

LETTER TO THE EDITOR

Update on the Basic Helix-Loop-Helix Transcription Factor Gene Family in *Arabidopsis thaliana*

Basic helix-loop-helix (bHLH) transcription factors represent a family of proteins that contain a bHLH domain, a motif involved in binding DNA. Recently, two groups independently analyzed the *BHLH* gene family of *Arabidopsis thaliana* (Heim et al., 2003; Toledo-Ortiz et al., 2003). These analyses revealed that this family is one of the largest transcription factor gene families in *Arabidopsis thaliana*. Although both analyses intended to give complete overviews of *AtBHLH* genes, some discrepancies were detected when the data sets were compared. After careful re-examination, we have resolved these discrepancies. In Table 1, we provide a uniform nomenclature for all of the genes that are mentioned in our two articles, and we encourage the use of this nomenclature in future reports concerning bHLH domain transcription factors (e.g., *AtBHLH042/TT8*).

Cross-referencing between the two data sets and further analysis have extended the total number of detected *AtBHLH* genes to 162 (Table 1). We assume that this count is very close to the final number of *AtBHLH* genes present in the *Arabidopsis thaliana* genome, but clearly, corrections or additions to the “complete” *Arabidopsis thaliana* genome sequence in the future still may cause this number to change. During examination and comparison of the data sets, we observed some common problems that contributed to the discrepancies. These problems arise commonly during the handling of large data sets and are discussed here to aid future attempts at gene family annotation. The main reasons for discrepancies were as follows.

(1) Differences between TIGR (www.tigr.org) or TAIR (www.arabidopsis.org) and MIPS (MAtdB; mips.gsf.de/projects/plants). Such differences are not easy to avoid, despite the best efforts of the database providers. Most problematic are differences in Arabidopsis Genome Initiative

Table 1. Summary of the *AtBHLH* Genes Detected

| Species ^a | Generic Name | AGI Gene Code | Entry Number ^b | Synonym(s) | Accession Number ^c | Reference ^d |
|----------------------|--------------|---------------|---------------------------|--------------------|-------------------------------|----------------------------|
| At | BHLH001 | At5g41315 | 31 | GL3 | AF246291 | Payne et al., 2000 |
| At | BHLH002 | At1g63650 | 30 | EGL1/EGL3/AtMYC146 | AF027732 | Zhang et al., 2003 |
| At | BHLH003 | At4g16430 | 34 | | AF251688 | |
| At | BHLH004 | At4g17880 | 37 | AtMYC4 | AF251689 | Abe et al., 2003 |
| At | BHLH005 | At5g46760 | 36 | ATR2/AtMYC3 | AF251690 | Smolen et al., 2002 |
| At | BHLH006 | At1g32640 | 38 | AtMYC2/RAP1 | X99548 | Abe et al., 2003 |
| At | BHLH007 | At1g03040 | 92 | | AF251692 | |
| At | BHLH008 | At1g09530 | 100 | PIF3 | AF251693 | Ni et al., 1998 |
| At | BHLH009 | At2g43010 | 102 | PIF4 | AF251694 | Huq and Quail, 2002 |
| At | BHLH010 | At2g31220 | 23 | | AF251695 | |
| At | BHLH011 | At4g36060 | 137 | | AF251696 | |
| At | BHLH012 | At4g00480 | 58 | AtMYC1 | AF251697 | Urao et al., 1996 |
| At | BHLH013 | At1g01260 | 39 | Myc7E | AY120752 | GenBank entry ^e |
| At | BHLH014 | At4g00870 | 33 | | AJ519812 | |
| At | BHLH015 | At2g20180 | 101 | PIL5 | AF488560 | Yamashino et al., 2003 |
| At | BHLH016 | At4g00050 | 108 | | AF488561 | |
| At | BHLH017 | At2g46510 | 35 | | AY094399 | |
| At | BHLH018 | At2g22750 | 28 | | AF488562 | |
| At | BHLH019 | At2g22760 | 26 | | AF488563 | |
| At | BHLH020 | At2g22770 | 27 | | AF488564 | |
| At | BHLH021 | At2g16910 | 48 | AMS | AF488565 | Sorensen et al., 2003 |
| At | BHLH022 | At4g21330 | 49 | | NM_118253 | |
| At | BHLH023 | At4g28790 | 107 | | AF488566 | |
| At | BHLH024 | At4g36930 | 99 | SPATULA | AF319540 | Heisler et al., 2001 |
| At | BHLH025 | At4g37850 | 29 | | AF488567 | |
| At | BHLH026 | At1g02340 | 68 | HFR1 | AF488568 | Fairchild et al., 2000 |
| At | BHLH027 | At4g29930 | 42 | | AF488569 | |
| At | BHLH028 | At5g46830 | 40 | | AF252636 | |
| At | BHLH029 | At2g28160 | 43 | | AF488570 | |
| At | BHLH030 | At1g68810 | 53 | | AY072161 | |
| At | BHLH031 | At1g59640 | 88 | ZCW32 | AB028232 | GenBank entry ^e |
| At | BHLH032 | At3g25710 | 54 | | AF488571 | |
| At | BHLH033 | At1g12860 | 44 | | AF488572 | |
| At | BHLH034 | At3g23210 | 135 | | AF488573 | |
| At | BHLH035 | At5g57150 | 41 | | AF488574 | |
| At | BHLH036 | At5g51780 | 6 | | AF488575 | |
| At | BHLH037 | At3g50330 | 117 | | NM_114893 | |
| At | BHLH038 | At3g56970 | 8 | ORG2 | AF488576 | Kang et al., 2003 |
| At | BHLH039 | At3g56980 | 9 | ORG3 | AF488577 | Kang et al., 2003 |
| At | BHLH040 | At4g00120 | 120 | | AF488578 | |
| At | BHLH041 | At5g56960 | 51 | | NM_125078 | |
| At | BHLH042 | At4g09820 | 32 | TT8 | AJ277509 | Nesi et al., 2000 |
| At | BHLH043 | At5g09750 | 119 | | NM_121012 | |
| At | BHLH044 | At1g18400 | 77 | BEE1 | AF488579 | Friedrichsen et al., 2002 |
| At | BHLH045 | At3g06120 | 20 | | AF488580 | |
| At | BHLH046 | At5g08130 | 126 | | AF488581 | |
| At | BHLH047 | At3g47640 | 139 | | AF488582 | |
| At | BHLH048 | At2g42300 | 97 | | AF488583 | |

