknow:26732738-26735377 | 140 | 15 717.04 | 6.51 | -0.387 |
| | Achn187281 | Chr25:14003284-14004218 | 169 | 18 752.31 | 7.74 | -0.562 |
| | Achn134411 | Chr11:9912189-9913100 | 164 | 18 374.93 | 8.82 | -0.553 |
| | Achn134421 | Chr11:9908206-9909034 | 164 | 18456.03 | 8.45 | -0.593 |
| | Achn106561 | Chr13:16582329-16583249 | 306 | 33 864.69 | 4.84 | -0.725 |
| | Achn245111 | Chr3:15705906-15707003 | 365 | 40 687.33 | 4.62 | -0.625 |
| DREB-A1 | Achn317211 | Chr14:10433754-10434461 | 235 | 26 250.23 | 5.80 | -0.601 |
| | Achn317221 | Chr14:10407771-10419345 | 451 | 50 740.09 | 5.26 | -0.501 |
| | Achn317201 | Chr14:10441240-10442576 | 281 | 31 096.94 | 6.25 | -0.418 |
| | Achn317191 | Chr14:10446395-10447609 | 261 | 29 182.51 | 5.58 | -0.607 |
| | Achn076481 | Chr18:14545440-14546153 | 237 | 26 030.98 | 5.25 | -0.433 |
| | Achn317171 | Chr14:10457348-10464229 | 155 | 17 307.63 | 9.35 | -0.562 |
| | Achn233741 | Chr24:14669913-14670611 | 232 | 25 064.98 | 5.56 | -0.506 |
| DREB-A2 | Achn037111 | Chr2:2509448-2513521 | 357 | 39 396.83 | 5.39 | -0.795 |
| | Achn054961 | Chr3:1736768-1737796 | 342 | 37 286.27 | 5.25 | -0.799 |
| | Achn077031 | Chr24:6357615-6358181 | 188 | 20 569.88 | 4.81 | -0.602 |
| | Achn049251 | Chr4:10833478-10833954 | 158 | 17 358.32 | 4.63 | -0.421 |
| | Achn230341 | Chr21:12427818-12428414 | 198 | 21 553.33 | 5.67 | -0.458 |
| | Achn025751 | Chr11:814588-816466 | 301 | 33 108.47 | 8.36 | -0.491 |
| DREB-A3 | Achn055051 | Chr3:1865926-1866684 | 252 | 27 161.07 | 6.04 | -0.338 |
| | Achn037211 | Chr2:2649779-2655033 | 290 | 31 180.45 | 8.80 | -0.499 |
| DREB-A4 | Achn200581 | Chr28:11528522-11529538 | 338 | 37 747.96 | 8.66 | -0.392 |
| | Achn005091 | Chr23:9696360- 9697103 | 247 | 27 480.10 | 8.71 | -0.606 |
| | Achn305641 | Chr19:2258250-2259032 | 260 | 28 922.90 | 9.40 | -0.505 |
| | Achn044861 | Chr15:10538627-10539259 | 210 | 22 862.23 | 4.78 | -0.501 |
| | Achn149081 | Chr8:19943540-19944166 | 208 | 22 442.87 | 5.06 | -0.394 |
| | Achn075201 | Chr12:4686149-4686745 | 198 | 20 394.49 | 5.02 | -0.320 |
| | Achn091741 | Chr20:6190959-6191537 | 192 | 20 205.36 | 5.34 | -0.404 |
| | Achn157941 | Chr3:595364-596119 | 251 | 26 736.65 | 4.95 | -0.561 |
| | Achn317161 | Chr14:10472411-10473037 | 208 | 22 309.15 | 5.30 | -0.430 |
| | Achn002521 | Chr15:6802852-6803673 | 207 | 21 792.74 | 7.69 | -0.404 |
| | Achn132541 | Chr25:10692250-10713472 | 461 | 50 517.85 | 7.02 | -0.342 |
| | Achn104551 | Chr8:20548952-20549499 | 165 | 18 192.42 | 5.03 | -0.512 |
| | Achn131671 | Unknow:1883111-1883527 | 138 | 15 519.32 | 9.12 | -0.995 |
| | Achn073021 | Chr3:10367125-10367649 | 174 | 19 052.35 | 5.15 | -0.245 |
| | Achn327741 | Chr1:13455957-13456529 | 190 | 20 527.01 | 5.34 | -0.229 |
| | Achn319581 | Chr24:13768090-13768680 | 196 | 21 070.50 | 5.06 | -0.257 |
| | Achn099771 | Unknow:29071905-29072809 | 258 | 28 559.83 | 5.29 | -0.526 |
| | Achn205631 | Chr14:9106706-9107359 | 217 | 23 761.52 | 5.48 | -0.495 |
| | Achn027091 | Chr14:3214326-3214706 | 126 | 14 074.87 | 9.80 | -0.855 |
| | Achn153231 | Chr7:5232469-5233188 | 239 | 26 582.50 | 8.49 | -0.741 |
| | Achn225571 | Unknow:7356808-7359115 | 224 | 24 913.60 | 8.62 | -0.871 |
| | Achn238481 | Unknow:52996111-52996902 | 263 | 28 834.58 | 7.71 | -0.868 |
| | Achn049811 | Chr11:13230053-13230682 | 209 | 22 974.53 | 4.96 | -0.492 |
| | Achn216471 | Chr16:9234327-9235381 | 215 | 23 759.53 | 5.78 | -0.581 |
| | Achn297481 | Chr25:13329282-13329911 | 209 | 22 945.72 | 5.05 | -0.491 |
| | Achn355461 | Unknow:95500473-95501096 | 207 | 22 550.12 | 4.84 | -0.507 |
| | Achn007081 | Unknow:112337298-112338038 | 246 | 26 285.15 | 4.79 | -0.382 |
| | Achn312401 | Unknow:40382126-40382800 | 224 | 24 989.79 | 5.73 | -0.701 |
| | Achn069471 | Chr12:10973118-10973822 | 234 | 25 255.82 | 5.15 | -0.453 |
| | Achn146171 | Unknow:37825689-37826402 | 237 | 25 469.99 | 5.26 | -0.436 |
| | Achn205451 | Chr11:10186610-10187155 | 181 | 19 990.46 | 5.01 | -0.402 |

