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The Genome 10K Project: A Way Forward

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Abstract

The Genome 10K Project was established in 2009 by a consortium of biologists and genome scientists determined to facilitate the sequencing and analysis of the complete genomes of 10,000 vertebrate species. Since then the number of selected and initiated species has risen from ~26 to 277 sequenced or ongoing with funding, an approximately tenfold increase in five years. Here we summarize the advances and commitments that have occurred by mid-2014 and outline the achievements and present challenges of reaching the 10,000-species goal. We summarize the status of known vertebrate genome projects, recommend standards for pronouncing a genome as sequenced or completed, and provide our present and future vision of the landscape of Genome 10K. The endeavor is ambitious, bold, expensive, and uncertain, but together the Genome 10K Consortium of Scientists and the worldwide genomics community are moving toward their goal of delivering to the coming generation the gift of genome empowerment for many vertebrate species.

Keywords

mammal; amphibian; reptile; bird; fish; genome

INTRODUCTION

The advent of low-cost, high-throughput sequencing has ushered in a new age of genome science and has forever changed the landscape of biological research. Projects that could only be dreamt of 10 years ago are now becoming a reality. The Genome 10K Project (hereafter the G10K Project) is one such project (1–3). Sequencing 10,000 vertebrate genomes is an ambitious and worthy goal that will provide a foundation for diverse research and exciting discovery for decades to come. We originally selected a goal of 10,000 species

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DISCLOSURE STATEMENT

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(from a total of over 62,000 named vertebrate species) (Figure 1) as a round number target that was achievable, and which includes nearly every species with even modest biological knowledge available plus several thousand species without much knowledge. A detailed description of the rationale is presented in the original G10K White paper (1).

The G10K Project was founded in 2009 by bringing together biologists, bioinformaticians, and computational scientists to accumulate and organize specimens, to develop standards for genome assembly and annotation, and to facilitate the release and use of the genome data created through the project. At the first G10K workshop in Santa Cruz, California (April 13–16, 2009), biologists who curated museum or personal frozen collections of biospecimens were convened and asked to develop a list of vertebrate specimens available in collections globally, which then would become the basis of the G10K Project. Amazingly, the group found that 16,203 vertebrate species had already been collected and were housed in existing collections. These were collated into a database (http://genome10k.soe.ucsc.edu) that became the foundation for developing initial plans for whole genome sequencing (WGS) (1).

Since 2009, the G10K Project has grown in membership, in responsibilities, in recognition, and in stewardship. At the most recent G10K workshop (April 24–28, 2013) in Fort Lauderdale, Florida, over 150 scientists gathered to develop plans for future genome sequencing and discuss analytical and computational challenges and the exciting results from the first ~270 vertebrate genomes sequenced to date. Here, we provide an overview of the goals, responsibilities, accomplishments, and insights of the G10K Project, where the project stands today with regard to the vertebrate genomes that have been sequenced thus far, and the remaining challenges involved in reaching the goal of sequencing 10,000 vertebrate genomes.

GENOME 10K RESPONSIBILITIES

The G10K Community of Scientists (G10KCOS) established six primary goals or responsibilities to drive the project forward (Table 1). Our first charge was to accumulate biospecimens that would provide the DNA necessary to develop reference-quality genomes. The 2009 G10K meeting identified over 16,000 species from existing collections in museums, universities, and zoos around the world and cataloged that inventory in an open-access database accessible to the entire community (https://genome10k.soe.ucsc.edu/biospecimen_database). Samples included in this virtual repository ranged from extracted genomic DNA to frozen tissues to cell lines. In addition to compiling this virtual list, we produced an in-depth report of best practices for obtaining and storing vertebrate biospecimens for WGS (4).

A second goal of the G10K Project is to foster the development of research communities centered either around the genomes of species or species groups (e.g., birds) or around bioinformatics themes, namely genome assembly, annotation, alignment, and comparative analyses. Such communities are vital because not only do they help establish criteria for the selection of species to be sequenced but they also ensure interdisciplinary collaboration among scientists with diverse research experiences. For example, whereas one scientist may

intend to use a reference genome to analyze genome architecture, another may use the same data to search for evidence of positive selection. Thus, an open-access genome becomes a commodity that drives multifaceted research programs in different fields. Within the G10K Project, communities of scientists are broadly organized around the major classes of vertebrates (fishes, amphibians, nonavian reptiles, birds, and mammals), and these communities strive to identify target species for genome sequencing that benefit the largest group of scientists and fill major genome sampling gaps across the vertebrate tree of life.

A third goal of the G10K Project is to develop a strong and scientifically vetted set of standards concerning specimen selection, DNA preparation, genome assembly, genome feature annotation, whole genome alignment, comparative analyses, and data release. Despite the tremendous progress that has been made in genomics, the field itself is still in an experimental state with no established best practices in the generation and analysis of genome data. Various genomic groups develop their own ideas about sample quality and quantity for de novo sequencing as well as about what constitutes a high-coverage genome. They often use home-brew or unvetted software, even though several groups have established that software programs developed for assembly, annotation, and alignment differ markedly in accuracy and efficiency (5–8). G10K scientists aim to develop a set of consensus-based best practices regarding genomic data generation and analysis. For example, given a shark, frog, or microbat, which tissue(s) would be most useful in producing genomic libraries? How should these biospecimens be preserved? How is DNA derived from them handled? Which sequencing libraries should be prepared? Given the choice of among 20+ genome assembly algorithms and programs, which one produces the most accurate assembly, and what parameters are best for evaluating this? The G10KCOS is developing informed guidelines in addressing issues such as these through collaborations between biologists and bioinformaticians. A preliminary snapshot of G10K endorsed standards is presented in the sidebar, Draft Standards for Genome 10K.

A fourth responsibility for the G10KCOS is to record the progress of vertebrate WGS by maintaining a database of completed and ongoing projects being carried out by genome sequencing centers and by independent research laboratories around the world (http://genome10k.soe.ucsc.edu/species). By doing this, we not only avoid duplication of efforts, given the still relatively high expense of generating and annotating reference-quality genomes, but also help to target the species that will maximize research dividends and increase breadth of phylogenetic coverage in the vertebrate tree of life (9). Table 2 presents a list of 164 vertebrate species with a published genome sequence, and Table 3 lists an additional 113 vertebrate species for which genome sequencing is accomplished or near completion.

The fifth goal of the G10K Project, raising funds, is an evolving exercise. The G10K Project was initially predicated on the expectation that the costs associated with genome sequencing would decrease rapidly, making it relatively affordable to sequence vertebrate genomes with size scales similar to the human genome (10–12). However, even as sequencing costs decline, the cost of data processing and bioinformatic analysis remains substantive. The G10KCOS is addressing this challenge by fostering training workshops that empower computer-savvy students in analysis of genome data (see below for these bioinformatics

challenges). The G10KCOS endorses research development grants and proposals that facilitate local funding of genome projects and encourage investigator-initiated fund development from government, corporate, and entrepreneurial resources. G10K has signed memorandums of understanding with large sequencing centers, such as BGI-Shenzhen and the Broad Institute, to work together to increase the quality and quantity of vertebrate genome sequencing endeavors. For example, in 2010 BGI-Shenzhen agreed to sequence and fund the first ~1% (105 species) of vertebrate genomes in close collaboration with the G10KCOS. At this writing, whole genome sequences have been completed for 70% of these species, and of these, 43 have been published (Tables 2 and 3).

Initial publication of a genome sequencing project frequently generates additional funding, particularly when the published genome of a species stirs excitement and enthusiasm in the public imagination. Whether it is the genome of the giant panda (13), with its revelations about the genetics of its ability to digest bamboo; the elephant shark (14), as a model for the evolution of the vertebrate body plan; or the minke whale (15), providing a glimpse into the adaptations associated with becoming aquatic, many of the opportunities we already have with today's sequencing technology are too enticing to pass up while waiting for technology to improve.

Lastly, the G10K Project has spread across biology to inspire similar large community initiatives to sequence the genomes of nonvertebrate species (our sixth goal), including insects (i5K), noninsect marine invertebrates (GIGA), plants (NSF Plant Genome Research Program), fungi (1000 Fungal Genomes Project), and microbes (100K Foodborne Pathogen Genome Project) (see Table 1).

BIOINFORMATICS CHALLENGES TO WHOLE GENOME SEQUENCE ANALYSES

The G10KCOS is presently working to identify and prioritize the next set of vertebrate species for genome sequencing (e.g., Reference 16). This process relies on insights from the bioinformaticians who will lead the assembly and analysis of the sequence data (17, 18). A critical first step in genome assembly is to determine what sequence data will be most useful to maximize the potential for de novo and reference-guided genome assembly. Large-insert genomic libraries, long sequence reads, and physical map–based technologies are crucial in assembling longer contiguous sequence fragments. High-quality (undegraded) DNAs in high-microgram quantities are required. Better methods for de novo genome sequencing from smaller (nanogram) amounts of DNA will make sample collection easier for many additional smaller species. Another important consideration for genome assembly is the size and repeat content of the target genome. Larger and more repetitive genomes will be more costly to sequence and assemble. Complex and abundant repeat families present in many species confound genome assembly, especially if the repeating units are long and highly similar to one another. Unfortunately, it is not always possible to determine the repeat content of a genome until some preliminary sequence sampling has been performed.

Another key bioinformatics challenge is sequence heterozygosity and its disposition across the genome. Available assembly algorithms erect a haploid reference genome by merging

the information from the two parental genome sequences, often making arbitrary phase assignments, frequently producing chimeric contigs and scaffolds. A highly heterozygous individual can make assembly inaccurate or impossible. This can be assuaged by selecting highly inbred or haploid individuals, but these are unavailable for most species. Abundant segmental duplications, which may appear as additional haplotypes, add to the problem. These may be polymorphic, and hence heterozygous as well. Mixtures of DNA from multiple individuals, undertaken to obtain sufficient input DNA for some sequencing libraries, create an additional layer of complexity.

Given the current challenges in assembling a large (>>3-Gbp), repeat-rich genome with a high level of heterozygosity, many such genome projects are being deferred until the future. Even for typical vertebrate genomes, there is constant awareness that the longer one waits to sequence one's favorite genome, the cheaper and higher quality it will become. Species for which genomic sequences were generated and assembled relatively early in the large-scale comparative genomics era can be of lower quality, with inaccurate assemblies, missed paralogs, and chimeric chromosomal segments [see, for example, the platypus (19) and giant panda (13) genomes; 20]. Assemblies for certain species that were first to be sequenced (e.g., chicken, chimpanzee) have been validated and improved using complementary mapping and assembly approaches, but they are expensive and time consuming. Prioritizing species for sequencing is a complex process that must balance the needs of individual communities, the overall G10K effort, funding constraints, and emerging technologies.