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(AGI) codes for the same gene between the different databases.

(2) Positions on pseudochromosomes that are not stable as a result of corrections in single BAC sequences that affect the entire area “downstream” of the corrected locus.

(3) BAC identifiers and BAC sequence coordinates that differ for the same gene when either the upper or the lower strand is considered. One option is to keep the gene orientation according to the direction of transcription; the other is to keep the original BAC sequence in its 5' to 3' arrangement. Clearly consistency is very important.

(4) Genes located at BAC borders that can result in either double entries of the same gene or failure to detect the gene as a result of the destruction of a continuous signature pattern.

(5) Sequence errors in the genome sequence that destroy open reading frames.

(6) Differences in the detailed definition of what constitutes a bHLH domain.

Both studies started with a subset of known bHLH domain transcription factors and used a consensus sequence described by Atchley et al. (1999) as a reference. However, whereas one analysis was based on bHLH proteins similar to *Zea mays* Sn (e.g., *ZmR*) that are involved in secondary metabolism and cell identity pathways (Heim et al., 2003), the other used a subset based on PHYTOCHROME-INTERACTING FACTOR3 (PIF3) as a starting point (Toledo-Ortiz et al., 2003). In addition, the set of databases used was not completely overlapping. Consequently, some genes were identified as encoding true bHLHs by one group but not by the other, and vice versa. These differences have been removed; there are now only two *BHLH* genes listed in Table 1 (*AtBHLH136/At5g39860* and *AtBHLH160/At1g71200*) that fit the criteria of Heim et al. (2003) but not those of Toledo-Ortiz et al. (2003). A third article analyzing plant bHLH domain proteins ap-

Table 1. (continued).