表1（续）　Table 1（continued）

| 亚族 Subfamily | 编号 Numbering | 染色体:位置 Chromosome: Location | 蛋白长度 Protien length/aa | 分子质量 Molecular mass/ku | 等电点 Isoelectric point | 总平均亲水性 GRAVY |
|---|---|---|---|---|---|---|
| DREB-A5 | Achn013101 | Chr9:2716599-2717030 | 143 | 16 111.92 | 5.95 | -1.010 |
| | Achn285481 | Chr1:8098347-8098778 | 143 | 16 212.04 | 6.63 | -1.106 |
| | Achn136171 | Chr1:15402234-15408344 | 236 | 26 325.85 | 6.99 | -0.531 |
| | Achn363841 | Chr5:2021349-2025666 | 205 | 22 601.88 | 9.59 | -0.413 |
| | Achn159401 | Chr4:9266540-9266908 | 122 | 13 517.88 | 5.39 | -0.825 |
| | Achn299651 | Chr21:10263060-10263524 | 154 | 17 075.88 | 8.93 | -0.990 |
| | Achn167681 | Chr12:12612719-12613737 | 297 | 32 842.79 | 9.39 | -0.561 |
| | Achn240471 | Unknow:61341510-61350073 | 324 | 35 703.75 | 6.60 | -0.465 |
| | Achn243111 | Chr4:2210966-2214988 | 273 | 30 012.67 | 9.36 | -0.543 |
| | Achn023091 | Chr1:3332530-3333003 | 157 | 17 702.69 | 6.97 | -0.768 |
| | Achn117281 | Chr21:4877586-4878128 | 180 | 19 249.27 | 9.48 | -0.559 |
| | Achn305041 | Unknow:79431333-79431911 | 192 | 21 373.09 | 5.75 | -0.358 |
| | Achn204851 | Chr4:623579-624070 | 163 | 18 099.19 | 7.84 | -0.605 |
| | Achn371851 | Chr21:3717321-3717812 | 163 | 18 077.08 | 5.91 | -0.666 |
| | Achn023491 | Chr1:4011199-4017439 | 244 | 27 789.42 | 5.86 | -0.582 |
| | Achn302861 | Unknow:79666380-79667000 | 206 | 23 266.13 | 5.52 | -0.582 |
| | Achn271311 | Chr26:7428255-7442061 | 692 | 77 054.11 | 6.43 | -0.334 |
| DREB-A6 | Achn087381 | Chr4:6624199-6625245 | 348 | 37 653.04 | 6.17 | -0.524 |
| | Achn266591 | Chr21:8202747-8203787 | 346 | 37 721.22 | 6.83 | -0.536 |
| | Achn253771 | Chr8:15039837-15044601 | 438 | 48 866.35 | 9.13 | -0.563 |
| | Achn189151 | Chr14:10788356-10789231 | 291 | 32 176.24 | 8.49 | -0.520 |




