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GENOMIC LEVEL IDENTIFICATION OF AUXIN RESPONSE FACTOR GENE FAMILY IN *GNETUM LUOFUENSE* C. Y. CHENG

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Abstract

In the auxin-mediated growth and development process of plants, auxin response factors (ARFs) act as an important component. ARF has so far been identified and characterized in a number of vascular plant species. *Gnetum* L. is a gymnosperm genus with dietary, industrial and medicinal uses, but little is known about its ARF genes. A comprehensive identification and characterization of ARF gene family in *Gnetum luofuense* C.Y. Cheng genome was performed. Twenty ARF genes were identified and categorized into two groups. Conserved motif analysis suggested that most proteins were in accordance with the typical ARF structural model. Additionally, the gene duplication analysis indicated the expanding state of *Gnetum* ARF gene family in the process of evolution, and some Coniferales species lost many ARF members recently. This study provides comprehensive understanding of *Gnetum* ARF gene family, and laid the theoretical foundation for further functional verification.

Introduction

Auxin response factor (ARF) protein is a key regulator of plant hormone gene expression (Tiwari 2003, Guilfoyle and Hagen 2007). In flowering plants, ARFs bind with specificity to TGTCTC auxin response elements (AuxRE) and function in combination with Aux/IAA (auxin/indole acetic acid) repressors (Guilfoyle and Hagen 2007). There is a growing interest of research about ARF family, and its regulation mechanisms in plant growth have been revealed. Members of the ARFs family have specific conserved domains to display their functions, most of them contained an amino-terminal DNA-binding domain (DBD) which acts as activation/ repression domain (Guilfoyle and Hagen 2007, Tiwari 2003). The rice (Yu *et al*. 2002) and *Arabidopsis* Heynh. in Holl & Heynh. (Cokus *et al*. 2008) genome sequencing provide the basis for the ARF family study in dicotyledons and monocotyledons. There are 22 members distributed on all the chromosomes, among them 1st chromosomes have the largest number, and most ARF members come from recent gene duplication events (Remington 2004). There are 25 ARF members distributed on 10 chromosomes of rice (Wang *et al*. 2007). And a large number of experiments show that ARF genes in *Arabidopsis* and rice are usually transcribed in a variety of tissues and organs. However, there is an exception that the expression of ARF gene cluster in *Arabidopsis* 1th chromosome seems to be limited to embryogenesis/seed development (Ulmasov *et al*. 1999, Okushima 2005).

Gene expression patterns of ARF members have also been studied, ARF1 in *Arabidopsis* expressed specifically during inflorescence development (Hardtke 2004). However, ARF2 is expressed in flower organs and regulated the light/dark growth of seedlings (Hardtke 2004, Schruff 2006), ARF5, ARF7, ARF8 and ARF12 expressed in embryo, seed and other tissues, respectively (Remington 2004, Okushima 2005, Ellis *et al*. 2005). At present, many studies

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showed that the most important role of ARF gene family was to regulate plant growth and development. For example, in seed germination it regulates the size of seeds and organization formation in embryo and so on (Sessions *et al.* 1997, Hardtke 1998, Hardtke 2004).

As a unique group in gymnosperm, *Gnetum* L. makes a key link involved in the angiosperm evolution because of its angiospermic characteristics, which has a long-standing controversial phylogenetic position (Ickertbond and Wojciechowski 2014, Wickett *et al.* 2014, Deng *et al.* 2019). *Gnetum* is considered to be an important economic crop for improving backward and malnourished areas in Africa due to its grain, oil and medicinal functions (Ali *et al.* 2011, Moise *et al*. 2012). In addition to their striking evolutionary divergence, many species of *Gnetum* are rich in bioactive compounds such as flavonoids, stilbenoids, alkaloids and volatile oils, providing medicinal and health benefits (Deng *et al*. 2016, 2017, 2019, Parage *et al*. 2012).

