

**PROPOSAL TO ENHANCE THE SEQUENCE OF THE CHICKEN GENOME****Jerry Dodgson, Michigan State University****Hans Cheng, USDA-ARS Avian Disease and Oncology Lab****Wes Warren, Washington University Genome Sequencing Center****Aleksey Zimin, U. of Maryland, Center for Bioinformatics and Computational Biology****I. Background and Current Status**

The chicken genome (~1.2 Gb) was sequenced with NIH support in response to a White Paper (see [http://genome.wustl.edu/genomes/view/gallus\\_gallus/](http://genome.wustl.edu/genomes/view/gallus_gallus/)) by the Washington U. Genome Sequencing Center (WUGSC) with the first draft sequence announced in March 2004. That draft was based on 6.6X WGS (Sanger) coverage, assembled and aligned to chromosomes using BAC end sequences and a comprehensive BAC physical map (Wallis et al., 2004). DNA from a single, partially inbred Red Jungle Fowl bird (the primary wild progenitor of domestic chickens) was sequenced. Subsequently, a second Build (WUGSC 2.1/galGal3) was generated, and this build is currently available on the genome browsers. It added an additional 198K reads focused on contig ends and regions of poor quality. Furthermore, the assembly was improved using early SNP mapping data that better aligned contigs on chromosomes. Total sequence in Build 2 includes 1.1 Gb of sequence, about 95% of which is anchored to autosomes 1-28 and 32, along with the Z and W sex chromosomes. A small amount of sequence is assigned to linkage groups for which numbered chromosomes are not available (chicken has 39 chromosome pairs) and 63.9 Mb of sequence remained on chrUn\_random. A relatively small part of the sequence is on chromosome-specific unassembled contigs. The Z and W sex chromosomes were sequenced only to ~3.3X due to their hemizygous state in the female bird used. Build 2.1 increased the size of chrZ from 33.6 to 74.6 Mb and decreased chrW from 4.9 Mb to 0.26 Mb due, in part, to several mistaken assignments of contigs to W in Build 1 that were actually on Z. For Build 2, the contig N50 = 45 kb, the supercontig N50 = 11.1 Mb and the ultracontig N50 = 15.5 Mb. The difference between the first two statistics reflects a fairly high frequency of short unsequenced gaps spanned by read pairs. Nevertheless, by a variety of measures, the Build 2 assembly is of very high quality. This is probably due, in part, to the much lower level of interspersed repeats in avian genomes (~10%) vs. mammalian genomes (>30%).

A third build of the genome (3.0) is available from WUGSC based on 12X 454 coverage and PCAP assembly. In addition, WUGSC currently has 70X Illumina coverage of the genome that isn't part of the above assemblies. A comprehensive hybrid assembly of all available Sanger-based sequence plus the 12X coverage by the 454 reads has been performed by the U. of Maryland in collaboration with WUGSC. This assembly also includes the high quality, BAC-by-BAC sequence of the Z chromosome done by Bellott et al. (2010). This assembly is currently being annotated and is expected to become available to the browsers in the next few months. Using a combination of Sanger and 454 sequence resulted in an increase of N50 contig size by 460% to 252 Kb. The supercontig N50 increased to 17.6 Mb. In addition to the much improved Z chromosome sequence, the new assembly removes about 10 Mb of artifactual duplications. The total amount of sequence mapped to the chromosomes increased by 15 Mb, accounting for duplication errors. These corrections derive from the fact that the bird used was incompletely inbred, leading to heterozygous alleles being mistakenly called as duplications.