EVALUATING GENOME ASSEMBLIES

The initial step in making a genome useful to the biological community that studies a species is to produce an assembly of the millions of short DNA reads obtained from next-generation sequencing technology into an ordered and oriented sequence of contigs that resembles the order in which the assembled sequence actually occurs on each chromosome (see References 20–22). Genome assembly begins with homology match detection of reads to build short contigs. Contigs are then joined with mate pair end reads to form scaffolds, which within ideal assemblies span millions of base pairs. The process is completed when scaffolds are assembled into chromosomes using independent physical framework maps. The G10KCOS has evaluated a dozen or more available computational assembly tools, termed assemblers, which have been developed to accomplish this process in the Assemblathon competitions (7, 8). The challenges are detecting and correcting assembly mistakes caused by repeat sequence families, by copy number variation of certain DNA stretches, and by single-nucleotide variants (SNPs), the stuff of evolution and the scourge of a basic assembler (e.g., Reference 21). Assemblathon competitions first compared different assembly tools using a simulated vertebrate genome (7) and then three genome sequences from a cichlid fish, a parakeet, and a snake (8). The Genome Assembly Gold-standard Evaluation consortium and study further evaluated assembly quality of genomes across a broad array of species (5).

Lessons learned from the Assemblathons and other evaluations have led to the development of new assemblers. DISCOVAR de novo (http://www.broadinstitute.org/software/discovar/blog/; 23) is a new assembler developed at the Broad Institute that avoids the need for

polymerase chain reaction (PCR) and in fact requires PCR-free libraries. This leads to improvements because compositional biases present in PCR-based approaches confound assemblers by generating nonuniform read depth. Although DISCOVAR is currently being used for resequencing projects, its real promise may be to assemble de novo genomes.

To evaluate assembly quality, new metrics have also been developed beyond N50 (the smallest length N such that at least 50% of the bases in the assembly are in contigs of that length or greater). Probabilistic measures based on likelihood statistics have been used and shown to provide more accurate and objective evaluations of assembly quality, independent of a reference genome (24–26). For example, the program CGAL uses the uniformity of genome coverage to evaluate the likelihood of assembly quality while simultaneously taking into account sequencing errors, insert size distribution, and extent of unassembled data (26). When CGAL was applied to the Assemblathon 1 data set, assemblies with a higher extent of coverage tended to be more accurate. These methods allow researchers to optimize parameters associated with assembly programs to obtain better-quality assemblies (with higher likelihood values) and are likely to become standard tools in obtaining high-quality assemblies (25).

A major finding of the Assemblathon studies is that there is considerable variation among output assemblies. Users cannot simply merge the outputs of many assemblers to arrive at an optimal consensus assembly. One assembly program, Metassembler (M. Schatz, unpublished data; http://schatzlab.cshl.edu/presentations/2011-11-03.Genome%20Informatics.pdf), actually does this, but its accuracy is no better than its best constituents. Assembly is a complex problem with many trade-offs, and there are no easy solutions (25). Has genome assembly with short reads reached a point of diminishing returns? At the G10K 2013 workshop, we learned that though many algorithms are still in development, accuracy is not substantially improved when only short reads are available, suggesting new sequencing approaches are needed to make the next quantum leap.

Large-Insert Sequencing Methods

New methods that improve the outlook for de novo genome assembly by sequencing large inserts with distinctly barcoded short reads are on the horizon. Protocols based on sequencing fosmid pools (~30 kb/fosmid) have gotten less expensive while still achieving long-range order and orientation of contigs (27, 28) (Table 4). Illumina-Moleculo technology, at approximately 10 kb per independently barcoded insert, provides similar benefits at lower cost. Its cost and overall feasibility for G10K have not been well established, though several groups have recently used Illumina-Moleculo reads to haplotype the human genome, with promising results (29).

Table 4 lists promising new long-read technologies, although each of these is as yet unproven for very large-scale (~3-Gbp) genome assembly. The single-molecule, real-time sequencing technology (SMRT) manufactured by Pacific Biosciences (PacBio) has been available for several years, but its higher relative cost and higher basic error rate have restricted its use to microbial genomes and eukaryote transcriptomes (30, 31). However, ongoing improvements in SMRT sequencing are beginning to ameliorate these concerns (32), and high-quality assemblies can often be obtained through hybrid approaches in which

assemblies are generated using both short reads (e.g., Illumina) and long reads (e.g., PacBio) (33). Oxford Nanopore long reads have evoked considerable hopefulness as genome scientists are piloting genome assembly for accuracy, feasibility, and cost effectiveness. As various long-read technologies improve and their prices fall, it is likely that they will become part of typical genome assembly efforts.

Mapping Methods to Assist in Assembly

Mapping methods can also be used to improve assembly. Richard Durbin from the Wellcome Trust Sanger Institute proposed at the 2013 G10K meeting the sequencing of trios (mother, father, child) to improve genome assembly through a direct haplotype-phase resolved linkage map (280). Using SNP variation as an information source in assembly is a unique and potentially powerful new strategy that would anchor scaffolds to an ad hoc haplotype map. However, this approach does require additional sequencing. These techniques are an addition to single-sperm genome amplification (producing individual genome-wide haplotypes as well as whole genome assemblies) and other sequencing approaches that in theory can build a recombination and/or physical map using bioinformatics analysis (34–36).

Framework physical maps have been a mainstay for anchoring genome assemblies of model species (human, mouse, rat, dog, cat, and others) (20). However, linkage and radiation hybrid physical maps for these genome projects are rather expensive for wider-scale use. Optical mapping, a relatively new tool for building an independent physical map to anchor assembled scaffolds of sequenced genomes (e.g., Reference 37), was evaluated favorably in Assemblathon 2 (8). Map-generating technologies pioneered by BioNano Genomics, the Irys System, use rare-cut genomic DNA subjected to electrophoretic current to produce physical maps as well (38, 39). Physical or optical mapping methods can be used to improve graph navigation (40), to validate chromosomal ordering of contigs, and to detect and break up chimeric contigs. Random fosmid sequencing was also used as a kind of physical map for evaluation in Assemblathon 2. Although laborious and expensive, clone-based sequencing has the advantage of reduced size and no sequence heterozygosity. Genome assemblers can benefit from transcriptome information (41) to guide their algorithms as well as from comparative syntenic similarity employed by the Reference-Assisted Chromosome Assembly algorithm (42). These avenues of research must be explored more thoroughly as genome alignment and comparative genome analyses become more central to the G10K Project.

GENOME ANNOTATION

Genome annotation encompasses the description of a variety of elements that can be identified in a species' genome, from protein-coding regions and intervening noncoding sequence to repeat families, noncoding RNAs, regulatory motifs, and specific elements (Table 5). For identification of protein-coding genes, transcriptome information via RNA-seq data is invaluable before, during, and after a genome has been assembled (6). Noncoding RNA genes, such as structural RNAs, microRNAs, and long noncoding RNAs, are also identified by RNA-seq in conjunction with bioinformatics sequence analysis and play key

roles in the cell (e.g., Reference 43). One of the main reasons to sequence a genome is to investigate its genes, and RNA-seq can provide some of this information at a fraction of the cost of a whole genome assembly. Flanking the genes, one finds a variety of regulatory elements, some of which are highly conserved between species and hence recognized from sequence, whereas others are more rapidly evolving and require experimental assays involving chromatin immunoprecipitation followed by sequencing (ChIP-seq) or DNase I hypersensitive site sequencing.

Available software programs for discerning genes and other features (Table 5) have been employed to unravel the secrets of new genomes on a regular basis. There are no precise best practices for gene selection, SNP discovery, or repeat annotation, although it has been shown that consistency may be low across different algorithms and methods [e.g., SNP calling (44) or reconstruction from RNA-seq data (45)]. The G10KCOS is considering an annotation-collaborative exercise (such as the Assemblathons and the Alignathon) to develop more explicit guidelines for vertebrate genome annotation.

GENOME ALIGNMENT

A comparative genomics approach between related species is fundamental to the identification and analysis of genes, their regulatory elements, and their adaptive natural history (6, 46–48). As such, comparative analyses of homologous genes in a syntenic context among related well-annotated species is a mainstay of annotation pipelines (49, 50). Such analysis depends heavily upon accurate multiple genome alignments. Exceptions to gene sequence conservation can indicate evolutionary gene changes, chromosome rearrangements, gene family expansion or contraction, and SNP-based signatures of historic selection. Discerning these genome modifications allows critical insights into the events occurring over the course of speciation and divergence of taxa. But comparative analysis of genomes from distantly related species is not simple, rather akin to comparing the assembly blueprints of a Boeing 747 to a Mercedes-Benz sedan, to a Yamaha motor scooter, and to a tricycle. A first step is to design an efficient strategy for aligning the entire gigabase-long genomes of related species.

Genome alignment, the task of aligning all the homologous nucleotides in a set of complete genomes, including those in noncoding regions, is critical if we are to establish the genetic relationships and, by extension, evolutionary history of our shared vertebrate ancestry. Genome alignment can be thought of as a generalized form of the DNA alignment problem, in that all other (classical) forms of alignment are a subclass of this general problem. The Alignathon competition invited participants to submit solutions to constructed or collected data sets (51). Three independent data sets, two simulated from primates and mammals and one a set of 20 *Drosophila* genomes, were offered for trial of various alignment algorithms. All the data sets involved genomes of approximately 200 Mbp in length, a decision made to create a meaningful challenge that was nonetheless accessible to the broadest possible range of tools. In all, 35 different analytical solutions were submitted by 10 teams using 12 distinct alignment pipelines (51).

Several important conclusions were reached through the Alignathon competition. First, relatively few groups and very few tools are currently capable of making precise genome alignments even at the scale of the 20-*Drosophila*-genome data set. For example, 11 of the 35 submitted alignments were computed using variants of the Multiz alignment pipeline (52), which is now over ten years old. Second, many current genome alignment tools have noticeable limitations. In particular, many of the entries were reference-based (genomes aligned to a reference genome as a key step), which produced a noticeable bias in the quality of alignments between nonreference genomes. Notably, only two of the alignment teams attempted to align multiple paralogous sequences. Third, there are few broad metrics for assessing genome alignments of real genomes that can be used to assess the quality of the alignment across the genome, and which do not rely on expert biological information (e.g., the location of annotations), and even fewer that have robust implementations. Fourth, consistent results were found between the simulation study and metrics for assessing the real alignments (53). Lastly, there exists tremendous variability in performance between alignment programs, though there is much less variance when aligning closely related organisms. With increasing evolutionary distance between compared species, all the various whole genome alignment tools get progressively less reliable.