At present, there is a lack of research on the identification of the transcription factor family in a genome wide scale. As a family with a large number of members in plants and widely reported in other plants, the ARF family of *Gnetum* has not been identified and reported. In the present research, the ARF transcription factor family at the genomic level based on the published genomic information was identified. The structure and evolutionary pattern of ARF family were investigated to lay a foundation for further exploration of the ARF function and the molecular mechanism of the development in *Gnetum.*

Materials and Methods

Representative species of different plant groups were selected according to their evolutionary link including ginkgo, pine, moss and fern. These species were *Ephedra przewalskii* Stapf, *Selaginella tamariscina* (P. Beauv.) Spring, *Amborella trichopoda* Baill. (Zuccolo *et al*. 2011), *Welwitschia mirabilis* Hook. f. (Wan *et al*. 2018), *Picea abies* (L.) H. Karst and *Ginkgo biloba* L. (Guan *et al*. 2016). The protein sequences of ARF family of conserved species were downloaded from the several resource database such as NCBI. ARF gene family of *Gnetum luofuense* C.Y. Cheng members named *GnARFs* were achieved by blast searches against *Arabidopsis* ARF proteins based on its genomic data. Next, the Pfam database was used to determine if each candidate ARF sequence was a member of the ARF gene family.

Complete protein sequences of *G. luofuense* ARFs were extracted and then multiple-sequence alignments done with ClusterW. They were used to construct the phylogenetic tree using MEGAx software by neighbor-joining (NJ) method with 1000 bootstrap replications. The model was p-distance, missing data processing method was pairwise deletion and other parameters were default values.

To examine the structural divergence among the *GnARFs*, the conserved motif was investigated in the encoded ARF proteins. Their complete amino acid sequences were subjected to MEME analysis online (http:// meme.nbcr.net/meme/cgi-bin/meme.cgi) with the following parameters: (1) optimum motif width was set from 6 - 50 and (2) the maximum number of motifs were set to identify eight motifs. To speculate the possible evolutionary patterns of ARF gene family in the amplification of the whole plant community, Notung (Chen *et al.* 2000) was used to perform large-scale analysis in seven plant species. The maximum number of ARF genes acquired and missing were estimated by coordinating each cluster/subclass in species.

Results and Discussion

In total, 20 ARF genes were identified from the *Gnetum luofuense* genome, and three functional domains were contained in GnARF proteins. At present, ARF have been identified and characterized in different species such as *Arabiopsis thaliana*, rice L. and *A. trichopoda* (Finet *et*

al. 2010), however, little detailed systematic investigation of the ARF family has been performed in gymnosperms, especially in Gnetales. In this study, the number of *GnARFs* was identified in *G. luofuense* genome, which is fewer members than *A. thaliana* (ARF number: 23), rice (ARF number: 25) (Wang *et al*. 2007) and *Zea mays* L. (ARF number: 35) (Liu *et al*. 2011a), while more than *Prunus persica* (L.) Batsch (ARF number: 19) (Li *et al*. 2015) and *Citrus sinensis* (L.) Osbeck (ARF number: 19) (Diao *et al*. 2020). The domains of *GnARF* family transcription factors consisted of N-terminal B3-like DNA binding domain (DBD) (PF02362.21), Auxin_resp (PF06507.13) and AUX_IAA (PF02309.16), a C-terminal dimerization domain (CTD) (Table 1).

The phylogenetic tree was constructed by all *GnARF* protein, indicating that the gene family could be divided into two subfamilies (Fig. 1A). A big difference existed in the lengths of *GnARF* genes, such as less than 1000 bp (TnS000445341t03) and close to 40000 bp (TnS000141003t01). It was noted that the exons number vary widely among family members, ranging from 1 - 14 and most of the family members (13) had UTR region, suggesting structural similarities within the two subfamilies (Fig. 1B). Results showed that the evolution of *G. luofuense* genes had contributed the expansion and contraction of exons subordinated *GnARF* genes and conserved gene structure existed in the same. The structure analysis of ARFs showed the difference in the gene length and number of exons, the phylogenetic tree suggested that the ARF gene family could be divided into two subfamilies with similar functional members. They might be formed in gene duplication by the analyses of ARF gene duplication and deletion. Among the conserved domains, 75 and 60% family members contained B3 and Auxin_resp domain, the structure diversity indicated that members may perform different functions in auxin signaling pathway to adapt the complex natural environment. The CTD structure had high similarity with III and IV domains in Aux/IAA gene family (Hagen and Guilfoyle 2002). It has therefore been hypothesized that Aux/IAA can regulate the activity of ARF protein (Guilfoyle and Hagen 2012, Korasick *et al*. 2015). Aux/IAA and ARF were both nucleoproteins, most ARF were located in nucleus, a few were localized in chloroplasts or mitochondria (Xia *et al*. 2019), which indicated ARF had other combination, such as auxin response gene with TGTCTC AuxREs element (Liu *et al.* 2011b).