**II. Need for refinement.**

The current chicken genome assembly surely suffers from many of the gaps and errors that have been proven to occur in other vertebrate genomes, even in highly "finished" genomes such as those of human and mouse. Being the first agricultural animal genome sequenced also means that the initial build was done at comparatively high cost and lower coverage with sequencing technology circa 2003. The new Build currently in progress addresses some of these deficits by adopting a hybrid approach that fuses NextGen and Sanger reads and by including the nearly finished quality Z sequence of Bellott et al. (2010). As with other vertebrate genomes, a major problem in the current sequence relates to segmental duplications. An obvious example of this comes from Bellott et al. (2010) who identified a tandem array of four testis-expressed genes that constitutes ~15% of the Z chromosome, one-fifth of all chicken segmental duplications and in total about a third of the protein-coding genes on Z. The

array exists in two blocks that were unassembled in Build 2 (partly in fragments on chrUn but mostly missing). It's well known that such duplications are frequently missed ("over-collapsed") in draft quality WGS assemblies, that they are common sites of copy number variation (CNV), and that such variation frequently has major phenotypic consequences (e.g., Conrad et al., 2010). Another example of obvious relevance is that Build 2 contains only two closely linked interferon genes (IFNA and IFNB) whereas Sick et al. (1996) showed that there are actually 11 or more tandemly duplicated genes in this cluster. A third example is that of the major histocompatibility complex (B-complex in chicken) on GGA16 (one of the smallest microchromosomes), a region of great immunological importance, and another region with many gene duplications and CNV. Directed sequencing of selected BACs was critical to elucidate the organization of this region (Shiina et al., 2007).

**However, the chicken genome assembly has a particular problem that appears not to be shared with those of mammals: the missing sequence/microchromosome problem.** Like most birds, chickens contain about 10 "macrochromosomes" with lengths typical of those in mammals, but the remaining 28 autosomes are "microchromosomes" that are too small to easily distinguish or order by standard cytogenetics. Moreover, as confirmed by the draft sequence (International Chicken Genome Sequencing Consortium, 2004), the microchromosomes are unusual in base composition (GC rich), recombination rate (high cM/Mb), gene density (high) and intron size (low). **Of primary importance to this white paper, microchromosome sequences are underrepresented or totally missing in both the sequence assembly and all clone libraries examined to date.** The reason for the missing sequence remains uncertain, but it is especially problematic for the smallest chromosomes, GGA16, 25 and 27-38. Representation of these chromosomes in both chicken and turkey BAC libraries is typically even less than that of the hemizygous Z chromosome, and no distinguishing BAC probes are available for GGA29 and higher. As a result, there either is no sequence alignment to these chromosomes (GGA29 and higher, except for ~1 kb on GGA32) or the assembly is incomplete and uncertain (GGA16, 25, 27, 28). This was demonstrated by the ordered resequencing of GGA28 by Gordon et al. (2007) which greatly reoriented its assembly. While a significant fraction of the missing sequence is likely repetitive, it's clear that a substantial number of genes are also missing. For example, the great majority of chicken genes homologous to those on HSA19q cannot be found in the assembly, and, for the most part, they are also missing in chicken BAC libraries and in the Trace Archives (Gordon, Stubbs and Groenen, personal communication).

It was initially thought that the missing microchromosome sequences arose from an inability to be cloned in *E. coli*. However, the recent turkey genome sequence assembly (Dalloul et al., 2010) was shown to be equally deficient in HSA19q orthologues, even though it was based on NextGen sequencing with no cloning involved! Similarly, extensive 454 and Illumina sequencing of chicken at WUGSC has not added substantially to the microchromosome assemblies. Thus, the explanation for the missing sequence remains uncertain, but it most likely involves a combination of poor clone representation, high GC content leading to poor sequence reads and a high density of simple tandemly repetitive sequences that interfere with assembly and may lead to reads being automatically filtered out as problematic during the assembly process. Much of the missing sequence may lie within the 39 Mb that still remain on chrUn\_random in the soon-to-be-released assembly. It also remains possible that some characteristic of these chromosomes makes it unusually difficult to recover DNA from them.

### III. Approach

Improving the chicken sequence will require a combination of clone-by-clone finishing, new sequencing technology and directed approaches focusing on the microchromosome problem.

