

A uniform gene and chromosome nomenclature system for oat (*Avena* spp.)

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ABSTRACT

Context. Several high-quality reference genomes for oat (*Avena sativa* L. and relatives) have been published, with the prospect of many additional whole-genome assemblies emerging in the near future. **Aims.** This has necessitated an effort by the International Oat Nomenclature Committee (IONC; all co-authors on this paper) to devise a universal system for naming oat genomes and subgenomes, chromosomes, genes, gene models and quantitative trait loci. **Methods.** We evaluated existing naming practices, recent data from oat whole-genome sequencing, and the newly published convention for wheat nomenclature. **Key results.** A framework for these rules has been posted on the GrainGenes database website (<https://wheat.pw.usda.gov/GG3/oatnomenclature>). The gene naming convention requires adoption of a numerical identifier for each genotype; we propose that these identifiers be assigned by contacting the GrainGenes curators, the curator of the *Oat Newsletter*, or a member of the IONC (as listed at the GrainGenes link above). **Conclusions.** We encourage oat researchers to refer to these resources, policies, procedures and conventions, adopting them as an international nomenclature standard. **Implications.** Adoption of these standards will facilitate communication and dissemination of oat research and allow programmatic access and data sharing across platforms, and will contribute to oat breeding and research worldwide.

Keywords: *Avena*, chromosome nomenclature, data standardisation, gene nomenclature, genome nomenclature, oat, plant breeding, QTL nomenclature.

Introduction

The past 4 years have witnessed the publication of the first whole-genome sequence assemblies of the oat genus *Avena* L., classified within subfamily Pooideae of the Poaceae, tribe Poeae, subtribe Aveninae. The first oat whole-genome sequences published were for A- and C-genome diploids (Maughan *et al.* 2019), and rapidly progressed further to hexaploid *A. sativa* L. ($2n = 6x = 42$, AACDD) with the online release of the hexaploid OT3098 sequence in 2020 on the GrainGenes database (Yao *et al.* 2022) website (<https://wheat.pw.usda.gov/jb/?data=/ggds/oat-ot3098-pepsico>). This release was followed by published assemblies of the OT3098 ver. 2 assembly in 2021, Swedish hulled oat cv. Sang (Kamal *et al.* 2022), and Chinese hullless cv. Sanfensan (Peng *et al.* 2022). Significantly, these whole-genome sequences permitted the assignment of each of the 21 oat chromosomes to their subgenome and homoeologous group. The group designations were based on synteny with the seven chromosomes of the non-Poeae grass barley (*Hordeum vulgare* L.). Whole-genome sequencing efforts are now progressing toward assemblies of multiple genotypes of common oat and closely related species in a coordinated international effort – the Oat Pangenome Project (PanOat). This has necessitated a reappraisal of the various existing oat chromosome, linkage group, gene and gene model designations and their unification into a single, universal nomenclature convention.

Oat geneticists in the 1960s were the first to suggest that *A. sativa* and its allohexaploid allied taxa – *A. byzantina* C. Koch (red oat), *A. fatua* L. (common wild oat) and *A. sterilis* L.

(wild animated oat) – carried the AA, CC and DD subgenomes (Rajhathy and Thomas 1974). Their original karyotype-based nomenclature system was based on chromosome morphology without molecular cytogenetic or chromosome banding data (Rajhathy 1963), and gene nomenclature generally followed rules established in other cereal species, particularly those in the tribe Triticeae (Simons *et al.* 1966, 1978). We present a universal genome, chromosome, transcriptome and gene identification system approved by the International Oat Nomenclature Committee (IONC) for application to all *Avena* genotypes that are analysed moving forward. This system follows the convention for chromosome nomenclature established for barley (Singh and Tsuchiya 1982; Wang *et al.* 1996) and the new system for wheat (Boden *et al.* 2023).