拟南芥RAV *Arabidopsis* RAV　　猕猴桃RAV Kiwifruit RAV　　拟南芥AP2/EREBP *Arabidopsis* AP2/EREBP　　猕猴桃AP2/EREBP Kiwifruit AP2/EREBP

**图4　拟南芥和猕猴桃AP2/EREBP蛋白三级结构**

**Fig. 4　The tertiary structure of AP2/EREBP protein in *Arabidopsis* and kiwifruit**

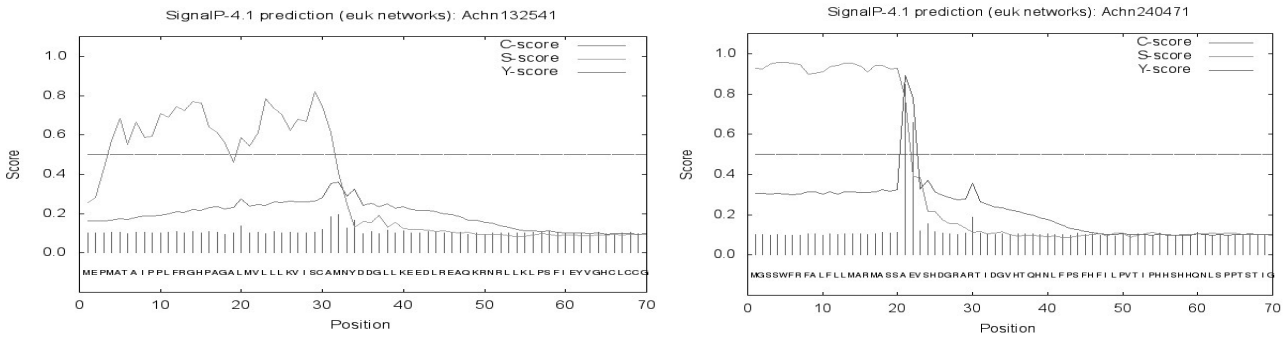



**图5　猕猴桃AP2/EREBP家族转录因子信号肽预测**

**Fig. 5　Signal peptide prediction of AP2/EREBP family transcription factors in kiwifruit**

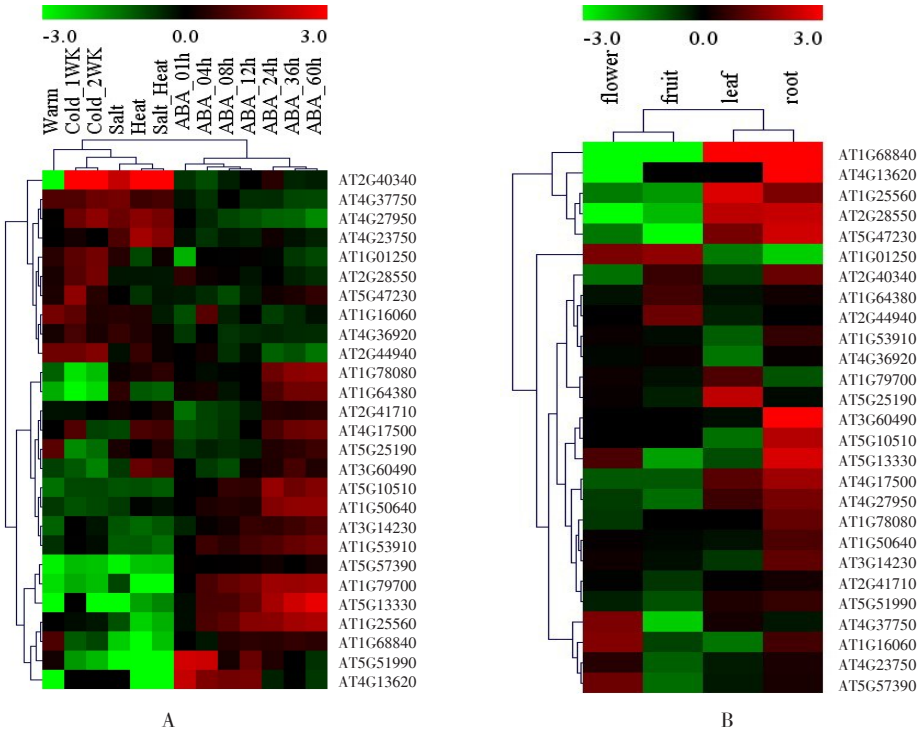
Achn132541和Achn240471存在信号肽，其余蛋白不存在信号肽，属于非分泌型蛋白。