**a. Clone by clone finishing.** This is the standard approach in use for human and other genomes and already shown to be effective for GGA28 (Gordon et al., 2007) and GGAZ (Bellott et al., 2010). BACs can be selected from the existing map (Wallis et al., 2004) and/or additional probing of existing BAC and fosmid libraries for finishing. In some cases, long range PCR can be used to cross gaps of appropriate size. Selected clones or clone pools can be sequenced using NextGen approaches to eliminate the need for subcloning. The primary focus of these directed efforts should be on areas of likely segmental duplication (Völker et al., 2010) and on those

microchromosomes that are partially assembled but unfinished. While this approach will clearly improve the sequence assembly in problem areas, by itself, it is unlikely to fully address the missing microchromosomes.

**b. Next generation sequencing technologies.** The development of new sequencing technologies is rapid, and at least some of these may help in addressing the missing sequence problem. A prime example is the long reads described for Pacific Biosciences instruments (Eid et al., 2009). Long reads across repetitive regions may allow for assembly of sequence contigs that currently either cannot be assembled at all or, at best, are consigned to chrUn\_random. However, based on the current experience at WUGSC, further developmental work will be needed before the current Pacific Biosciences sequencers are ready to tackle the problem. Other new technologies may be more robust to high GC or simple repetitive sequences. Perhaps DNA ligase-based approaches might prove more effective than polymerase-based sequencing for the missing regions. New assembly software might also help in addressing this special problem. It will also be important to map existing Illumina data onto the new assembly (based solely on Sanger and 454 data) in hopes of filling remaining small gaps. Furthermore, a number of NextGen sequences of various chickens or chicken lines and deep RNA-seq experiments have been performed or are underway (e.g., Rubin et al., 2010). Currently, those reads that don't map to the existing framework sequence are largely ignored, but these may well contain many sequences that fall in the microchromosomal regions. If these could be captured, even in very small sequence contigs, they could provide useful starting points for the directed approaches described below.

**c. Directed approaches at the missing, likely microchromosomal, sequence.** A variety of approaches can be used to address this issue. First, one could enrich for microchromosomal DNA by flow sorting or microdissection (Griffin et al., 1999) prior to amplification and NextGen sequencing. An alternate approach might involve the use of pulsed field gel electrophoresis to enrich for the smallest chromosomes (Spence et al., 2006). These approaches should succeed if the major obstacle involves isolating microchromosomal DNA in the first place and/or cloning it. Another category of approaches are based on the idea that at least small segments of sequence within the missing regions can be identified. As noted above, many segments of the missing microchromosomes may currently exist in chrUn\_random. Oligonucleotide sequences within the various chrUn\_random sequence contigs could be used either as probes to isolate and identify BACs or other clones for sequence finishing or in an array capture approach to enrich DNA for NextGen sequencing. An effort was made to capture at least the large contigs on chrUn\_random by SNP chip mapping, but this did not expand microchromosome coverage significantly. Another source of sequences of interest might be within Trace Archives or within existing unassembled NextGen reads (see part IIIb. above). These could be searched for significant homology to missing genes such as those identified on HSA19q (Dalloul et al., 2010). Then those oligonucleotides could be used for array capture sequencing or as probes. Likely fragments of some of the HSA19q orthologues have been identified within the Trace Archives, but this approach is rather narrow in that it can only focus on segments with homology to human genes, a small percentage of what's likely to be missing. However, at this point, any handle that would allow us to better understand the nature of the problem and give us an entry into the missing microchromosomes would be a useful start.