In order to better understand the diversity and evolutionary relationship of ARF proteins in *Gnetum*, the conservative motif of *GnARFs* was analyzed (Fig. 2). Among the eight conserved motif, some conserved sequences were missing in several genes, such as motif 7 was missing in six genes, including TnS000522447t02, TnS000522447t03, TnS000997253t01, TnS000441-621t07, TnS000445341t03 and TnS000660247t01. Motifs 2, 3, 4, 5, 6 and 8 were mainly found in the first subfamily, while last three motifs existed in another group. Some motifs only existed in specific genes, suggesting that these motifs may contribute to the specific functions of these genes, whereas motifs that existed in all ARF family members were responsible for the basic function.

A phylogenetic tree was constructed to evaluate the possible differences on homologous and evolutionary relationships of ARF genes among different species comprising several representative terrestrial plant species, including *E. przewalskii*, *S. tamariscina*, *A. trichopoda*, *W. mirabilis*, *P. abies* and *Gi. biloba* (Fig. 3). The tree revealed that all ARFs among seven species were divided into three groups named Classes I, II and III containing 14, 20 and 21 members, respectively. Interestingly, the ARF genes of *Gnetum* and *Gi. biloba* were both present in Classes II while except *P. abies*, suggesting ARF genes in Pinaceae may be lost during evolution. This further implied different evolutionary histories of ARFs in different species. Conserved sequence analysis results showed common motif compositions in all ARF genes and different groups, suggesting the functional similarities by forming conserved domains through combination. The phylogenetic analysis indicated that there is a large number of paragenetic homologous genes in *Gnetum*. Furthermore, low support rate in phylogenetic tree indicated that insertion, deletion and

Table 1. ARF gene members and domain structure of *Gnetum*.