### 2.7　‘红阳’猕猴桃AP2/EREBP转录因子家族表达模式分析

用猕猴桃204条AP2/EREBP蛋白序列Blast同源搜索拟南芥全基因组序列，去冗余后共获得27个同源拟南芥基因，并进行表达模式分析，其中GSE80565、GSE67332、GSE72806中的RNA-seq数据分别为脱落酸（ABA）、不同程度的冰冻耐受性和盐、热胁迫下的表达数据，结果（图6-A）显示，在

ABA处理后，AP2/EREBP家族基因表达明显上调，保持较高表达量，并且在对冰冻耐受性和盐热胁迫表达中，该家族基因也明显表现出上调趋势，从这些数据和对表达谱的分析情况来看，AP2/EREBP家族基因响应非生物胁迫，对低温、干旱高盐和其他环境胁迫都有一定的调控作用。

植物根系是作为吸收养分和营养物质以及激素的一个主要器官，能够很快适应周围环境的变化，植物叶片也是适应外界逆境和吸收营养物质的重要器官。从AP2/EREBP家族基因在植物不同组织中的表达情况分析（图6-B）来看，该家族基因在植物的根系和叶中的表达量较高，说明AP2/EREBP家族基




A. 同源拟南芥基因分别在冷热处理、盐处理和 10 μmol·L$^{-1}$ ABA 处理中的表达谱；B. 同源拟南芥基因分别在植物花、果实、叶和根部中的表达谱。ABA_01h、ABA_04h、ABA_08h、ABA_12h、ABA_24h、ABA_36h、ABA_60h. ABA 处理 0、4、8、12、24、36、60 h；Warm. 温暖处理；Cold_1WK、Cold_2WK. 冷处理 1、2 周；Salt. 盐处理；Heat. 热激处理。flower. 花；fruit. 果实；leaf. 叶；root. 根。图中用绿、黑、红三色代表基因表达水平。绿色越亮表达越弱，红色越亮表达越强。

A. The expression profiles of homologous *Arabidopsis* genes under the treatment of warm, cold, salt and 10 μmol·L$^{-1}$ ABA. B. The expression profiles of homologous *Arabidopsis* genes in plant flowers, fruits, leaves and roots, respectively. ABA_01h, ABA_04h, ABA_08h, ABA_12h, ABA_24h, ABA_36h, ABA_60h. ABA 处理 0, 4, 8, 12, 24, 36, 60 h; Warm. Warm treatment; Cold_1WK, Cold_2WK. Cold treatment 1 week and 2 week; Salt. Salt treatment; Heat. Heat treatment. The gene expression level is displayed with green, black, red scheme in the picture. The brighter the green, the weaker the expression; the brighter the red, the stronger the expression.

**图 6 猕猴桃 AP2/EREBP 转录因子同源拟南芥基因表达谱**

**Fig. 6 Expression profile of AP2/EREBP transcription factor homologous to *Arabidopsis* gene in kiwifruit**

因对调节植物抗逆性有一定作用。

## 3 讨 论

转录因子能特异性地结合启动子区的顺式作用元件，调控植物下游逆境应答基因的表达，因而转录因子在植物受外界环境胁迫时所发挥的关键作用备受关注。AP2/EREBP转录因子在植物生长、发育和胁迫应答等过程中发挥重要作用。RAV亚族转录因子与植物对信号的传导过程有关[26]，AP2亚族转录因子有调控花、种子和胚珠发育的功能，EREBP亚族转录因子有调节植物对激素、病原和胁迫应答反应等功能[27]。AP2结构域可以直接与DRE/CRT元件或者GCC-box结合，而这些元件常存在于编码病原和胁迫等相关基因的启动子区域。ERF类蛋白能特异性地结合GCC-box顺式作用元件，DREB类蛋白特异地与DRE/CRT元件结合，在植物生长、发育和胁迫应答等过程中发挥重要作用。目前，关于AP2/EREBP转录因子的研究在很多植物上均得

到开展，且获得了很多新的发现和研究成果。因此，随着猕猴桃全基因组测序的完成[24]，开展AP2/EREBP家族转录因子的研究，可进一步给猕猴桃AP2/EREBP转录因子结构、表达调控网络和相互作用研究奠定基础，有助于构建和完善AP2/EREBP转录因子在生物和非生物胁迫中的信号调节途径。