The nomenclature rules

Genomes and subgenomes

Whole-genome sequence assemblies (Kamal *et al.* 2022; Peng *et al.* 2022) along with prior work by various authors including Yan *et al.* 2016 and Latta *et al.* (2019) have confirmed the unique identities of the A, B, C and D genomes/subgenomes of *Avena*. In addition, we herein propose a separate genome designator for the perennial autotetraploid oat *A. macrostachya*, EE, because of its uniquely long chromosomes with dense pericentromeric heterochromatin patterns, highly symmetrical karyotype (Badaeva *et al.* 2010), and recalcitrance to crossing with other *Avena* species having genomes A, B and D, albeit with somewhat greater homology to genome C (Leggett 2011). In the current proposal, the subgenomes of *A. sativa* are indicated with the subscript 's'. Diploid genomes will follow several new conventions: A_a represents the *A. atlantica-strigosa* biological species group, A_c is for the *A. canariensis* genome, A_d for *A. damascena*, A_l for *A. longiglumis*, and A_p for *A. prostrata*. For the CC diploids, C_e represents the genome of the *A. eriantha-clauda* group and C_v is used for *A. ventricosa*. The *A. barbata* group contains subgenomes A_b and B (which has not been identified in any other biological species). The C- and D-subgenomes in the Section Pachycarpa tetraploids are represented as C_i and D_i in *A. insularis*, C_g and D_g in *A. magna* (syn. *A. maroccana*), and C_y and D_y in *A. murphyi*. Use of the subscript 'm' is discouraged owing to potential confusion with multiple tetraploid species names beginning with the letter 'm'.

Species/taxon designation code

For the gene models, each *Avena* biological species-group has a five-letter species designator beginning with 'AVxxx' and each genotype is to be assigned its own specific five-digit code, beginning with the first set of assembled reference genomes (Table 1). Hereafter, each new sequenced genotype should be assigned a number after consultation between the

researcher and the GrainGenes curation team. Genotypes of the same species are grouped within specified numerical ranges, as follows. Numbers 00001–09999 are reserved for natural hexaploids of the *A. sativa* group. Tetraploids are numbered 10000–15999. Diploids are numbered 20000–26999. Synthetics will be designated with numbers in the 30000s.

Chromosome correspondences

Homoeologous chromosome groups were identified and subgenome assignments made based on common synteny within *Avena* and with chromosomes 1H–7H of *Hordeum vulgare*, along with distributions of subgenome-abundant repetitive motifs (Jiang *et al.* 2021; Kamal *et al.* 2022; Peng *et al.* 2022) (Table 2).

Quantitative trait loci, genes and proteins

Quantitative trait loci

The IONC recognises the utility of having a consistent naming system for QTL. However, many quantitative trait loci (QTLs) have been identified in oat over the years, and changing the older names could cause confusion. Therefore, the committee proposes that:

1. The names of previously published QTLs be kept as is, unless this would duplicate a name used elsewhere. In such cases, the name would be modified, staying close to the original.
2. The names of new QTLs and previously published QTLs with no names assigned be given names using the following convention, which has been derived from the standard used by the GrainGenes database (Yao *et al.* 2022; <https://wheat.pw.usda.gov/>), and informed by the new wheat nomenclature rules outlined by Boden *et al.* (2023):

QField1.Field2_Field3

Field1 is the main trait name (two to five letters). If any additional trait or environment information is necessary to distinguish the QTL, then a dash followed by two to five more letters is added.

Field2 is the map name, with the year and a dash added if necessary to distinguish the work. Typically, the map name would either be an abbreviated version of the pedigree for a biparental cross, or the name given to an association mapping population.

Field3 is the linkage group name. If the group has been assigned to an 'Mrg' linkage group from the 2018 hexaploid oat consensus map (Bekele *et al.* 2018), then 'Mrg' is included in the name. If more than one QTL for the same trait is found on one linkage group, then a period is added, followed by a number to distinguish the QTL.

Table 1. Correspondence between five-letter species designator codes, genome/subgenome formulae, and commonly accepted *Avena* taxa, excluding lesser used taxa identified in Baum (1977) or Loskutov and Rines (2011).