| Species ^a | Generic Name | AGI Gene Code | Entry Number ^b | Synonym(s) | Accession Number ^c | Reference ^d |
|----------------------|--------------|---------------|---------------------------|------------|-------------------------------|-----------------------------|
| At | BHLH049 | At1g68920 | 82 | | AF488584 | |
| At | BHLH050 | At1g73830 | 76 | BEE3 | AF488585 | Friedrichsen et al., 2002 |
| At | BHLH059 | At4g02590 | 93 | | AF488592 | |
| At | BHLH060 | At3g57800 | 91 | | AF488593 | |
| At | BHLH061 | At5g10570 | 46 | | AF488594 | |
| At | BHLH062 | At3g07340 | 85 | | AF488595 | |
| At | BHLH063 | At4g34530 | 84 | | AF488596 | |
| At | BHLH064 | At2g18300 | 79 | | AF488597 | |
| At | BHLH065 | At3g59060 | 103 | PIL6 | AF488598 | Yamashino et al., 2003 |
| At | BHLH066 | At2g24260 | 95 | | AF488599 | |
| At | BHLH067 | At3g61950 | 11 | | AF488600 | |
| At | BHLH068 | At4g29100 | 60 | | AF488634 | |
| At | BHLH069 | At4g30980 | 94 | | AF488601 | |
| At | BHLH070 | At2g46810 | 13 | | AF488602 | |
| At | BHLH071 | At5g46690 | 17 | | AF488603 | |
| At | BHLH072 | At5g61270 | 109 | | AF488604 | |
| At | BHLH073 | At5g67110 | 98 | ALCATRAZ | AF488605 | Rajani and Sundaresan, 2001 |
| At | BHLH074 | At1g10120 | 90 | | AF488606 | |
| At | BHLH075 | At1g25330 | 78 | | AF488607 | |
| At | BHLH076 | At1g26260 | 83 | | AF488608 | |
| At | BHLH077 | At3g23690 | 87 | | AF488609 | |
| At | BHLH078 | At5g48560 | 86 | | AF488610 | |
| At | BHLH079 | At5g62610 | 81 | | AF488611 | |
| At | BHLH080 | At1g35460 | 71 | | AF488612 | |
| At | BHLH081 | At4g09180 | 72 | | AF488613 | |
| At | BHLH082 | At5g58010 | 96 | | AF488614 | |
| At | BHLH083 | At1g66470 | 112 | | AF488615 | |
| At | BHLH084 | At2g14760 | | | AJ577584 | |
| At | BHLH085 | At4g33880 | 115 | | AF488616 | |
| At | BHLH086 | At5g37800 | 113 | | NM_123139 | |
| At | BHLH087 | At3g21330 | 121 | | AF488617 | |
| At | BHLH088 | At5g67060 | 118 | | AF488618 | |
| At | BHLH089 | At1g06170 | 24 | | AF488619 | |
| At | BHLH090 | At1g10610 | 50 | | AF488620 | |
| At | BHLH091 | At2g31210 | 25 | | AJ519809 | |
| At | BHLH092 | At5g43650 | 22 | | AY065390 | |
| At | BHLH093 | At5g65640 | 47 | | AF488621 | |
| At | BHLH094 | At1g22490 | 16 | | AF488622 | |
| At | BHLH095 | At1g49770 | 21 | | AF488623 | |
| At | BHLH096 | At1g72210 | 15 | | AJ459771 | |
| At | BHLH097 | At3g24140 | 14 | | AF488624 | |
| At | BHLH098 | At5g53210 | 19 | | NM_124700 | |
| At | BHLH099 | At5g65320 | 18 | | AF488625 | |
| At | BHLH100 | At2g41240 | 7 | | AF488626 | |
| At | BHLH101 | At5g04150 | 10 | | AJ519810 | |
| At | BHLH102 | At1g69010 | 125 | | AF488627 | |
| At | BHLH103 | At4g21340 | 62 | | AY065362 | |
| At | BHLH104 | At4g14410 | 136 | | AF488628 | |
| At | BHLH105 | At5g54680 | 133 | | AF488629 | |
| At | BHLH106 | At2g41130 | 56 | | AY074639 | |
| At | BHLH107 | At3g56770 | 55 | | NM_115536 | |
| At | BHLH108 | At1g25310 | 132 | | NM_102341 | |
| At | BHLH109 | At1g68240 | | | AJ577585 | |
| At | BHLH110 | At1g27660 | 59 | | NM_102531 | |
| At | BHLH111 | At1g31050 | 66 | | AA395190 | |

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peared recently (Buck and Atchley, 2003) reporting ~118 *AtBHLH* genes. Of these, 116 correspond to those listed in Table 1. The remaining two (At1g49830 and At5g33210) do not fit the criteria used for Table 1.