The Alignathon was successful in revealing both the strengths and weaknesses of available whole genome alignment tools, but there remain several important directions for future work that, when pursued, will provide valuable information for the G10K and eukaryotic genomics community as a whole. A proposed second Alignathon competition in the future would address the following topics:

1. the impact of assembly errors on alignment. Addressing this would ideally be an integrative analysis with the Assemblathon group.
2. scaling to larger genome sizes with greater complexity and more repeats; i.e., evaluating and comparing results of full-size vertebrate genome alignments.
3. a comparison of methods for the alignment of genes within genome alignments.
4. the accuracy of cross-validation methods; one way to assess genome alignments is to set aside the sequence of a target genome and then assess how closely an imputed ancestral genome based upon a genome alignment of the other genomes matches the target genome. Such approaches have been used previously (52, 54) but never for complete genomes and genome alignments.

Computing genome alignments is computationally intense and requires several thousand CPU hours per genome. One of the main problems encountered in the first Alignathon was the lack of groups with sufficient computational power to compete. This is a critical problem that must be addressed by the development of more efficient methods, coupled to an increased commitment to provisioning more powerful computer resources for multiple alignments.

PROGRESS AND FUTURE PLANS FOR WHOLE GENOME SEQUENCING OF 10,000 SPECIES

In the five years since Genome 10K was proposed, the genomes of 277 vertebrate species have been proposed, funded, accomplished at some level, and released; of these, the genomes of 164 species have been reviewed and published (Tables 2 and 3). These achievements reflect efforts from larger sequencing centers, independent projects from individual teams, the BGI-G10K collaboration, and other G10KCOS initiatives, altogether a remarkable accomplishment. An additional 200+ species are named on websites of sequencing centers (BGI, the Broad Institute, the Baylor College of Medicine Human Genome Sequencing Center, The Genome Institute at Washington University, and others) as pending, with a substantial degree of uncertainty about their timetable for completion. The initial G10KCOS selection of species has been discussed (1), and a wealth of vertebrate evolutionary genomic diversity is beginning to be produced. Next, we summarize the challenges, accomplishments, and insights of G10K to date regarding the five principal taxonomic classes of vertebrates (Figure 1).

FISHES

More than half of all vertebrate species are fishes, which include the jawless (Agnatha), cartilaginous (Chondrichthyes), lobe-fin (Sarcopterygii), and ray-fin (Actinopterygii) fishes, with the latter group being the most diverse in number of species (Figure 2). The first nonhuman vertebrate genomes to be sequenced were those of the teleost fishes, a group that contains many species with genomes that are unusually small in size and therefore amenable to whole genome shotgun sequencing (e.g., fugu, *Takifugu rubripes*; 55, 56). Since then, a draft genome sequence from another pufferfish species, *Tetraodon nigroviridis*, has been produced (57), along with the genomes of the medaka (*Oryzias latipes*), three-spined stickleback (*Gasterosteus aculeatus*), zebrafish (*Danio rerio*), and platyfish (*Xiphophorus maculatus*), all of which serve as important model organisms for studies of gene function in development and adaptive evolution (58–61). Annotation of the zebrafish genome revealed over 26,000 protein-coding genes as well as the highest number of species-specific genes yet found for any vertebrate species whole genome sequenced to date. This large gene number is likely due to the whole genome duplication event that occurred early in the history of teleost fishes, resulting in the formation of numerous functional gene duplicates (60). Since these earlier studies, the number of fish WGS projects, both published and ongoing, has increased dramatically, providing many key insights related to physiological adaptations and vertebrate evolution (62, 63).

Given the breadth of vertebrate species diversity represented by the fishes, the majority of species planned to be de novo sequenced by the G10K Project will be fishes, particularly the teleosts (see Reference 16). As a first step toward that goal, 30 of the first 105 species to be selected for WGS through the collaborative efforts of BGI and G10K are fishes, including one cartilaginous fish, the elasmobranch great hammerhead shark (*Sphyrna mokarran*); two representatives of the early-branching Chondrostei; and 27 species of teleost fishes that encompass 12 orders. At this writing, the genomes of 24 fish species are published and 47

others are near completion (Tables 2 and 3). In anticipation of future genome sequencing efforts, the G10K fish community has identified a global list of 100 fish species that were nominated as gold standards, in that besides WGS, transcriptomes and stable cell lines will be generated for these species (16).

AMPHIBIANS

Amphibians comprise approximately 11% of vertebrate species. New taxa are described and reported for this group every year, implying that total amphibian biodiversity may be greatly underestimated (64). Among 7,300 named amphibian species, we currently have whole genome sequences available for only two species, both being anurans and from the same genus, the western clawed frog [*Xenopus* (*Silurana*) *tropicalis*] and the African clawed frog [*Xenopus* (*Silurana*) *laevis*] (Tables 2 and 3) (65; see also http://www.xenbase.org/entry/). Genome size is extremely variable within amphibians, varying by as much as ~130-fold (66, 67). Further, amphibians harbor some of the largest genomes, which has significantly hampered progress in the sequencing of additional amphibian genomes. The largest tetrapod genomes are found within the salamanders (Caudata), with sizes ranging from ~14 to ~120 Gb (68). Preliminary genomic scans of several salamander taxa indicate that large genome size may be related to the extensive proliferation of long terminal repeat retrotransposons (69). Such large genomes increase the cost of collecting raw data (many more libraries are needed to achieve adequate coverage) and increase the computational complexity of the assembly and analysis of those data. Additionally, the small physical size of most amphibians limits the amount of tissue that is available for making large-insert mate-pair libraries.

Despite the challenges and high costs of obtaining a diversity of amphibian genomes, there are reasons that these costs may be justifiable to some extent, considering how underrepresented this important group is currently among the list of completed vertebrate genomes (Table 2). Future developments in assembly strategies, especially the use of long reads discussed above (Table 4), may enable large genomes to be assembled more readily. Given the remarkable and unique adaptations developed in this vertebrate class, the complete absence of an understanding of the diversity of amphibian genome structure, content, and evolution poses a major gap in our knowledge of living vertebrates (66).

Among the first 105 species nominated for WGS through the BGI-G10K collaborative effort, nine amphibians were chosen to represent a broad level of divergence across the (mostly) anuran tree of life (Table 3). Species targeted for WGS include the coastal tailed frog (*Ascaphus truei*), a member of the Archaeobatrachia, which includes species showing primitive characteristics not found in other anurans and therefore represents a key lineage in the anuran tree of life. Also included is a member of the amphibian order Gymnophiona (caecilians), represented by the Banna caecilian (*Ichthyophis bannanicus*). At present, sequencing has been completed for the Tibetan frog (*Nanorana parkeri*), now in the draft assembly stage. At least one other independent anuran genome project is under way, that of the cane toad (*Rhinella marina*), a species originally found in Central and South America but later introduced into Hawaii, Australia, and parts of Oceania, where it has become an invasive (70). This species is also in the assembly stage.

WGS has also begun on well-studied frog species with relatively small genome sizes, such as the túngara frog (*Physalaemus pustulosus*), important in studies of sexual selection (71); the coqui frog (*Eleutherodactylus coqui*), important in studies of the evolution of direct development (72); and the plains spadefoot toad (*Spea bombifrons*), important in studies of speciation and adaptive hybridization (73). An additional small-genome species, the eastern banjo frog from Australia (*Limnodynastes dumerilii*), provides phylogenetic breadth. BGI-G10K is also taking on one large-genome species, the strawberry dart-poison frog (*Oophaga pumilio*), important for studies of rapid phenotypic evolution under natural and sexual selection (74). WGS data collection should begin soon on the last of the nine amphibian G10K species, including the horned marsupial frog (*Gastrotheca cornuta*), with its unusual reproductive biology and high conservation concern (75).

Looking toward the future, we see three main priorities for sequencing the genomes of additional amphibian species. First, a high-quality assembly should be provided from at least one member of each of the three extant amphibian orders (Anura, Caudata, and Gymnophiona). The BGI-G10K-selected amphibian species will meet two-thirds of this goal with sequencing the genomes of nine Anura and one Gymnophiona species (Table 3). As for Caudata, independent efforts are currently under way to sequence and assemble the genome of the Mexican axolotl (*Ambystoma mexicanum*), an important model organism used for research in a variety of fields, including embryogenesis, regenerative biology and medicine, neurology, and sensory biology (see http://www.ambystoma.org/). Amphibians are the sister group to amniotes, and complete genomes from representatives of all three amphibian orders could therefore provide new information about the characteristics of the amniote ancestral genome and how vertebrate lineages have diverged since this ancestor (76).

The second priority would expand WGS and annotation to incorporate species with smaller-sized genomes. Because a reference genome assembly is paramount to genome analyses, frog species with small genomes remain high-priority targets for platinum genome sequencing projects today (see sidebar, Draft Standards for Genome 10K). Furthermore, the availability of high-quality RNA samples for transcriptome sequencing from frozen viable cell cultures opens new opportunities for assisting the advancement of amphibian genomics.

A third priority would target species pairs or larger groups that allow genomic analysis of one of the many biological phenomena that are prominent in amphibian evolution. These include species that produce medically important skin toxins and antimicrobial peptides (77). Genomic data may also be important to many conservation interventions in amphibians and to understanding susceptibility and resistance to chytrid fungal infection and decline, e.g., of *Atelopus* and *Lithobates* (78, 79). Finally, the next round of amphibian genome sequencing will certainly need to greatly increase phylogenetic coverage of the amphibian tree of life to facilitate comparative genomic analyses, and in so doing will hopefully provide greater geographical representation as well.