Gene	Start	End	HMM code	HMM name	HMM start	HMM end	HMM length	E value
TnS000522447t02	129	230	PF02362.21	B3	1	100	101	1.40E-21
TnS000522447t02	255	338	PF06507.13	Auxin_resp	1	83	83	4.20E-35
TnS000015975t02	113	214	PF02362.21	B3	1	100	101	6.00E-21
TnS000015975t02	239	322	PF06507.13	Auxin_resp	1	83	83	1.00E-33
TnS000015975t02	898	975	PF02309.16	AUX_IAA	138	234	237	5.10E-08
TnS000138797t02	127	228	PF02362.21	B3	1	100	101	8.50E-22
TnS000138797t02	253	336	PF06507.13	Auxin_resp	1	83	83	1.00E-33
TnS000138797t02	878	963	PF02309.16	AUX_IAA	123	228	237	8.20E-07
TnS000936593t02	125	226	PF02362.21	B3	1	100	101	4.20E-22
TnS000936593t02	251	334	PF06507.13	Auxin_resp	1	83	83	1.50E-33
TnS000936593t02	844	881	PF02309.16	AUX_IAA	192	229	237	2.10E-05
TnS000141003t01	163	264	PF02362.21	B3	1	100	101	1.20E-21
TnS000141003t01	289	371	PF06507.13	Auxin_resp	1	83	83	2.80E-36
TnS000811647t03	143	243	PF02362.21	B3	1	99	101	1.90E-20
TnS000811647t03	269	351	PF06507.13	Auxin_resp	1	83	83	4.50E-37
TnS000811647t03	682	808	PF02309.16	AUX_IAA	86	232	237	3.90E-12
TnS000426595t04	147	205	PF02362.21	B3	1	55	101	1.70E-07
TnS000426595t04	248	330	PF06507.13	Auxin_resp	1	83	83	5.20E-34
TnS000426595t04	773	864	PF02309.16	AUX_IAA	123	234	237	6.50E-08
TnS000006441t03	122	224	PF02362.21	B3	1	100	101	9.40E-21
TnS000006441t03	278	361	PF06507.13	Auxin_resp	1	83	83	3.80E-29
TnS000332527t09	403	504	PF02362.21	B3	1	100	101	2.20E-20
TnS000332527t09	561	644	PF06507.13	Auxin_resp	1	83	83	1.40E-29
TnS000060703t05	161	227	PF06507.13	Auxin_resp	18	83	83	4.40E-25
TnS000200419t01	32	99	PF02362.21	B3	1	64	101	5.40E-08
TnS000084833t11	9	91	PF06507.13	Auxin_resp	1	83	83	1.10E-36
TnS000084833t11	446	558	PF02309.16	AUX_IAA	115	237	237	3.30E-08
TnS000522447t03	129	230	PF02362.21	B3	1	100	101	2.50E-21
TnS000522447t03	255	338	PF06507.13	Auxin_resp	1	83	83	6.60E-35
TnS000820461t01	128	216	PF02362.21	B3	1	86	101	1.50E-27
TnS000867017t28	130	480	PF02309.16	AUX_IAA	1	233	237	4.30E-64
TnS000653177t04	37	199	PF02309.16	AUX_IAA	67	230	237	5.20E-50
TnS000441621t07	233	340	PF02362.21	B3	1	100	101	3.60E-28
TnS000445341t03	8	98	PF02362.21	B3	1	88	101	4.60E-28
TnS000053353t02	9	381	PF02309.16	AUX_IAA	1	237	237	1.90E-85
TnS000142615t19	83	443	PF02309.16	AUX_IAA	2	237	237	2.30E-79
TnS000997253t01	324	424	PF02362.21	B3	1	100	101	1.30E-16
TnS000498063t52	88	273	PF02309.16	AUX_IAA	46	237	237	7.00E-52
TnS000660247t01	337	408	PF02362.21	B3	1	69	101	5.30E-19

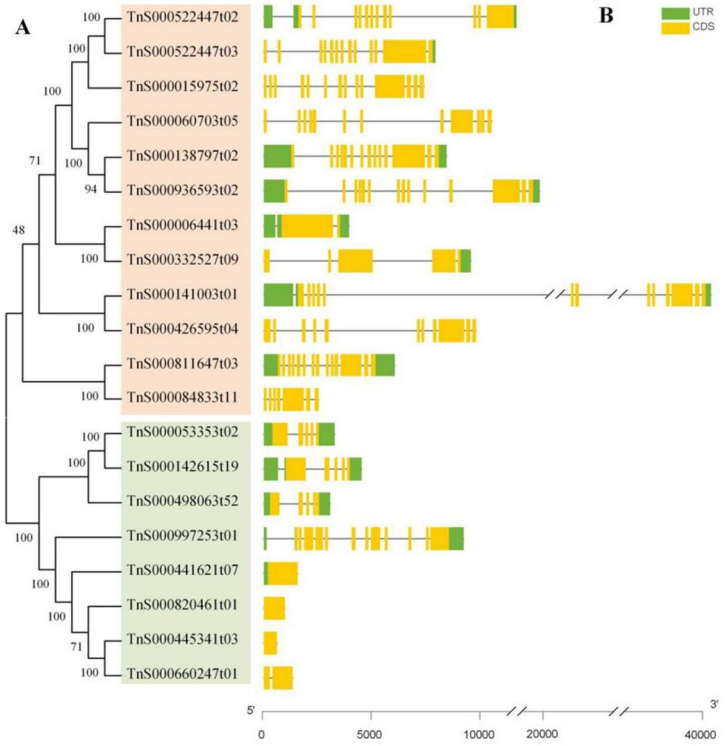

Fig. 1. Evolutionary analysis of ARF gene family of *Gnetum* (A) and gene structure (B).