Search engines have been greatly improved in the last few years, but they still often are not exact enough to identify certain motifs. This is not necessarily the result of deficiencies in the search algorithms but may result from the structure of matrices that describe known motifs (e.g., *AtBHLH125* spanned two separate BAC ends, and two separate predictions had to be fused). Even the continuous optimization of our bHLH domain matrix never resulted in the identification of all 162 *AtBHLH* genes in one search. Additionally, gene prediction tools are sometimes not flexible enough to respond to variable intron lengths and exon distribution (e.g., the prediction NM_105789 for *AtBHLH160* contains an intron that causes an overestimate of the length of the loop structure). It sounds obvious, but it is worth emphasizing that cDNA sequences, even from reverse transcriptase-mediated PCR experiments, should be deposited in GenBank (<http://www.ncbi.nlm.nih.gov/>) or EMBL (<http://www.ebi.ac.uk/Databases/>) even if the genomic sequence is already in the database, and the "metadata" of the database entry should be written with care. The most unambiguous identifier of any given gene (unless a sequence-identical duplication exists) is its DNA sequence, and only this information allows designations and identifier assignments to be checked and rechecked.

It is an interesting and critical point that even with a combination of all available BLAST (Basic Local Alignment Search Tool) tools, both groups were unable to obtain a full set of Arabidopsis bHLH domain transcription factors in their initial analyses. Both studies relied on BLAST search capabilities (TBLASTN and BLASTP) and subsequent evaluation of the hits for the respective bHLH consensus sequences. In addition, position-specific iterated BLAST was used by one of the two groups to identify remaining unidentified bHLH domain-encoding sequences. Nevertheless, several true *BHLH*

Table 1. (continued).

| Species ^a | Generic Name | AGI Gene Code | Entry Number ^b | Synonym(s) | Accession Number ^c | Reference ^d |
|----------------------|--------------|---------------|---------------------------|------------|-------------------------------|-------------------------|
| At | BHLH112 | At1g61660 | 64 | | AF488630 | |
| At | BHLH113 | At3g19500 | 61 | | AF488631 | |
| At | BHLH114 | At4g05170 | 65 | | NM_116756 | |
| At | BHLH115 | At1g51070 | 134 | | AF488632 | |
| At | BHLH116 | At3g26744 | 45 | ICE1 | AY079016 | Chinnusamy et al., 2003 |
| At | BHLH117 | At3g22100 | 140 | | NM_113106 | |
| At | BHLH118 | At4g25400 | 5 | | NM_118672 | |
| At | BHLH119 | At4g28811 | 104 | | AJ519811 | |
| At | BHLH120 | At5g51790 | 4 | | NM_124558 | |
| At | BHLH121 | At3g19860 | 138 | | AF488633 | |
| At | BHLH122 | At1g51140 | 70 | | AY063120 | |
| At | BHLH123 | At3g20640 | 63 | | AU238908 | |
| At | BHLH124 | At2g46970 | 110 | PIL1 | AB090873 | Yamashino et al., 2003 |
| At | BHLH125 | At1g62975 | 2 | | AF506369 | |
| At | BHLH126 | At4g25410 | 3 | | Z46563 | |
| At | BHLH127 | At4g28815 | | | AJ577586 | |
| At | BHLH128 | At1g05805 | 74 | | AY045907 | |
| At | BHLH129 | At2g43140 | 73 | | AU237473 | |
| At | BHLH130 | At2g42280 | 69 | | NM_129790 | |
| At | BHLH131 | At4g38071 | | | AJ577587 | |
| At | BHLH132 | At3g62090 | 111 | PIL2 | AB090874 | Yamashino et al., 2003 |
| At | BHLH133 | At2g20095 | | | AJ577588 | |
| At | BHLH134 | At5g15160 | 52 | | AK118887 | |
| At | BHLH135 | At1g74500 | 67 | | AY088286 | |
| At | BHLH136 | At5g39860 | | | AY088246 | |
| At | BHLH137 | At5g50915 | 89 | | AY087602 | |
| At | BHLH138 | At2g31215 | | | NM_179830 | |
| At | BHLH139 | At5g43175 | 116 | | NM_148080 | |
| At | BHLH140 | At5g01310 | 122 | | NM_120209 | |
| At | BHLH141 | At5g38860 | 127 | | NM_123247 | |
| At | BHLH142 | At5g64340 | 128 | | AY062561 | |
| At | BHLH143 | At5g09460 | 129 | | BT000009 | |
| At | BHLH144 | At1g29950 | 130 | | AF361607 | |
| At | BHLH145 | At5g50010 | 131 | | BT005301 | |
| At | BHLH146 | At4g30180 | 141 | | AU237244 | |
| At | BHLH147 | At3g17100 | 142 | | NM_180270 | |
| At | BHLH148 | At3g06590 | 143 | | NM_111535 | |
| At | BHLH149 | At1g09250 | 144 | | BT003052 | |
| At | BHLH150 | At3g05800 | 145 | | NM_111454 | |
| At | BHLH151 | At2g47270 | 146 | | NM_130295 | |
| At | BHLH152 | At1g22380 | 147 | | NM_102088 | |
| At | BHLH153 | At1g05710 | | | AJ576040 | |
| At | BHLH154 | At2g31730 | | | AJ576041 | |
| At | BHLH155 | At2g31280 | | | AJ576042 | |
| At | BHLH156 | At2g27230 | | | AJ576043 | |
| At | BHLH157 | At1g64625 | | | AJ576044 | |
| At | BHLH158 | At2g43060 | | | AJ576045 | |
| At | BHLH159 | At4g30410 | | | AJ576046 | |
| At | BHLH160 | At1g71200 | | | NM_105789 | |
| At | BHLH161 | At3g47710 | | | NM_114639 | |
| At | BHLH162 | At4g20970 | | | NM_118215 | |