**IV. Expected value, benefit and impact.** As noted in the original White Paper for chicken sequencing, the chicken is the premier non-mammalian vertebrate model organism. We won't repeat the extensive justification provided in that document but will simply note that all of it remains in force. Rather, we hope to briefly highlight a few of the major impacts derived from the initial draft sequence of the chicken. First, the chicken sequence clearly delivered on its promise as an outgroup for comparative analysis of the human genome. Background (non-selected) homology between the chicken and human genomes is essentially nil, so the chicken-human comparison identified the ~5% of the human genome under selective pressure. Remarkably, more than half of this sequence is not within protein coding genes and, on average, is located farther away from genes than it would be in a random distribution (International Chicken Genome Sequencing Consortium, 2004, cited 783 times according to ISI Web of Knowledge). The sequence formed the framework for SNP discovery (International Chicken Polymorphism Map Consortium, 2004) and the development of SNP chips. This provided the opportunity to assess the worldwide genetic diversity of the chicken (Muir et al., 2008), a first for any agricultural animal and done to a depth greater than perhaps any animal species other than human. The

development of larger SNP chips has enabled whole genome association studies for quantitative traits and is currently allowing the major poultry breeders to implement whole genome-based selection strategies. Due to the relatively short generation time of chickens, the effectiveness of such approaches can be experimentally assessed much more easily than in cattle or swine. More recently, the reference sequence provided the basis for extensive resequencing of a variety of chicken genomes (e.g., Rubin et al., 2010) to examine the diversity in even greater detail and to reveal the many marks of selection that have occurred in both the domestication of the chicken and in experimental breeding populations such as high and low body weight lines. The draft sequence and associated maps also provided the framework for the sequence of the chicken Z chromosome which generated critical insights into the evolution of sex determination (Bellott et al., 2010). The chicken sequence also fulfilled its promise as the sequence of the model bird (and even the model dinosaur!) and was critical to the subsequent sequencing of the zebra finch (Warren et al., 2010) and the turkey (Dalloul et al., 2010), as it will be to all the avian sequences generated as part of the Genome 10K initiative (about half the total species proposed by the Genome 10K Community of Scientists, 2009). The sequence was also critical in the recent study of chicken centromeres (Shang et al., 2010) that suggests that at least some chicken centromeres are among the smallest known in vertebrates, of a size easily amenable to *in vitro* mutagenesis. As with Bellott et al. (2010), the Shang et al. paper (2010) specifically demonstrates the importance of finished quality sequence, as the chicken centromeres invariably fall within regions of segmental duplications that are poorly assembled.

To assess the continued relevance of the chicken as a model organism in the major biomedical fields and the size of the interested community, we repeated the PubMed search from the first White Paper, this time scanning only the period since the publication of the chicken sequence paper to the present. The result was the same – with the possible exception of neurology, there were many more citations for chicken than several other model non-mammalian vertebrates.

**Table 1. PubMed entries, 12/09/2004 to present (09/20/2010)**

Keyword	total hits	and development	and virus	and cancer	and neuron	and immunology	and pathology	and disease
chicken	17,678	4,077	3,062	1058	804	2,710	1539	2,892
Xenopus	8,533	2,285	136	560	978	191	348	414
zebrafish	7,340	3,627	101	610	1128	306	591	770
fugu	475	ND	ND	ND	ND	ND	ND	ND
tetraodon	160	ND	ND	ND	ND	ND	ND	ND

ND: not determined

It goes without saying that chicken is equally important as a source of high quality protein at a time when worldwide demand for this source of nutrition is growing rapidly (Rosegrant et al., 2001). Beyond the importance of a safe and nutritious food supply to human life, the enormous world-wide interest in raising poultry for food provides a collateral source of scientific data that inform our understanding of biology in general. The huge commercial populations means that large scale breeding studies can be done in the chicken. In many cases the traits that are of interest (nutrition, growth, disease resistance, reproductive success) to the poultry industry who possess the largest flocks are traits that are of similar importance to human health, so studies of chicken genetics and human medicine are often complementary.