通过对猕猴桃全基因组数据的检索与筛选，本文共鉴定出204个猕猴桃AP2/EREBP转录因子家族成员，同时与拟南芥AP2/EREBP转录因子家族聚类分析，初步划分为AP2、RAV、ERF和DREB 4个亚家族，与拟南芥全基因组进行比对，进一步将ERF亚家族分为B1~B6亚组，DREB亚家族分为A1~A6亚组，分别对其理化性质、结构域、染色体分布和保守元件分布等多种生物信息学进行分析，表明这些基因在进化过程中比较保守，且普遍含有一个AP2保守结构域，将为后续RNA研究验证功能提供靶序列；猕猴桃AP2/EREBP家族在染色体上分布不均匀，在Chr14上存在串联复制现象，这与响应生物及非生物胁迫的相关基因扩增有密切的关系[28]。此外，发现Chr10上没有分布该家族基因，而拟南芥AP2/EREBP基因则在5条染色体上均有分布，表明‘红阳’猕猴桃基因组在长期进化过程中，由于面对一定的选择压力，可能造成Chr10上AP2/EREBP家族基因的丢失；与此同时，发现29条序列无法定位到已知染色体上，可能是‘红阳’猕猴桃全基因组组装不尽完善，导致这29条序列无法组装在猕猴桃29条染色体上，它们可能分布在其他任何一条染色体上；猕猴桃AP2/EREBP转录因子还含有其他保守结构域，说明猕猴桃AP2/EREBP转录因子可能具有更加广泛的生物学功能；‘红阳’猕猴桃204条蛋白只有2条具有信号肽，信号肽具有蛋白质定向转运功能和其他生理功能。基于Walter、Blobel和Gilmore等[29-30]提出的‘信号假说’，建议重点关注这2条蛋白的功能。同时，这些基因含有3个保守元件，与拟南芥AP2/EREBP转录因子家族结构、特征和系谱进化等基本相似，推测该家族转录因子功能和拟南芥相似。在对猕猴桃AP2/EREBP转录因子家族的同源拟南芥表达谱研究中，发现AP2/EREBP基因家族对非生物胁迫具有一定的调控作用，特别是在低温、高温、高盐和ABA等胁迫下，表达尤为明显。Shen等[31]从经高盐浓度处理的盐生植物山菠菜（*Atriples hortensis*）中分离得到编码AP2/EREBP类蛋白的基因AhDREB1，转入烟草中，结果AhDREB1在烟草中的超表达明显地提高烟草的耐盐性；刘强等[32]将从拟南芥分离得到的DREB1A基因导入植株，由于DREB1A的超表达，植株对干旱及低温的耐性大大增强。说明AP2/EREBP转录因子在植物抵抗非生物胁迫过程中发挥重要作用[33-35]。在拟南芥不同植物组织的表达谱中，发现AP2/EREBP转录因子在根叶中大量表达，在花和果中表达水平较低，说明AP2/EREBP参与了植物生长发育的调节[13-18]，且不同亚族基因在不同组织中的表达量也有差别。如Shen等[36]在对拟南芥和山菠菜的研究中发现，正常生长条件下，AtDREB2A和AhDREB1在根、茎和叶中均有表达，而在盐胁迫下，AhDREB1在根组织中大量表达，但在茎和叶中的表达量低；西府海棠（*Malus micromalus* Makino）MrDREB6在叶中的表达量最高，其次是种子，而在茎中的表达量最少[37]。说明植物间不同的抗性机制影响不同的植物组织表达，也可能与植物的进化历程和对环境的适应性有关。但由于拟南芥和猕猴桃种属之间差异较大，建议根据同源表达结果挑选最具有显著性的序列进行克隆和表达，并导入拟南芥进行试验验证。

通过这些研究分析，为进一步了解猕猴桃AP2/EREBP家族成员间结构与功能的关系以及该转录因子在猕猴桃生长发育及胁迫应答中的功能研究奠定了一定的理论基础。随着分子生物学的发展，运用GEO和RNA-Seq等表达数据库和生物信息学等方法进行全基因组分析，有助于推动转录因子间互作网络及信号传导网络的研究与发展。

## 4　结　论

利用生物信息学方法获得204条猕猴桃AP2/EREBP家族转录因子，并与拟南芥AP2/EREBP转录因子进行系谱进化、结构域、基因定位和同源表达等分析，表明猕猴桃AP2/EREBP转录因子在进化过程中比较保守，参与植物发育和胁迫应答调控，这可为今后利用基因工程探索AP2/EREBP转录因子功能奠定基础。

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