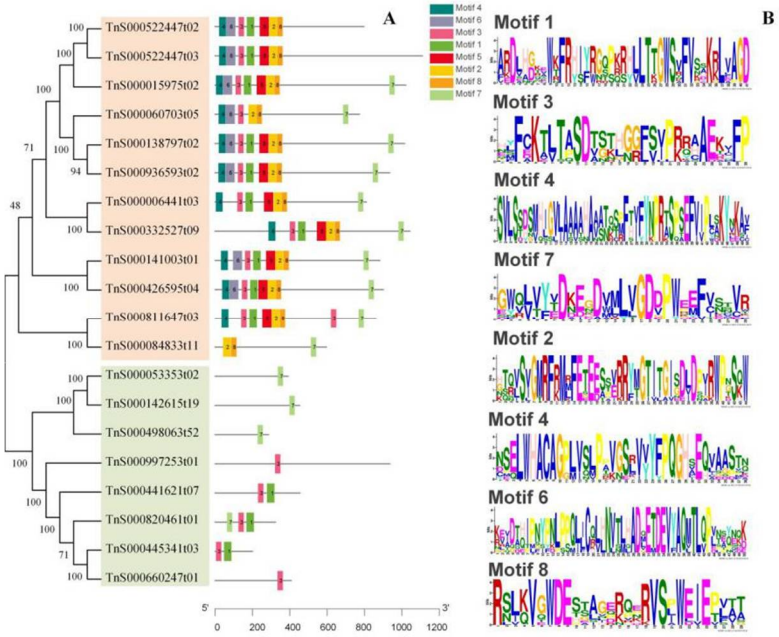

Fig. 2. Results of motif prediction (A) and sequence logo of motif (B) of *Gnetum* ARF gene.

other events occurred outside the conserved domain of ARF gene members in the replication process as other species (Morgenstern and Atchley 1999).