The chicken genome sequence assemblies have been done either at WUGSC or at U. Md. CBCB in collaboration with WUGSC and are maintained and made publicly available by WUGSC. As noted, they are also made available to the community on the major genome browsers. As part of this white paper, scientists in both the agricultural and biomedical communities were consulted. Emails of support were received from 84 scientists, worldwide (list attached), **including Dr. Jesus Arango, current President of the Poultry Breeders of America, speaking on their behalf and Jim McKay, Neil O’Sullivan, Rudolf Preisinger, Alfons Koerhuis, and Ron Okimoto who direct research at some of the major poultry breeding companies, worldwide.** This testifies to the substantial interest of the poultry industry leaders who are actively using the sequence and associated SNP with their whole genome-assisted selection efforts.

**V. Turkey genome.** Although less important as a model organism, the turkey is also a major food source, the fourth largest meat commodity in the U.S. and a growing source of protein, worldwide. As noted above, the turkey genome sequence was recently published (Dalloul et al., 2010), based on a hybrid approach using combined Illumina and 454 sequencing reads and aligning the contigs to a detailed comparative(turkey-chicken)/physical BAC map. Last year, USDA-NIFA AFRI supported a Tools grant designed to enhance this sequence by accumulating additional data and extensive further annotation. Thus, it's likely premature to do additional extensive finishing in the turkey of the sort proposed above for chicken. **However, the overall turkey assembly still depends significantly on comparison to the chicken genome and appears to be missing the same microchromosome segments, so efforts to enhance the chicken sequence will have important collateral benefits for the turkey genome.**

As noted above, the goals for enhancing the chicken genome sequence are two-fold. First, finishing existing chromosome assemblies, particularly in areas of like segmental duplications. This is a task for a high volume sequencing center such as WUGSC. On the other hand, addressing the missing sequence/microchromosome problem may require novel enrichment approaches such as those described above. This might be more amenable to a competitive grant-based funding mechanism such as those of USDA-NIFA AFRI or NIH NHGRI R01 applications. We believe that such projects could fit within the funding range of typical R01 grants or previous AFRI Animal Genome Tools programs.

## VII. References

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## Appendix 1, Expressions of support received for enhanced sequence assembly for the chicken genome

Jesus Arango	President, Poultry Breeders of America on their behalf	Industry
Neil O'Sullivan,	Director of Res. and Development, Hy-Line International	Industry
Jim McKay,	Group Director for Science and Technology EW Group	Industry
Rudolf Preisinger,	Director of Research and Development, Lohmann Tierzucht	Industry
Alfons Koerhuis	Director of Research and Development, Aviagen	Industry
Ron Okimoto	Cobb-Vantress	industry, quant. genetics
Shane Burgess	Miss. State U.	proteomics, bioinformatics
Hans Cheng	ARS Avian Disease and Oncology Lab	genomics, virology
Mary Delany	UC Davis	chromosome structure, avian diversity
Doug Foster	U. Minn.	cell biology
Wayne Kuenzel	U. Ark.	neurobiology
Sue Lamont	Iowa State	genomics, Salmonella and other diseases
Bill Muir	Purdue	genomics, quantitative genetics
F. Abel Ponce de Leon	U. Minn.	genomics, cytogenetics
Tom Porter	U. Maryland	molecular neurobiology
Kent Reed	U. Minn.	turkey genomics and biology
Carl Schmidt	U. Delaware	genomics, bioinformatics
Lisa Taneyhill	U. Maryland	developmental biology
Huanmin Zhang	ARS Avian Disease and Oncology Lab	virology, quantitative genetics
Huaijun Zhou	Texas A&M	genomics, bioinformatics, diseases
Robin Morgan	U. Delaware	genomics, virology
Hsiao-Ching Liu	North Carolina State	genomics, virology
Mark Parcels	U. Delaware	virology
Henry Hunt	ARS Avian Disease and Oncology Lab	immunology, virology
Ed Smith	Virginia Tech	turkey genomics and avian biology
Titus Brown	Mich. State U.	bioinformatics, devel. biology
Martien Groenen	Wageningen U.	genomics, quantitative genetics
A.P. Jackson	U. of Cambridge	proteomics, cell biol.
Sean Kennedy	Environment Canada	toxicological genomics
Steffen Weigend	Friedrich Loeffler Institut	diversity genomics
Erich Jarvis	Duke University Medical Center	neurobiology
Roger Sawyer	U. of South Carolina	connective tissue development
David Clayton	University of Illinois	avian genomics, behavioral biology
Leif Andersson	Uppsala University	genomics
Revaz Solomonias	Iliia State University Tbilisi, Georgia	visual imprinting
Hermann Rohrer	U. of Vermont	neurobiology
Jez Guggenheim	Cardiff University	eye development
Craig Boote	Cardiff University	eye development
Avigdor Cahaner	Hebrew U. of Jerusalem	genomics
Paula Bovolenta	Instituto Cajal, CSIC	developmental biology
Susan Chapman	Clemson U.	genomics
Claudio Stern	University College London	developmental biology
Mirian Einat	ARO, Volcani Center, Israel	proteomics, genomics
Andrew Bendall	University of Guelph	genomics
Frank Schubert	University of Portsmouth	brain development
Luis Puellas	Univ.of Murcia,	brain development
Guojun Sheng	RIKEN Center for Developmental Biology	developmental biology
Hisato Kondoh	Osaka University	developmental biology
Paul Layer	Technische Universit Darmstadt (TUD)	brain development
Ruth Diez del Corral	Instituto Cajal, CSIC	developmental biology