NONAVIAN REPTILES

Living “reptiles” comprise three main lineages: (*a*) turtles (Testudines); (*b*) tuatara, lizards, and snakes (Lepidosauria); and (*c*) alligators and crocodiles (Crocodylia). Reptiles are an

ancient group, which is reflected in their extensive diversity; for example, the divergence among major squamate groups (e.g., snakes and lizards) is similar in magnitude to that between humans and kangaroos (~175 My) (80). This diversity manifests across many traits, reflected in appreciable genetic and morphological innovation across reptilian lineages. For example, across reptile species there exists a broad range of life history traits related to reproduction and sex determination. Among the most remarkable are repeated transitions across the phylogeny between environmental and genotypic sex determination (81). Furthermore, species with genotypic sex determination can have sex chromosome systems with either female (ZZ/ZW) or male (XX/XY) heterogamety. These sex chromosomes, and presumably the sex-determining genes they contain, are not conserved across lineages even though the basic syntenic blocks making up the karyotype are conserved (reviewed in Reference 82). Reptiles are therefore excellent models for the study of evolution of sex determination, and of sex chromosomes. Annotation, mapping, and comparison of whole genome sequences from both sexes are invaluable tools for understanding the evolutionary processes governing sex determination (83) and promise to identify, for the first time, a sex-determining gene in a reptile. Squamates (lizards and snakes) are also the only vertebrate group to have true parthenogenesis, or asexual reproduction without any input (genetic or otherwise) from males (84). They are thus excellent systems to investigate the consequences of asexuality in amniotes on a whole genome scale (85).

Despite the extreme variations in genomic content and characteristics present within reptiles (86), they have remained a relatively neglected target of large-scale genome sequencing efforts. A handful of recent nonavian reptile genome sequencing and assembly projects have been motivated by addressing phylogenetic questions and the genomic basis of specific biological questions. The first published nonavian reptile genome, that of the green anole lizard, *Anolis carolinensis*, revealed a nucleotide organization (isochores) unlike that of any other sequenced vertebrate to date (87–89). Since then, genomes for two snake species, the Burmese python (*Python molurus bivittatus*) and the king cobra (*Ophiophagus hannah*), have been published and indicate that snakes may have reevolved GC isochore structure (90–92). Analyses of snake genomes also suggest that the ancestral snake lineage experienced unprecedented levels of positive selection on protein-coding genes, that repeat element content varies widely across snakes, and that snake organ remodeling after feeding is associated with massive shifts in gene expression (90, 91). Draft genome sequences for four species of crocodilians, the American alligator (*Alligator mississippiensis*), the gharial (*Gavialis gangeticus*), the saltwater crocodile (*Crocodylus porosus*), and the Chinese alligator (*Alligator sinensis*), have been completed and published (93, 94). Together, these crocodilian genomes provide important insights into the ancestral genomes of archosaurs and amniotes and hold potential for understanding characteristics of dinosaur genomes (93). The sister phylogenetic relationship of turtles and archosaurs (birds and crocodiles) was recently affirmed with the complete genome sequence from the western painted turtle, *Chrysemys picta* (95), which also found that turtles have evolved at a remarkably slow rate at the molecular level. Crocodiles have an even slower rate (93). Thus, current reptilian genomics projects are largely motivated by the specific biological and evolutionary questions that their genomes can address, and ongoing or proposed projects continue to

develop among independent research groups or through research consortiums (e.g., the Consortium for Snake Genomics) (Table 1).

Eleven nonavian reptile species were nominated for de novo genome sequencing and assembly through the BGI-G10K collaboration (Tables 2 and 3). Draft assemblies have been completed for eight of these species, of which three have been published (94, 96). Among the species chosen is the tuatara, *Sphenodon punctatus*, the sole representative of the relictual lineage Rhyncocephalia, which is likely sister to the squamate reptiles. The rarity and significance of this species made obtaining samples for WGS a permitting challenge, and the relatively large genome size (~5 Gb) has also hampered efforts to obtain a reference genome at high coverage.

Other reptilian target species were chosen to address particular questions with regard to key biological characteristics. The Gila monster, *Heloderma suspectum*, is being sequenced to identify the genes involved in venom evolution (e.g., Reference 97). The Australian central bearded dragon lizard, *Pogona vitticeps*, is also being targeted because this species provides an ideal model to examine the genomic underpinnings of environmental and genetic sex determination. Gender in this lizard is usually determined by a pair of ZZ or ZW sex microchromosomes (98), but ZZ individuals can be reversed to the female phenotype at high temperatures (99). An annotated genome sequence for the dragon lizard *P. vitticeps* is currently available online (https://genomics.canberra.edu.au), and a partial physical map for this species is nearing completion. For two turtle species published, the green turtle (*Chelonia mydas*), a marine species, and the soft-shelled turtle (*Pelodiscus sinensis*) (96), genome sizes averaged about 2.2 Gb. Comparative genomic analyses indicated dramatic expansion in the olfactory receptor gene family in both species and the loss of several orthologous genes involved in normal development and energy homeostasis (96). Whole-embryo gene expression analysis of both turtle species showed global repatterning of gene regulation following the divergence between the turtle and chicken lineages through which the unique body plan of turtles may have evolved (96).

Future priorities for WGS of additional taxa of nonavian reptiles is collectively based on the number of interesting biological questions such genomes may address, the availability of samples, species having smaller genome sizes and low heterozygosity, and overall vertebrate genome diversity. Species selected for the next round of WGS have been prioritized to address such questions, including the following: (*a*) the evolution and molecular mechanisms underlying genetic and temperature-dependent sex determination; (*b*) molecular underpinnings of extreme morphological and molecular convergent evolution; (*c*) extreme phenotypes (e.g., horns, gliding in lizards, adhesive toe pads, projectile tongues); (*d*) responses of widely distributed species to past and present climate change; (*e*) evolution and persistence of parthenogenetic lineages, evolution of deadly venom toxins, and loss of limbs and sight; (*f*) evolution of viviparity; and (*g*) the evolutionary placement of debated lineages within the evolutionary tree of nonavian reptiles. Because there are several independent research groups producing moderate-quality genomes of reptiles, the G10KCOS is targeting species that could add value to these other genomes by providing a platinum reference genome of related species.

BIRDS

Modern birds trace their origins to the Jurassic epoch (over 150 Mya), when a theropod lineage of the widespread and successful reptilian dinosaurs spawned a group that would be the only survivors of the Cretaceous-Paleogene dinosaur extinction (~66 Mya) (100). Today, Aves represents the most specious class of terrestrial vertebrates, with some 10,500 bird species occupying a plethora of adaptive niches. One hypothesis is that Neoaves birds and placental mammals, comprising more than 95% of all living bird and mammal species, have captured the ecological niche opportunities that emerged from the cataclysm of the Cretaceous-Paleogene extinction event 66 Mya, which led to the extinction of dinosaurs. An alternative hypothesis is that modern birds radiated 10–80 millions of years before that event (101, 102).

This detailed history, enriched by morphological, behavioral, molecular, and paleontological inference, has produced a fascinating vertebrate group that has informed evolutionary processes, neuroscience, developmental biology, and species conservation. Further, several domestic bird species have significant economic impact (chicken, turkey, ostrich, quail, and others), and many species have been introduced in the pet trade.

During recent decades, the avian systematics community has developed large repositories that house high-quality genetic samples of a substantial number of avian species. These collections provide an essential resource for genomic analyses of avian structural, functional, and behavioral diversity. With representation from 15 natural history collections distributed globally, the G10K biospecimen list (1) includes specimens from 100% of the 32 orders, 91% of the 230 families, 73% of the 2,172 genera, and approximately 50% of the 10,500 species of birds (Figure 3). Each order is represented in multiple biospecimen collections, as are all but 17 families and all but 585 genera, ensuring at least one sample of high quality.

Until recently, whole genome sequence assessment was limited to three species, the chicken (*Gallus gallus*), domestic turkey (*Meleagris gallopavo*), and zebra finch (*Taeniopygia guttata*) (103–105). Further, the phylogenetic relationships among many bird taxa were unresolved or controversial except for the most coarse-grained divergences (106–108). The smaller genome size of birds relative to other vertebrates (68) and reduced sequencing costs made it possible to expand WGS efforts into nonmodel species to expand our understanding of the structure and function of avian genomes (109).

The avian genomics community has achieved a seminal realization of the vision outlined by Genome 10K for comparative genomic analyses. With unparalleled collaborative interaction, a comprehensive multifactorial WGS approach has been mounted by an international team (led by investigators from BGI, Duke University, and the University of Copenhagen) for 48 avian species representing each order of the Neognathae infraclass (Table 2) and two Palaeognath orders (110–112), and complemented by a group of reptilian outgroup species genomes, the American alligator (*A. mississippiensis*) (93) green sea turtle (*C. mydas*) (96), and green anole lizard (*A. carolinensis*) (87). In a December 2014 release of some 28 papers

published in *Science*, *Genome Biology*, and other outlets, the richest comparative genomics analysis of any vertebrate group has appeared.

The findings of the collaborative Avian Phylogenomics Group address a wide variety of inquiries that we shall mention here only briefly, referring the reader to the more detailed reports for added substance (111–113; see also http://www.sciencemag.org/content/346/6215/1308.short and http://www.sciencemag.org/content/346/6215/1308/suppl/DC1). For starters, the studies provided a robust redrawing of the phylogenetic history of avian orders and a genomics inquiry into the making of a bird, or rather a bird genome (Figure 3). The findings help resolve the debate on the timing of the Neoaves divergence, dating it to around 66 Mya in a nearly starlike, big bang radiation of species. Targeted genomic screens for association were offered for special adaptations that are unique to birds, including vocal learning, skeletal adaptations to flight, feather development, dietary and developmental components to endentulism (toothlessness), wide-wavelength visual capacity, sex determination, sexual adaptations, behaviors, plumage color varieties, endogenous retroviral footprints, genome contraction relative to reptiles and mammals, genome exchange breakpoints, and ecological accommodation. Inspired by their own success, the G10K example, and the vast biospecimen collections already inventoried, the Avian Phylogenomics Group and an international consortium of scientists are pursuing a Bird 10K initiative to capture whole genome sequences for every living bird species.

The avian phylogenomic efforts have also addressed and informed many of the bioinformatics challenges listed here that in turn inform all envisioned interspecies comparative genomic efforts. Better ad hoc phylogenetic algorithms were developed and more robust and comparable assemblies and alignment stipulations were tested with real species by the bird exercise. In many ways, the genomes generated from the 48 bird species offer a refreshing preview to the hopes and perils of the coming adventures for the G10K Project.