Five-letter species designator code	Ploidy	Subgenomes	Included <i>Avena</i> taxa	Reserved genotype identifier codes
AVAGA	4x	A'A'B'B'	<i>agadiriana</i>	11000–11999
AVATL	2x	A _a A _a , sometimes A _a A _a A _a A _a	<i>atlantica</i> <i>brevis</i> <i>hirtula</i> <i>hispanica</i> <i>nuda</i> <i>nudibrevis</i> <i>strigosa</i> <i>wiestii</i>	20000–20999
AVBAR	4x	A _b A _b BB	<i>abyssinica</i> <i>barbata</i> <i>vaviloviana</i>	10000–10999
AVCAN	2x	A _c A _c	<i>canariensis</i>	21000–21999
AVDAM	2x	A _d A _d	<i>damascena</i>	22000–22999
AVERI	2x	C _e C _e	<i>clauda</i> <i>eriantha</i> <i>pilosa</i>	25000–25999
AVINS	4x	C _i C _i D _i D _i	<i>insularis</i>	12000–12999
AVLON	2x	A _l A _l	<i>longiglumis</i>	23000–23999
AVMAG	4x	C _g C _g D _g D _g	<i>maroccana</i> <i>magna</i>	13000–13999
AVMAC	4x	EEEE (possibly EEE'E')	<i>macrostachya</i>	15000–15999
AVMUR	4x	C _y C _y D _y D _y	<i>murphyi</i>	14000–14999
AVPRO	2x	A _p A _p	<i>prostrata</i>	24000–24999
AVESA	6x	A _s A _s C _s C _s D _s D _s	<i>byzantina</i> <i>fatua</i> <i>ludoviciana</i> <i>occidentalis</i> <i>sativa</i> <i>sativa</i> subsp. <i>nuda</i> <i>sterilis</i>	00001–09999
AVSYN	4x-10x	Various	Synthetic allopolyploids, e.g. Amagalon	30000–30999
AVVEN	2x	C _v C _v	<i>bruhsiana</i> <i>ventricosa</i>	26000–26999

Designations generally follow biological species concept groups as outlined by Ladizinsky (2012).

A simple example of a name created using this system would be 'QHDNV.U8xU605_6' (QTL for heading date using non-vernalised plants, mapped in the UFRGS 8/UFRGS 930605 (U8xU605) population on linkage group 6). A more complex example would be 'QHD-Far11.2016-CORE_Mrg20.2' (QTL for heading date recorded at Fargo, ND, in 2011, mapped using the CORE set of lines in 2016 on linkage group Mrg20, the second of two HD QTLs on that group).

Examples of other styles of QTLs already in the literature include 'Days to heading', 'KxO-11-c' and 'QPlumps.Aberd17.2A' (in this last case, the chromosome number is identified).

Gene model identifiers

We recognise the importance of consistent use of gene model identifiers across *Avena* genotypes to facilitate analysis and interpretation across studies (Schnable 2020).

Table 2. Correspondence of chromosome, pseudochromosome, and linkage-group designation systems in *Avena* hexaploids and diploids *A. atlantica* and *A. eriantha*.