Delphine Duprez	U. Pierre and Marie Curie	muscle development
Ian Dunn	University of Guelph	development, QTL
Wolfgang Schneider	Medical University Vienna	genomics
Paul Hocking	University of Edinburgh	reproduction and development
Andrea Munsterberg	University of East Anglia	genomics
David Hume	University of Edinburgh	developmental biology
Thomas Brand	Imperial College London	developmental biology
Brian McCabe	U. of Cambridge	neurobiology
Dalit Sela-Donenfeld	The Hebrew University Of Jerusalem	neurobiology
Raquel Andrade	U. of Minho	developmental biology
Roger Keynes	U. of Cambridge	developmental biology
Imelda McGonnell	Royal Veterinary College, London	neurobiology, skeletal bio.
Olivier Gandrillon	U. of Lyon	genomics
Darren Griffin	University of Kent	cytogenetics
D.B. Hales	Southern Illinois U. School of Medicine	ovarian cancer
Juan Carlos Izpisua Belmonte	The Salk Institute for Biological Studies	developmental biology
Joy Richman	Life Sciences Institute, UBC	molecular biology, transcription factors
Seema Agarwala	University of Texas at Austin	neurobiology
Julian Sale	MRC Laboratory of Molecular Biology	DNA replication and repair
Clare Baker	University of Cambridge	neurobiology
Bertrand Pain	Ecole Normale Sup eure de Lyon	reproduction and development
Berta Alsina	Universitat Pompeu Fabra/PRBB	developmental biology
Dave Burt	Roslin Institute and U. of Edinburgh	genomics, dev. biol.
Helen Sang	Roslin Institute and U. of Edinburgh	reproduction and development
Andrea Streit	King's College London	developmental biology
Kate Storey	University of Dundee	neurobiology
Mike Skinner	Imperial College London	virology
Diana Darnell	Department of Cell Biology and Anatomy, U. of Arizona	gene regulation
Cliff Ragsdale	The University of Chicago	brain development
Susanne Dietrich	King's College London	neurobiology
Susan Mackem	NIH	limb development
Jose Maria Frade Lopez	Cajal Institute (CSIC)	developmental biology
William Upholt	University of Connecticut Health Center	developmental biology
Raj Ladher	RIKEN Centre for Developmental Biology	developmental biology