MAMMALS

Mammals comprise approximately 9% of the total diversity of vertebrates, but they have received a disproportionate focus from WGS studies. This no doubt stems from the fact that humans are nested among the eutherian mammals and that understanding the genomes of our closest mammalian relatives will provide insights into our own biology. A recent comparative genomic analysis of the functional elements among 29 eutherian genomes showed that up to 5.5% of the human genome has evolved through purifying selection and also allowed identification of ~4.2% of the genome that is comprised of constrained bases (i.e., nucleotide positions that show conservation across most or all 29 eutherian genomes) (114). Moreover, this analysis provided strong evidence for the dispersal of transposable elements across mammalian genomes and the accelerated evolution of specific elements along the primate lineage. The mammal and bird genome studies illustrate a timely glimpse of the profound insights gained when a large number of phylogenetically diverse genomes are analyzed in a comparative context.

Many but not all projects for sequencing mammalian genomes were initiated at major genome sequencing centers (the Broad Institute, the Genome Institute at Washington University, Baylor College of Medicine Human Genome Sequencing Center, and BGI-Shenzhen). Species targeted for de novo sequencing by these research centers and independent groups have been sampled from across the mammalian supra-ordinal groups (Monotremata, Marsupialia, Afrotheria, Laurasiatheria, Euarchontoglires, and Xenarthra). Emphases have concentrated among four orders of mammals: Carnivora (cats, dogs, bears, and their allies), Cetartiodactyla (ungulates, dolphins, and whales), Primates (great apes and monkeys), and Rodentia (mice, rats, and allies) (Tables 2 and 3) (Figure 4). Eutherian mammalian outgroups for which there are published genome sequences include two marsupials and one monotreme mammal (Table 2). The number of mammals sequenced has risen to 111 (66 published and 45 near completion) (Tables 2 and 3). Indeed, 41% of accomplished vertebrate genome sequence analyses involve mammals.

The mammal species selected for WGS by the initial BGI-G10K collaboration were chosen for reasons described previously (1) with attention to avoiding competitive overlap between the different genome sequencing centers. This has provided an opportunity to begin filling in the branches of the mammal tree of life by focusing on family-level representatives and/or closely related species (Figure 4). Our selection from Carnivora includes four species of large cats (tiger, *Panthera tigris*; African lion, *Panthera leo*; cheetah, *Acinonyx jubatus*; and American puma, *Puma concolor*). Combined with the felid genome projects being carried out by other research groups, this means that reference genomes will be available for four of the eight major lineages of the Felidae (115). The largest focus of the BGI-G10K collaborative project is in the Cetartiodactyla, with 16 species targeted for de novo sequencing, for which draft assemblies have been completed for 11 species, with a dozen more in progress. Species in this group were chosen not only to address questions related to domestication and understanding of the genetic basis of particular adaptations [e.g., high-altitude adaptation in the domestic yak (116)] but also with an emphasis on understanding the role of genomic architecture and chromosomal rearrangement in genome and organismal evolution (e.g., Reference 42). Primate studies have received focused efforts owing to interest in organization, evolution, and adaptation of the human genome (117). Studies of great apes, including chimpanzees, bonobos, gorillas, and orangutans, have contributed insights into population expansions and reductions as well as phylogeography of our closest relatives, all of which are endangered species (e.g., Reference 118).

The G10KCOS identified several broad research themes that will be used to choose the next round of mammal species for WGS. Species were chosen not only based on their phylogenetic distribution but also with regard to addressing fundamental questions in evolution, behavior, ecology, physiology, and conservation. For example, pairs or groups of species from canids to Old World primates were identified that could be used to address fundamental questions on the genomics of speciation, such as the identification of regions (or islands) of high divergence that may be involved in reproductive isolation that change in size and dimension over time (see, e.g., Reference 119). Another theme revolved around comparing species, particularly within bats and marsupials, that differ dramatically in metabolic rate and how this relates to differences in body size and longevity (e.g., Reference 120). Many mammals, such as bears, squirrels, bats, and opossums, undergo hibernation as

part of their life history, and therefore, pairs of species within each of these groups were identified for WGS to explore the genomic basis of hibernation and the ability to deal with deleterious effects of hibernation (e.g., Reference 121). Finally, given the potential revolutionary impact of genomics on conservation genetics and management (122), several species will be targeted for WGS that are amenable to addressing fundamental questions related to inbreeding and outbreeding depression, disease resistance, and use of genomic information to guide and inform deextinction efforts.

ANCIENT VERTEBRATE PALEOGENOMES

Although de novo genome sequencing of extant species exploits high-quality DNA extracted from purposefully collected tissues, another topic that fires the public imagination is paleogenomics— the sequencing and analysis of genome-scale information from historic or ancient samples, particularly those representing extinct species. Until recently, the sequencing of paleogenomes would have been inconceivable, owing to the sheer number of PCR-based Sanger sequencing reactions required to recover the gigabases of information within a preserved eukaryotic cell. Following publication of draft genomes of ancient humans, horses, and extinct species of Neandertals, Denisovans, the woolly mammoth, and passenger pigeons, popular perception has moved from asking if paleogenomes can be sequenced to when it will happen (124–128).

Considerable challenges to paleogenomic sequencing remain, however. Firstly, although the achievements thus far are undeniably impressive, the financial and physical resource requirements for paleogenomic sequencing remain beyond the capabilities of most research programs. Secondly, although experimental protocols for isolating paleogenomic data have improved considerably within the past several years, different preservation contexts clearly require different experimental approaches, and the field remains in the early stages of fully understanding how and why DNA is sometimes preserved. Thirdly, even if specimens are identified that contain high concentrations of target DNA relative to DNA from exogenous sources that colonize the sample postmortem, this target DNA will be heavily fragmented and damaged, precluding the generation of large-insert libraries or ultra-long reads that are critical for scaffolding de novo genome assemblies. As a result, most extinct genomes will, at best, be assembled via mapping to high-quality genomes of extant relative species—the success of which is limited by evolutionary distance. For example, extrapolation from in silico and experimental data sets based around mapping ancient sequencing reads to various mammal genomes suggests that at 5–6 My divergence (e.g., elephant-mammoth), 60–80% of the genome will map, whereas at >60 My (e.g., moa-extant ratite), success could fall below 20% (129, 130).

THE GENOMIC ROAD AHEAD

The G10K Project has fostered and witnessed many accomplishments and discoveries since its inception in 2009. The number of vertebrate species for which whole genomes are being produced or have been published has increased dramatically and will likely continue to rise exponentially in the future. By bringing together biologists, bioinformaticians, and computational scientists, the G10KCOS has tried to lead the way in establishing best

practices in biospecimen collection and preparation as well as in genome assembly and alignment. As we have shown in this review, such efforts will need to be applied to other areas of analysis, especially for genomes of large size. The successes so far provide optimism for the future. Genome science continues to be a dynamic field with advancing technologies. Although the vast majority of genome sequencing performed today is on the Illumina platform, and assembly algorithms are dominated by de Bruijn graphs, this may not be true in five years. It is difficult to estimate how genome science will change in the next decade. There are a variety of exciting new technologies, but it is impossible to perform cost-benefit analyses without the products themselves and the algorithms designed to use them. These advances afford new opportunities for elucidating the changes in genome structure and sequence that have resulted in the diversity of vertebrate life. The generation of reference genomes is finding application in health and well-being of humans and other vertebrates and is being applied to efforts for stewardship of our planetary biodiversity and efforts to conserve species threatened with extinction.

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DRAFT STANDARDS FOR GENOME 10K

The G10KCOS continued an ongoing process of setting standards for "doing a vertebrate genome" that actually began in 2009 with the first G10K workshop. The groups recognized nine important areas for discussion and recommendations that all bear on what a G10K species genome project should encompass. Detailed reports about each of these areas have been or will be published separately and deposited on the G10K website for guidance in nomination and sequence analyses of present and future selected species. Similar recommendations for standards have appeared for other genome consortia (Table 1). The areas of consideration, discussed throughout this article but summarized here, include

1. **Standards for biospecimen collections and DNA provision**. In general, approximately 100 μg of high–smolecular weight DNA (>50 Kbp) are ideal for construction of high–molecular weight mate-pair libraries. These should be from a single individual selected for minimal heterozygosity to optimize assembly. A detailed description of standards for DNA collection, storage, and processing for G10K has appeared (4).
2. **Recommendations for WGS of males and females**. G10K recommends that sequencing of both a male and female be considered for each new species. Comparisons of male to female genomes implicate specific (Y or W) sequences, including dosage-dependent gene regions critical for pinpointing the sex-determining gene (s) (e.g., Reference 131). If sequencing both sexes is not possible, the heterogametic sex should be chosen, because XY males and ZW females represent both sex chromosomes and comprise unabridged sex chromosome genes useful for quality control, population, and forensic applications.
3. **Sequencing standards**. These standards involve optimal quality control standards for current generation sequencing, including >60× coverage to assure that >98% of the species' euchromatic genome is represented.
4. **Assembly standards**. G10K standards for assembly encourage large contig and scaffold N50 (on the order of megabases), while minimizing (to a very few) the number of false joins that create chimeric scaffolds using an independent physical map–based framework. There is a cost-benefit consideration here, as some physical maps are very accurate but impractical owing to expense in many species (e.g., a pedigree linkage map in a humpback whale). Physical maps can be generated by various methods (Table 4), and a promising but as-yet-unfulfilled hope is the connecting of contigs to scaffolds using long-read technologies that are not yet optimized or scaled to larger vertebrate genomes (Table 4). Nonetheless, every good genome sequence seems to benefit from high-resolution physical maps (20).
5. **Genome annotation standards**. A G10K genome should have genes, SNPs, indels, repetitive elements, and other genome features annotated so the noncomputational user can access the genomic features and aspects readily.

Table5 gives a listing of some standard genome features and publically available software that help annotate them.

6. **Standards for archiving and placing a genome in a browser**. It is essential that a final genome assembly be submitted to the International Nucleotide Sequence Database Collaboration (INSDC, http://www.insdc.org/) so that it is available in a standard repository to all scientists. Submission to the INSDC can occur through the National Center for Biotechnology Information (NCBI) (http://www.ncbi.nlm.nih.gov/genbank/), European Bioinformatics Institute (http://www.ebi.ac.uk/ena), or DNA Databank of Japan (http://www.ddbj.nig.ac.jp/). The G10KCOS also encourages that all new genomes should be loaded into a genome browser, such as Gbrowse (132), JBrowse (133), track data hubs on the UCSC Genome Browser (134), NCBI, or Ensembl, for viewing and downloading. This format for viewing genomes is convenient and familiar and very much more useful to biological researchers than a trace archive or raw reads.