PepsiCo, Yao et al. (2022), Jiang et al. (2021)	Chaffin et al. (2016) Mrg consensus linkage group	Sanz et al. (2010) chromosome designation	Maughan et al. (2019) diploid oat assemblies	NEW 2x chromosome designation	NEW 6x chromosome designation
Genome A					
1A _s (-)	Mrg18(-)	17A	AA2(+)	1A_a	1A_s
2A _s (+)	Mrg33(+)	15A	AA5(-)	2A_a	2A_s
3A _s (+)	Mrg23(+)	11A	AA3(+)	3A_a	3A_s
4A _s (+)	Mrg20(+)	19A	AA4(-)	4A_a	4A_s
5A _s (+)	Mrg24(+)	8A	AA6(-)	5A_a	5A_s
6A _s (+)	Mrg05(+)	16A	AA7(-)	6A_a	6A_s
7A _s (+)	Mrg12(+)	13A	AA1(-)	7A_a	7A_s
Genome C					
1C _s (-)	Mrg28(-)	7C	AE5(+)	1C_e	1C_s
2C _s (+)	Mrg13(+)	5C	AE4(-)	2C_e	2C_s
3C _s (+)	Mrg15(-)	2C	AE3(-)	3C_e	3C_s
7C _s (+)	Mrg11(+)	1C	AE1(-)	4C_e	4C_s
5C _s (-)	Mrg03(-)	4C	AE6(-)	5C_e	5C_s
6C _s (-)	Mrg17(-)	3C	AE2(-)	6C_e	6C_s
4C _s (-)	Mrg09(-)	6C	AE7(-)	7C_e	7C_s
Genome D					
1D _s (-)	Mrg01(-)	14D	-	-	1D_s
2D _s (-)	Mrg08(-)	12D	-	-	2D_s
3D _s (+)	Mrg19(+)	21D	-	-	3D_s
4D _s (+)	Mrg21(+)	20D	-	-	4D_s
5D _s (-)	Mrg06(-)	10D	-	-	5D_s
6D _s (-)	Mrg04(-)	18D	-	-	6D_s
7D _s (-)	Mrg02(-)	9D	-	-	7D_s

The new chromosome numbering system (bolded columns) is based on synteny with pericentromeric core chromosome regions of *Hordeum vulgare*. The suffixes (+) and (-) denote the orientations of chromosomes relative to the new system (Kamal et al. 2022). As new *Avena* species are sequenced, their chromosomes will be oriented and numbered relative to the information presented here, using the genome and subgenome designations presented in Table 1. The reference for the PepsiCo release of OT3098 is as follows: *Avena sativa* – OT3098 v1, PepsiCo, https://wheat.pw.usda.gov/GG3/graingenes_downloads/oat-ot3098-pepsico. Note that in this table, chromosomes 4C_s and 7C_s are switched from the designation used in the PepsiCo OT3098 (Jiang et al. 2021; Yao et al. 2022) and Sanfensan genomes (Peng et al. 2022), in keeping with the analyses reported by Kamal et al. (2022).

It is important to emphasise that no perfect solution for gene model nomenclature exists, and each choice has advantages and disadvantages. Indeed, we are aware that different plant researcher communities adopted slightly different guidelines for their species. With this in mind, we propose the adoption of the following gene-model syntax for *Avena*:

Field1. Field2. Field3. Field4. Field5

Field1 is a five-character-long descriptor for species as shown in Table 1 ('designator code'). It will be shown in all upper case letters.

Field2 is a six-character-long descriptor for oat genotypes. The first five characters will be numerical, and the last character will be alphanumeric. The currently assigned genotype

identifiers are shown in Table 3. The last character (shown as 'x' in Table 3 as a placeholder) will be to give flexibility to account for genotype variants, or in case more than one assembly exists for the very same cultivar (e.g. assemblies done by the same or different research groups). The six-character-long identifier in this field will be assigned by the IONC and will be publicly available through GrainGenes (Yao et al. 2022) at <https://wheat.pw.usda.gov/GG3/oatnomenclature>. To obtain a new identifier, researchers are encouraged to reach out to the IONC through GrainGenes (feedback@graingenes.org).

Field3 is a two-character-long descriptor for the annotation release version for a given assembly. The first release will be r1, the second r2, and so forth. One example could be the same group working on the same assembly creating a second set of annotations.

Table 3. Initial oat genotype numerical assignments (in bold) for Field2 as described above and in Table 1.