^a The prefix At indicates *Arabidopsis thaliana* (see text).

^b BHLH "entry numbers" (Toledo-Ortiz et al., 2003).

^c GenBank accession number of the cDNA sequence representing the open reading frame used to evaluate the presence or absence of a proper bHLH domain signature.

^d References for the synonyms that are used in the literature.

^e The synonym was found only in a GenBank entry but not in an article.

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genes were not detected. Some of these initial false negatives were found by searching for the term "helix-loop-helix" in the annotation databases (e.g., *AtBHLH134* and *AtBHLH136*). However, this search also resulted in many false positives that had to be excluded as a result of misannotations based on weak homology or of "inherited misannotation," in which a single wrong annotation text had been used as a reference during annotation. In essence, we were unable to detect slightly divergent or mispredicted *BHLH* genes. The only solution to this problem may involve systematic annotation by expert annotators, comprehensive EST data production from normalized libraries, and the generation of full-length cDNA at least for protein-coding gene sequences. A significant part of the improvement of the data set presented in Table 1 is based on the reannotation of the Arabidopsis genome by the TIGR group, which followed this approach.

We were able to improve gene annotation further by comparing closely related *BHLH* genes for their exon/intron structures. This powerful similarity-based approach (used here within a single species) led to the correction of some gene annotations and, consequently, to a further increase in the total number of *AtBHLH* genes detected. Several of the genes that escaped the initial screens by both groups contain short introns in the region that encodes the loop of the HLH region. These comparably short introns, and also short exons that are part of the bHLH open reading frame, resulted in mispredictions that were a significant cause of false negatives in our initial analyses. One example is *AtBHLH160*, for which we found a formerly unpredicted intron after comparison with the most closely related genes *AtBHLH038/ORG2*, *AtBHLH039/ORG3*, *AtBHLH100*, and *AtBHLH101*.

The combined effort of our two groups and the lessons we have learned from the comparison of the two data sets have resulted in an (almost) complete view of the *AtBHLH* transcription factor gene family, now provided with unambiguous generic names and reference to synonyms. We hope that this work will serve as a solid foundation for further investigations into the functions

of the different members of this interesting gene family in plants.

Paul C. Bailey and Cathie Martin
John Innes Centre
Colney Lane
NR4 7UH Norwich, UK

Gabriela Toledo-Ortiz and Peter H. Quail
Department of Plant and
Microbial Biology
University of California
Berkeley, CA 94720
and United States Department
of Agriculture
Agricultural Research Service Plant
Gene Expression Center
Albany, CA 94710

Enamul Huq
Section of Molecular Cell and
Developmental Biology
University of Texas
1 University Station, A6700
Austin, TX 78712

**Marc A. Heim, Marc Jakoby,
and Martin Werber**
Max-Planck-Institute for Plant
Breeding Research,
50829 Köln, Germany

Bernd Weisshaar
Institute for Genome Research,
Bielefeld University,
33594 Bielefeld, Germany

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