7. **Standards for genome alignment**. Every species' genome has an evolutionary context and is indisputably connected to all others in a deep evolutionary genealogy that must be better understood. The first step in comparative genomics is to align homologous segments across related genomes so that comparative analyses can be achieved. No perfect algorithm for genome alignment has been developed or claimed, especially for the large vertebrate genomes we discuss here. The Alignathon community of G10K has endeavored to maximize consensus experience in the Alignathon competition discussed elsewhere in this article (51). Achievement of best practices and transfer of these alignment methods to the next generation of genome scientists are goals that the G10KCOS embraces.

8. **G10K data release**. The G10KCOS endorses rapid publication and release of genome sequences in the spirit of facilitating wide uses and application. All species' genome sequences, assembly, and annotation shall be released freely with public access upon publication or within two years of delivery of a sample to a sequencing facility, whichever comes first. The latter clause is intended to handle cases of delayed publication.

9. **Platinum Genome 10K species**. Owing to cost limitation, not all species will enjoy the scientific rigor demanded by the standards outlined above; indeed, some light-coverage sequences will be assessed, e.g., for SNP discovery, with no attention to de novo assembly and annotation. To facilitate genomic studies of such genomes, selected reference genomes called platinum genomes should be nominated for major taxonomic groups (e.g., orders or large families that differ by 30–50 My of evolutionary time). The G10KCOS will nominate reference species for which high-resolution physical maps or a long-insert sequencing equivalent will be generated and monitor the progress

of such projects to maximize genome opportunities for these platinum species.

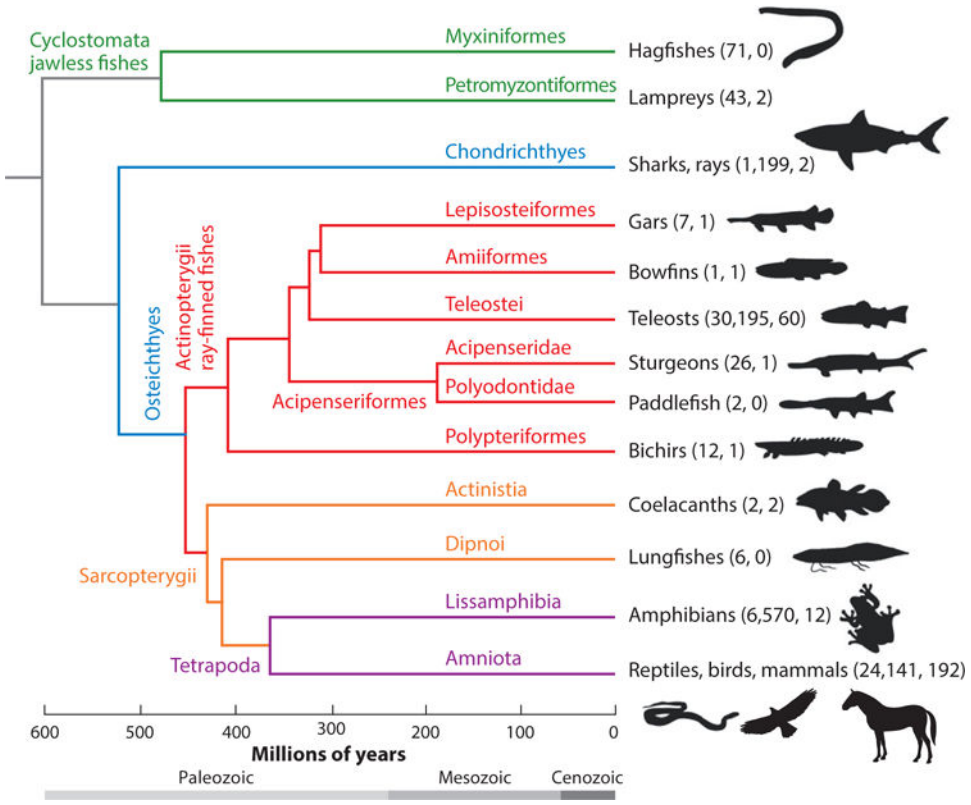

Figure 1.

Consensus phylogeny of the major lineages of vertebrates. Topology and divergence dates (Ma) are consensus estimates derived from References 1 and 276 and included citations. Following the common names of taxon groups in parentheses are number of living species for that group and number of species with published and/or pending genomes (see Tables 2 and 3).

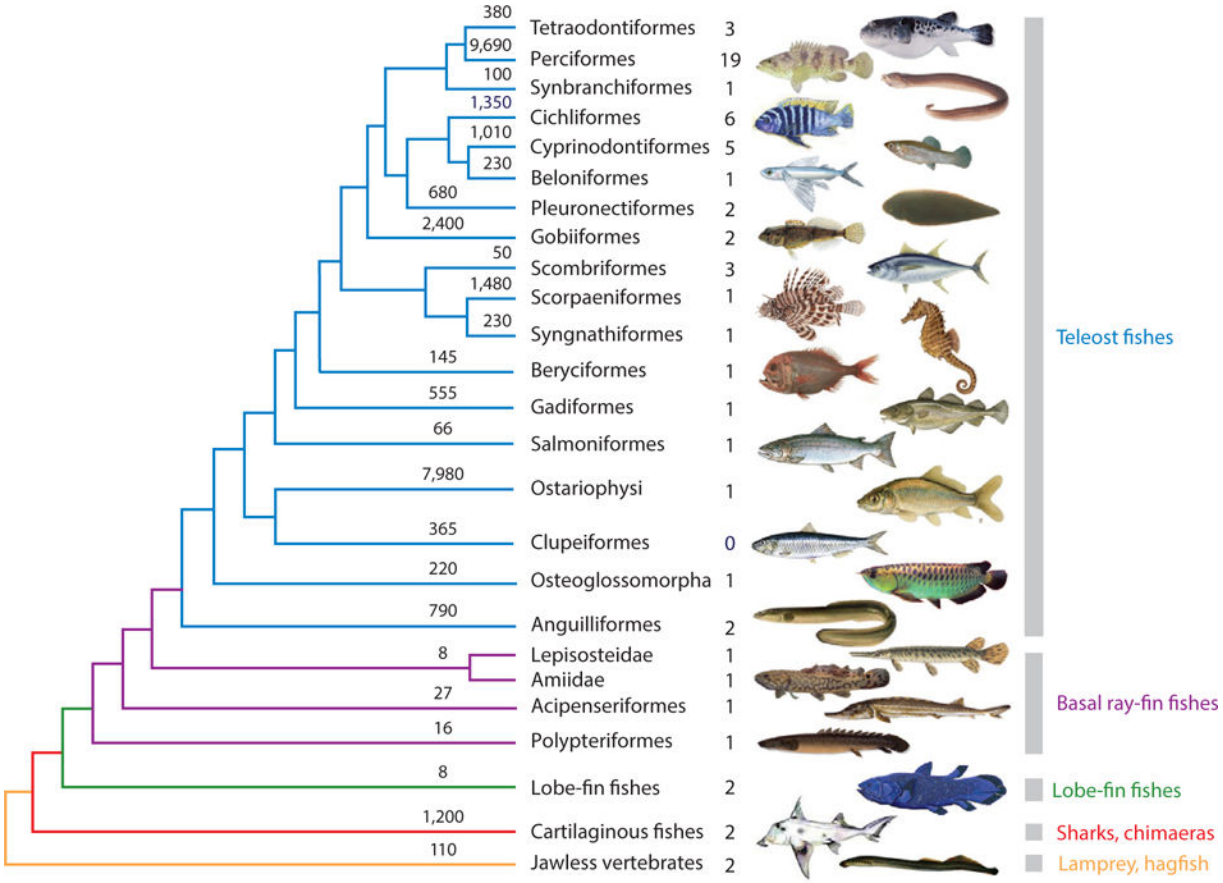

Figure 2.

Consensus phylogeny of the major lineages of fishes. Topology and dates (Ma) are derived from combined data tree reported in Reference 1. On the ends of the limbs is the number of living species for that group. Following the common names of taxon groups is number of species with published and/or pending genomes (see Tables 2 and 3).

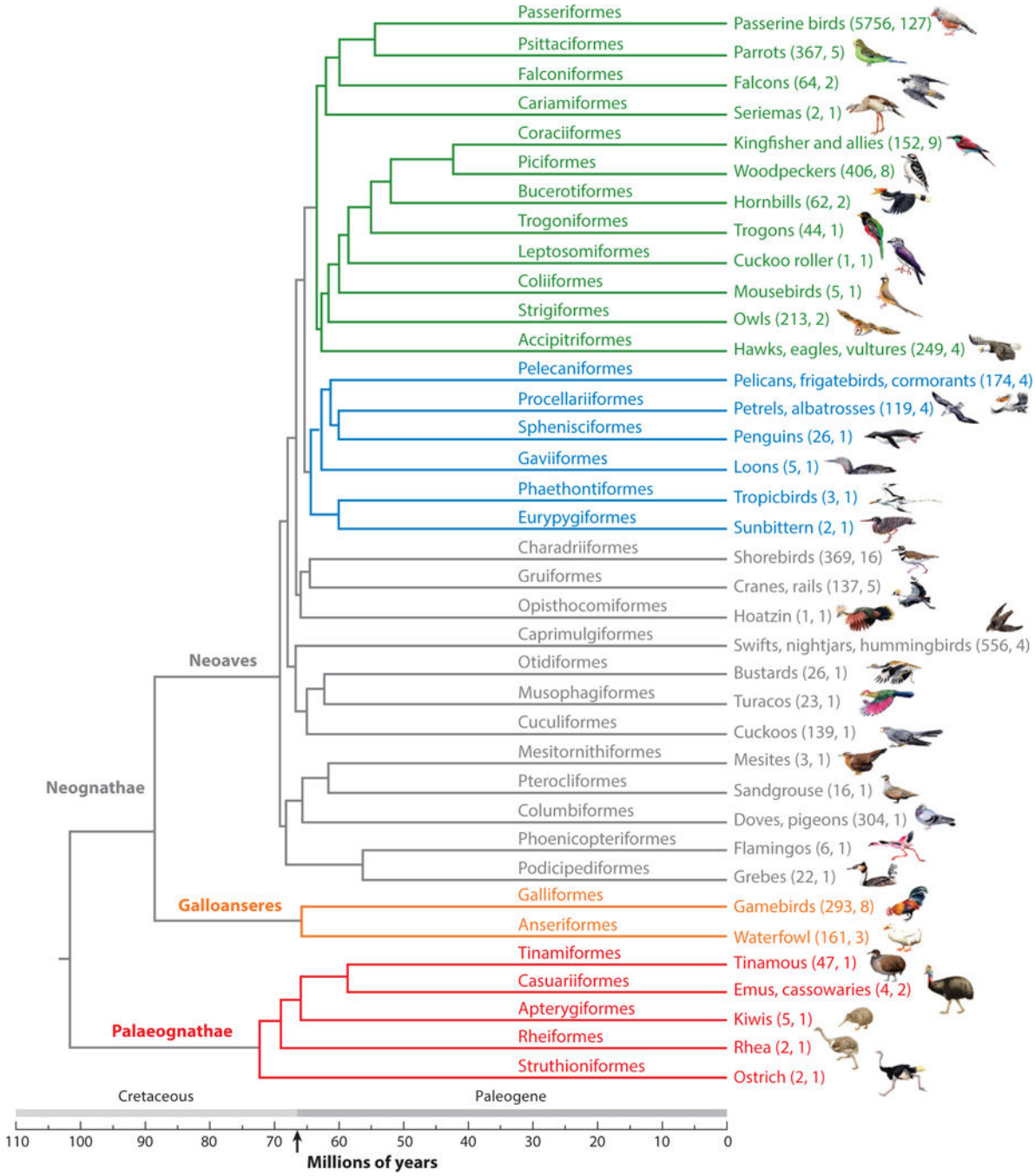

Figure 3.