Common name	Source	<i>Avena</i> taxa	Five-letter species designator code	Number
OT 3098	PanOat/PepsiCo	<i>sativa</i>	AVESA	0001x
GMI 423	PanOat/GMI	<i>sativa</i>	AVESA	0002x
Bingo	PanOat	<i>sativa</i>	AVESA	0003x
FMI3	PanOat	<i>sativa</i>	AVESA	0004x
Hative des Alpes	PanOat	<i>sativa</i>	AVESA	0005x
Bannister	PanOat	<i>sativa</i>	AVESA	0006x
Bilby	PanOat	<i>sativa</i>	AVESA	0007x
Clintland 60 (Clav 7234)	PanOat/USDA	<i>sativa</i>	AVESA	0008x
Nicolas	PanOat/Canada	<i>sativa</i>	AVESA	0009x
Sang	PanOat/Scanoat	<i>sativa</i>	AVESA	0010x
OT 380	PanOat/USDA	<i>sativa</i>	AVESA	0011x
Aslak	PanOat/LUKE	<i>sativa</i>	AVESA	0012x
Lion	PanOat	<i>sativa</i>	AVESA	0013x
Rhapsody	PanOat	<i>sativa</i>	AVESA	0014x
Delfin	PanOat	<i>sativa</i>	AVESA	0015x
HiFi	PanOat/Canada	<i>sativa</i>	AVESA	0016x
Park	PanOat/Canada	<i>sativa</i>	AVESA	0017x
GS7; 94197A1-9-2-2-2-5	PanOat/Canada	<i>sativa</i>	AVESA	0018x
Leggett	AAFC	<i>sativa</i>	AVESA	0019x
AC Morgan	AAFC	<i>sativa</i>	AVESA	0020x
Sanfensan	Yuanying Peng	<i>sativa</i> subsp. <i>nuda</i>	AVESA	00400x
PI 182478	PanOat/USDA	<i>sativa</i> subsp. <i>nuda</i>	AVESA	00401x
Gehl	PanOat/Canada	<i>sativa</i> subsp. <i>nuda</i>	AVESA	00402x
PI 258586	PanOat/IBERS	<i>byzantina</i>	AVESA	00500x
Victoria	PanOat	<i>byzantina</i>	AVESA	00501x
CN 25955	PanOat	<i>fatua</i>	AVESA	00600x
Tn1	PanOat/IBERS	<i>sterilis</i>	AVESA	00700x
Tn5	PanOat/IBERS	<i>sterilis</i>	AVESA	00701x
PI 388828	PanOat/USDA	<i>barbata</i>	AVBAR	10000x
PI 411152	BYU/USDA	<i>abyssinica</i>	AVBAR	10001x
BYU 209	PanOat	<i>insularis</i>	AVINS	12000x
CN 108634	Yuanying Peng	<i>insularis</i>	AVINS	12001x
CN 58138	PanOat	<i>longiglumis</i>	AVLON	23000x
CN 58139	Yuanying Peng	<i>longiglumis</i>	AVLON	23001x
Amagon	PanOat	<i>magna</i> X <i>longiglumis</i>	AVSYN	30000x

Note that 'x' in the number column is only used as a placeholder (as described in the text) to account for genotype variants, or in case more than one assembly exists for the same cultivar.

Field4 is a 10-character-long descriptor. The first two characters are alphanumeric and designate the chromosome (e.g. 4D). The third character is 'g' for gene locus, even for transcripts or proteins. The lower case, as opposed to upper case, 'g' was selected to increase the readability of the preceding chromosome descriptor. The following seven characters are the gene model identifier based on the position

ordering from the 5' to 3' DNA sequence for each chromosome (i.e. first predicted gene loci on the 1A chromosome will be 1Ag0000001, 1Ag0000002, and so forth; first predicted gene locus on the 2A chromosome will be 2Ag0000001). There is a caveat for researchers: these numbers are dependent on the annotation pipelines/assemblies, and therefore, the same gene identifier may not point to the

same gene locus for different releases or between different genotypes. To obtain orthologous relationships between the individual gene models of all genotypes included in PanOat, we will provide an orthologous gene framework with the pan-genome analysis.

Field5 is a flexible-length descriptor to show transcripts, isoforms/splice variants, and proteins. Field5 will be blank for gene loci. For gene models, gene transcripts, isoforms and proteins, the field will be numbered as 1, 2, and so forth.