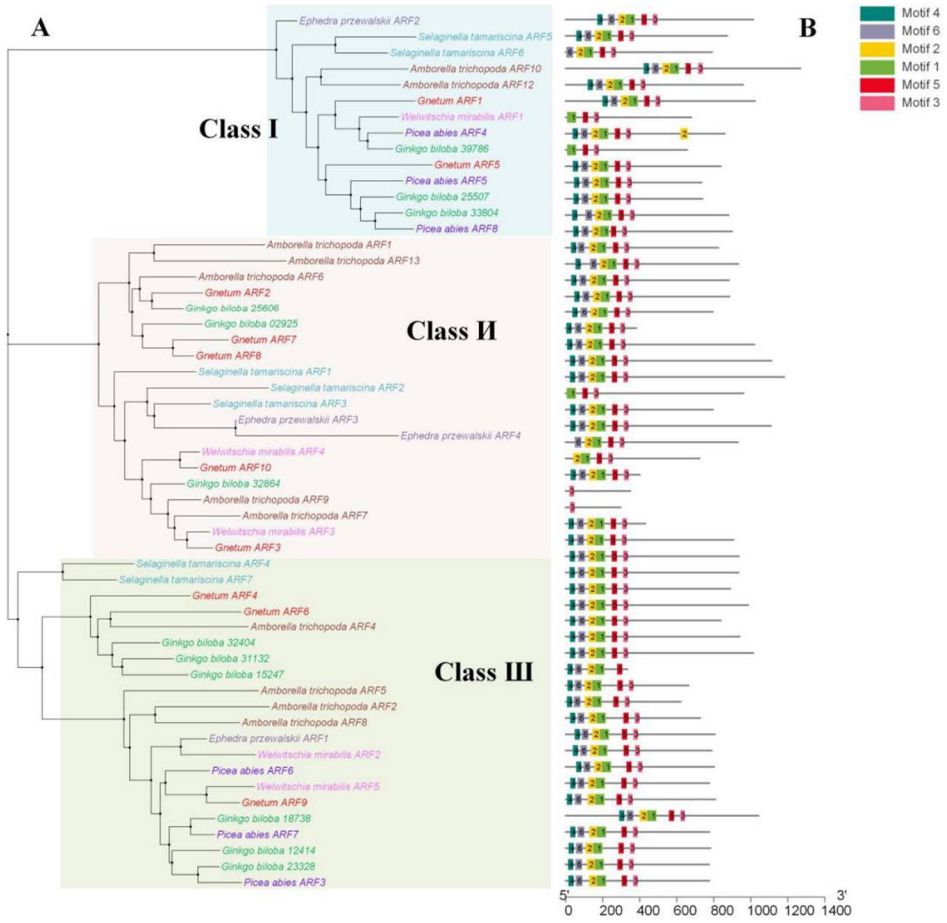

Fig. 3. Evolutionary analysis of ARF gene family among 7 species. A: NJ tree of ARF gene B: result of motif prediction.

To investigate the expansion and deletion of ARF gene families, evolutionary trees provided some valuable information and ARF gene members subordinated recent common ancestor of every species above were estimated (Fig. 4). Large-scale duplication event occurred early in the plant origin, and gene deletion was accompanied by the duplication event subsequently, especially in Pinaceae, whereas more duplication events were found in ferns and bryophytes. Multiple duplication patterns of *G. lofuense* occurred in *GnARF* recently.

Next, the duplication and loss numbers of ARF gene among plant species were explored (Fig. 5). The results showed that ARF gene underwent an uneven expansion process during evolution, which started from tracheophytes formation and expanded in several stages except euphyllophytes. Though multiple gene lost patterns were observed in a common ancestor among the species of *Gnetum* and in the family Pinaceae, the recent expansion resulted in more *GnARFs* (20), whereas the relatively small number of ARF genes in Pinaceae due to the gene deletion, especially in *P. taeda*.

Fig. 4. Duplication and loss events of *ARF* gene family among land plant.

Gene duplication can play an important role in a succession of genomic rearrangements, expansions, speciation, and the patterning of new life forms (Vision *et al*. 2000, Shukla *et al*. 2014). In the present study, it was observed that ARF gene families in several terrestrial plants had different evolution processes, specifically in expansion time and scale, which indicated that fragment replication, partial replication and transposon can play an important role in a succession

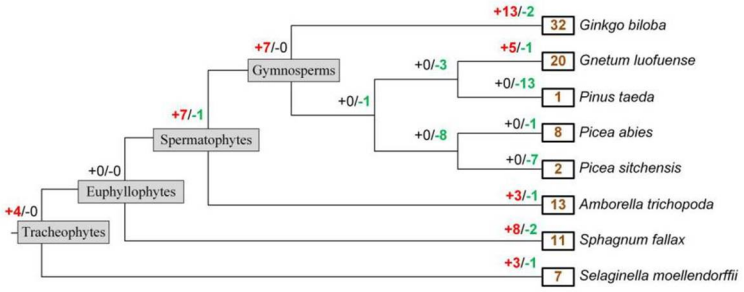

Fig. 5. Duplication and loss numbers of ARF gene among land plant.

of genomic rearrangements and expansions (Morgenstern and Atchley 1999). The ARF gene family of *Gnetum luofuense* were performed multiple expansions during evolution (Figs 4 and 5) and GnARF8, GnARF9, GnARF1, GnARF12, GnARF13, GnARF14 and GnARF15 were generated by gene duplication event recently, these duplicated genes may be modified as pseudogenization, subfunctionalization and neofunctionalization (Lynch 2000, Zhang 2003), and the function of these genes in *Gnetum* development regulation need further experimental results to verify. Additionally, many *GnARFs* seem to have corresponding relationship with *Ginkgo* and indicated that the proteins exist prior to the last common ancestor and are highly conserved with similar function (Finet *et al*. 2010). It is noteworthy that most ARFs in Pinaceae, closer phylogenetic relationship with *G. luofuense* were deleted recently, which should be further investigated.

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