Consensus phylogeny of the major lineages of birds. In parentheses are the number of living species as defined by Howard and Moore (277), with the exception of the Passerine species count, which is taken from (1)/number of species with published and/or pending genomes (Tables 2 and 3). Data include both those genomes published to date as listed in Table 2 and those currently undergoing final assembly and annotation as part of the Avian Phylogenomic Consortium (Table 3). The underlying time-calibrated phylogenetic tree is a composite of

the Neognath phylogeny published by Jarvis et al. (112) and Palaeognath phylogeny published by Mitchell et al. (278). Illustrations courtesy of Jon Fjeldå.

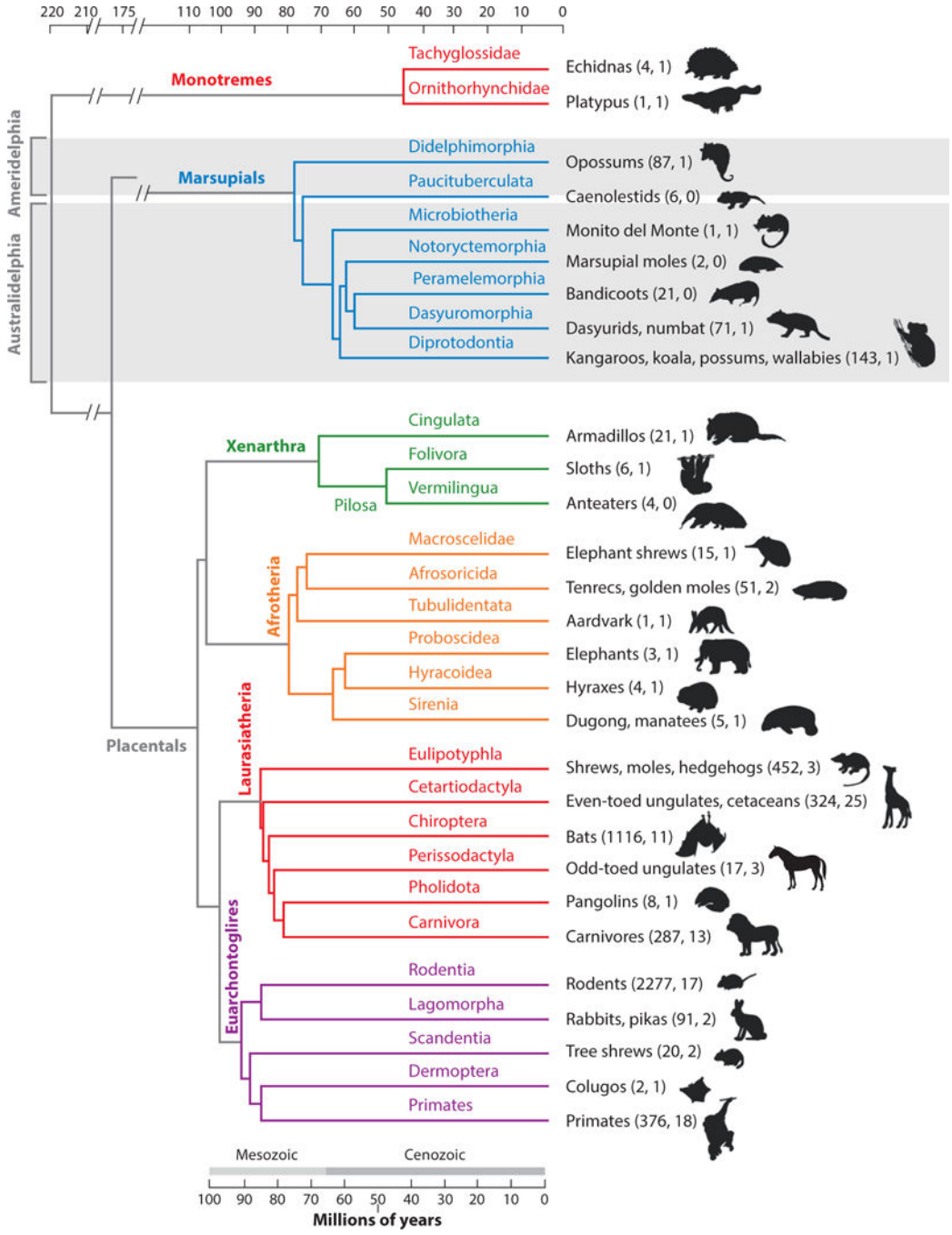

Figure 4.

Consensus phylogeny of the major lineages of mammals. Topology and dates (Ma) are consensus estimates derived from References 1 and 276 and included citations. Following the common names of taxon groups in parentheses are the number of living species for that group and number of species with published and/or pending genomes (see Tables 2 and 3).

Table 1

Goals of the Genome 10K Project (see text for details)

1. Gather and validate voucher biospecimens for whole genome sequencing (WGS)
2. Develop scientific communities around the species, taxonomic groups, and analytical themes (e.g., assembly, annotation, alignment, comparative genomic analyses)
3. Set standards for genome
a. Assembly
b. Annotation
c. Release on browsers
d. Rapid data release
4. Monitor progress on vertebrae WGS projects
5. Raise funds
6. Foster and support other genome consortia, such as the following:
a. **Insect 5K (i5K)** http://www.arthropodgenomes.org/wiki/i5K
b. **Global Invertebrate Genomics Alliance (GIGA)** http://www.nova.edu/ocean/giga/
c. **Consortium for Snake Genomics** http://www.snakegenomics.org/SnakeGenomics/Home.html
d. **1000 Fungal Genomes Project (1KFG)** http://1000.fungalgenomes.org/home/
e. **NSF Plant Genome Research Program (PGRP)** http://www.nsf.gov/pubs/2014/nsf14533/nsf14533.htm
f. **100K Foodborne Pathogen Genome Project** http://100kgenome.vetmed.ucdavis.edu

Table 2

List of 164 vertebrate genomes that have been published as of December 9, 2014[1]

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION	BIOPROJECT ID	REFERENCE
CYCLOSTOMATA						
Lethenteron camtschaticum	Arctic lamprey	Petromyzontiformes	Petromyzontidae	APJL00000000	PRJNA192554	135
Petromyzon marinus	Sea lamprey	Petromyzontiformes	Petromyzontidae	AEFG00000000	PRJNA12880	136
CHONDRICHTHYES						
Callorhinchus milii	Elephant shark	Chimaeriformes	Callorhinchidae	AAVX00000000	PRJNA18361	14
ACTINOPTERYGII						
Takifugu rubripes	Fugu	Tetraodontiformes	Tetraodontidae	CAAB00000000	PRJNA1434	56, 137
Tetraodon nigroviridis	Freshwater pufferfish	Tetraodontiformes	Tetraodontidae	CAAE00000000	PRJNA12350	57
Oryzias latipes	Japanese medaka	Beloniformes	Adrianichthyidae	BAAF00000000	PRJNA16702	58
Gadus morhua	Atlantic cod	Gadiformes	Gadidae	CAEA00000000	PRJNA41391	138
Anguilla japonica	Japanese eel	Anguilliformes	Anguillidae	AVPY00000000	PRJNA158309	139
Gasterosteus aculeatus	Three-spined stickleback	Gasterosteiformes	Gasterosteidae	AANH00000000	PRJNA13579	59
Danio rerio	Zebrafish	Cypriniformes	Cyprinidae	CABZ00000000	PRJNA11776	60
Thunnus orientalis	Pacific bluefin tuna	Scombriformes	Scombridae	BADN00000000	PRJDA68701	140
Xiphophorus maculatus	Southern platyfish	Cyprinodontiformes	Poeciliidae	AGAJ00000000	PRJNA72525	61
Cynoglossus semilaevis	**Tongue sole**	**Pleuronectiformes**	**Cynoglossidae**	**AGRG00000000**	PRJNA73987	131
Oncorhynchus mykiss	Rainbow trout	Salmoniformes	Salmonidae	CCAF000000000	PRJEB4421	141
Electrophorus electricus	Electric eel	Gymnotiformes	Gymnotidae		PRJNA249073	142
Cyprinus carpio	Common carp	Cypriniformes	Cyprinidae		PRJNA202478	143
Astyanax mexicanus	Mexican tetra	Characiformes	Characidae	APWO00000000	PRJNA89115	144
Larimichthys crocea	Large yellow croaker		Sciaenidae	JPYK00000000	PRJNA237858	145
Boleophthalmus pectinirostris	**Blue-spotted mudskipper**	**Gobiiformes**	**Gobiidae**	**JACK00000000**	PRJNA232434	146
Periophthalmus magnusspinnatus	Giant-fin mudskipper	Gobiiformes	Gobiidae	JACL00000000	PRJNA232435	146
Periophthalmodon schlosseri	**Giant mudskipper**	**Gobiiformes**	**Gobiidae**	**JACM00000000**	**PRJNA232436**	146
Scartelaos histophorus	Blue mudskipper	Gobiiformes	Gobiidae	JACN00000000	PRJNA232437	146
SARCOPTERYGII						