As an example, the following is an acceptable instance for *Avena sativa* (therefore 'AVESA') OT3098 genotype's ('00001') ver. 1 assembly ('a'; if this was ver. 2 assembly, it would have been 'b') and ver. 2 annotation set ('r2'), on the 1A chromosome ('1A'), for the first gene locus ('0000001'):

- Gene locus: AVESA.00001a.r2.1Ag0000001
- Gene models/transcripts/isoforms/proteins: AVESA.00001a.r2.1Ag0000001.1, AVESA.00001a.r2.1Ag0000001.2, and so on.

Functional gene names

Existing oat gene names will continue to be used, but moving forward, the guidelines developed for wheat gene nomenclature detailed in Boden *et al.* (2023) will be followed.

Pathogenic disease reaction

The system for designating loci controlling reaction to biotic agents that attack oat proposed by Simons *et al.* (1978) (Table 4) will continue to be followed but with the omission of the hyphen in designations (e.g. 'Pc1' rather than 'Pc-1') to reflect the more common usage of the former in publications since 1978. It should be noted that the chromosomal locations of many of the loci that have been catalogued to date remain unknown, and that some of these may prove to be allelic once this is resolved. If this arises, it will be necessary to change the numbering of the locus/loci involved, and possibly delete others from the catalogue, as has occurred in wheat (e.g. the deletion of *Sr1* due to synonymy with *Sr9d*, and of *Sr3* and *Sr4* due to a lack of single gene stocks; McIntosh *et al.* 1995) (Park *et al.* 2022).

Proteins

The protein notation for gene models is specified in the *Gene model Identifiers* section above. For the protein names associated with gene loci, Boden *et al.* (2023) will be followed.

Discussion

The rules and guidelines outlined above represent an effort to accommodate over 100 years of gene, genome and chromosome nomenclature in *Avena*, while providing for standardisation, not only within the oat research community,

Table 4. Locus designations for genes controlling pathogenic disease reaction in *Avena*.

Pathogen	Disease	Gene designation	Notes
<i>Blumeria graminis</i> f. sp. <i>avenae</i> (syn. <i>Erysiphe graminis</i>)	Powdery mildew	Pm	Formerly Eg (Hsam <i>et al.</i> 2014)
<i>Ditylenchus dipsaci</i>	Stem nematode	Dd	
<i>Heterodera avenae</i>	Cereal cyst nematode	Ha	
<i>Helminthosporium</i> (<i>Cochliobolus</i>) <i>victoriae</i>	Victoria blight	Hv	
<i>Puccinia coronata</i> f. sp. <i>avenae</i>	Crown rust	Pc	
<i>Puccinia graminis</i> f. sp. <i>avenae</i>	Stem rust	Pg	
<i>Pseudomonas coronafaciens</i> pv. <i>coronafaciens</i>	Halo blight	Psc	Kim (2020)
<i>Pseudomonas coronafaciens</i> pv. <i>striaefaciens</i>	Stripe blight	Pcs	Dutta <i>et al.</i> (2018)
<i>Schizaphis graminum</i>	Greenbug	Grb	Radchenko <i>et al.</i> (2018)
<i>Ustilago kollerii</i>	Covered smut	U	
<i>Ustilago avenae</i>	Loose smut	U	

but also extending to the broader cereal grass research community working on barley, wheat, rye and triticale. The time is ripe for this standardised nomenclature system, given the rapid expansion of oat and Triticeae genome sequencing efforts. It is our expectation that genome sequence information from other cereal grass genera will be essential resources to leverage in identifying economically important gene homologs within the *A. sativa* genome. We strongly encourage all oat researchers to familiarise themselves with this nomenclature and with the online resources and personnel at GrainGenes (<https://wheat.pw.usda.gov/GG3/>; Yao *et al.* 2022) and to adhere to the policies above through consultation with the GrainGenes team.

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Data availability. Data sharing is not applicable because no new data were generated or analysed during this study.

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