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION	BIOPROJECT ID	REFERENCE
Latimeria chalumnae	African coelacanth	Coelacanthiformes	Coelacanthidae	AFYH00000000; BAHO00000000	PRJNA56111; PRJDB500	147, 148
Latimeria menadoensis	Indonesian coelacanth	Coelacanthiformes	Coelacanthidae		PRJNA38001	148
AMPHIBIA						
Xenopus (Silurana) tropicalis	Western clawed frog	Anura	Pipidae	AAMC00000000	PRJNA12348	65
"**REPTILIA**"						
Anolis carolinensis	Green anole	Squamata	Iguanidae	AAWZ00000000	PRJNA18787; PRJNA60547	87
Python bivittatus	Burmese python	Squamata	Pythonidae	AEQU00000000	PRJNA61243; PRJNA238085	90
Alligator mississippiensis	American alligator	Crocodylia	Alligatoridae	AKHW00000000	PRJNA159843; PRJNA221578	93
Crocodylus porosus	Saltwater crocodile	Crocodylia	Crocodylidae		PRJNA163131	93
Gavialis gangeticus	Indian gharial	Crocodylia	Gavialidae		PRJNA172383	93
Ophiophagus hannah	King cobra	Squamata	Elapidae	AZIM00000000	PRJNA201683	92
Alligator sinensis	**Chinese alligator**	**Crocodylia**	**Alligatoridae**	**AVPB00000000**	**PRJNA221633**	94
Chelonia mydas	**Green turtle**	**Testudines**	**Cheloniidae**	**AJIM00000000**	**PRJNA104937; PRJNA234097**	96
Pelodiscus sinensis	**Chinese softshell turtle**	**Testudines**	**Trionychidae**	**AGCU00000000**	**PRJNA68233; PRJNA221645**	96
Chrysemys picta	Western painted turtle	Testudines	Emydidae	AHGY00000000	PRJNA78657	95
Crotalus mitchellii	Speckled rattlesnake	Serpentes	Viperidae	JPMF01000000	PRJNA255393	149
AVES						
Gallus gallus	Red jungle fowl	Galliformes	Phasianidae	AADN00000000	PRJNA13342	103
Meleagris gallopavo	Wild turkey	Galliformes	Phasianidae	ADDD00000000	PRJNA42129	104
Taeniopygia guttata	Zebra finch	Passeriformes	Estrildidae	ABQF00000000	PRJNA17289	105
Amazona vittata	Puerto Rican parrot	Psittaciformes	Psittacidae	AOCU00000000	PRJNA171587	150
Ficedula albicollis	Collared flycatcher	Passeriformes	Muscicapidae	AGTO00000000	PRJNA208061	119
Ficedula hypoleuca	Pied flycatcher	Passeriformes	Muscicapidae			119
Geospiza fortis	**Mallard duck**	**Anseriformes**	**Anatidae**	**ADON00000000**	**PRJNA46621**	151
Ara macao	Scarlet macaw	Psittaciformes	Psittacidae	AOUJ00000000	PRJNA189648	152
Columba livia	Rock pigeon	Columbiformes	Columbidae	AKCR00000000	PRJNA167554; PRJNA170656	153
Coturnix japonica	Japanese quail	Galliformes	Phasianidae	BASJ00000000	PRJDB1146	154
Falco cherrug	**Saker falcon**	**Falconiformes**	**Falconidae**	**AKMU00000000**	**PRJNA217049**	155
Falco peregrinus	**Peregrine falcon**	**Falconiformes**	**Falconidae**	**AKMT00000000**	**PRJNA198010**	155

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION	BIOPROJECT ID	REFERENCE
Geospiza magnirostris	Large ground finch	Passeriformes	Thraupidae		PRJNA178982	156
Melopsittacus undulatus	Australian parakeet (budgerigar)	Psittaciformes	Psittacidae	AGAI00000000	PRJNA197262	157
Pseudopodoces humilis	Ground tit	Passeriformes	Paridae	ANZD00000000	PRJNA217046	158, 159
Aquila chrysaetos	Golden eagle	Accipitriformes	Accipitridae	JDSB00000000	PRJNA222866	160
Colinus virginianus	Northern bobwhite	Galliformes	Odontophoridae	AWGT00000000	PRJNA188411	161
Corvus cornix	Hooded crow	Passeriformes	Corvidae	PRJNA208001		162
Lyrurus (Tetrao) tetrix	Black grouse	Galliformes	Phasianidae	JDSL00000000	PRJNA179551	163
Geospiza fortis	**Medium ground finch**	**Passeriformes**	**Fringillidae**	**AKZB00000000**	**PRJNA156703**	112, 113
Aptenodytes forsteri	**Emperor penguin**	**Sphenisciformes**	**Spheniscidae**	**JMFQ00000000**	**PRJNA235982**	112, 113
Pygoscelis adeliae	**Adelie penguin**	**Sphenisciformes**	**Spheniscidae**	**JMFP00000000**	**PRJNA235983**	112, 113
Acanthisitta chloris	Rifleman	Passeriformes	Acanthisittidae	JJRS00000000	PRJNA212877	112, 113
Antrostomus carolinensis	Chuck-will's-widow	Caprimulgiformes	Caprimulgidae	JMFU00000000	PRJNA212888	112, 113
Apaloderma vittatum	Bar-tailed trogon	Trogoniformes	Trogonidae	JMFV00000000	PRJNA212878	112, 113
Balearica regulorum	Crowned crane	Gruiformes	Gruidae	JJRR00000000	PRJNA212879	112, 113
Buceros rhinoceros	Javan rhinoceros hornbill	Bucerotiformes	Bucerotidae	JMFK00000000	PRJNA212887	112, 113
Calypte anna	**Anna's hummingbird**	**Trochiliformes**	**Trochilidae**	**JJRV00000000**	**PRJNA212866**	112, 113
Cariama cristata	Red-legged seriema	Gruiformes	Cariamidae	JJRQ00000000	PRJNA212889	112, 113
Cathartes aura	Turkey vulture	Cathartiformes	Cathartidae	JMFT00000000	PRJNA212890	112, 113
Chaetura pelagica	**Chimney swift**	**Apodiformes**	**Apodidae**		**PRJNA210808**	112, 113
Charadrius vociferus	**Killdeer**	**Charadriiformes**	**Charadriidae**	**JMFX00000000**	**PRJNA212867**	112, 113
Chlamydotis macqueenii	MacQueen's bustard	Gruiformes	Otididae	JMFJ00000000	PRJNA212891	112, 113
Colius striatus	Speckled mousebird	Coliiformes	Coliidae	JJRP00000000	PRJNA212892	112, 113
Corvus brachyrhynchos	**American crow**	**Passeriformes**	**Corvidae**	JMFN01000000	PRJNA212869	112, 113
Cuculus canorus	**Common cuckoo**	**Cuculiformes**	**Cuculidae**	**JNOX01000000**	**PRJNA212870**	112, 113
Egretta garzetta	Little egret	Ciconiiformes	Ardeidae	JJRC00000000	PRJNA232959	112, 113
Eurypyga helias	Sunbittern	Gruiformes	Eurypygidae	JJRO00000000	PRJNA212893	112, 113
Fulmarus glacialis	Northern fulmar	Procellariiformes	Procellariidae	JJRN00000000	PRJNA212894	112, 113
Gavia stellata	Red-throated loon	Gaviiformes	Gaviidae	JJRM00000000	PRJNA212895	112, 113
Haliaeetus albicilla	**White-tailed eagle**	**Falconiformes**	**Accipitridae**	**JJRL00000000**	**PRJNA212896**	112, 113

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION	BIOPROJECT ID	REFERENCE
Haliaeetus leucocephalus	Bald eagle	Falconiformes	Accipitridae		PRJNA237821	112, 113
Leptosomus discolor	Cuckoo roller	Coraciiformes	Leptosomatidae	JJRK00000000	PRJNA212897	112, 113
Manacus vitellinus	**Golden-collared manakin**	**Passeriformes**	**Pipridae**	**JMFM00000000**	**PRJNA212872**	112, 113
Merops nubicus	Northern carmine bee-eater	Coraciiformes	Meropidae	JJRJ00000000	PRJNA212898	112, 113
Mesitornis unicolor	Brown mesite	Gruiformes	Mesitornithidae	JJRI00000000	PRJNA212899	112, 113
Nestor notabilis	Kea	Psittaciformes	Psittacidae	JJRH00000000	PRJNA212900	112, 113
Nipponia nippon	**Crested ibis**	**Ciconiiformes**	**Threskiornithidae**	**JMFH00000000**	**PRJNA232572**	112, 113
Opisthocomus hoazin	**Hoatzin**	**Opisthocomiformes**	**Opisthocomidae**	**JMFL00000000**	**PRJNA212873**	112, 113
Pelecanus crispus	Dalmatian pelican	Pelicaniformes	Pelicanidae	JJRG00000000	PRJNA212901	112, 113
Phaethon lepturus	White-tailed tropicbird	Phaethontiformes	Phaethontidae	JJRF00000000	PRJNA212902	112, 113
Phalacrocorax carbo	Great black cormorant	Pelicaniformes	Phalacrocoracidae	JMFI00000000	PRJNA212903	112, 113
Phoenicopterus ruber ruber	Caribbean flamingo	Phoenicopteriformes	Phoenicopteridae	JJRE00000000	PRJNA212904	112, 113
Picoides pubescens	**Downy woodpecker**	**Piciformes**	**Picidae**	**JJRU00000000**	**PRJNA212874**	112, 113
Podiceps cristatus	Great-crested grebe	Podicipediformes	Podicipedidae	JMFS00000000	PRJNA212905	112, 113
Pterocles gutturalis	Yellow-throated sandgrouse	Ciconiiformes	Pteroclidae	JMFR00000000	PRJNA212906	112, 113
Struthio camelus	**Ostrich**	**Struthioniformes**	**Struthionidae**	**JJRT00000000**	**PRJNA212875**	112, 113
Tauraco erythrolophus	Angola turaco	Musophagiformes	Musophagidae	JNOY00000000	PRJNA212908	112, 113
Tinamus guttatus	**White-throated tinamou**	**Tinamiformes**	**Tinamidae**	**JMFW00000000**	**PRJNA212876**	112, 113
Tyto alba	Barn owl	Strigiformes	Tytonidae	JJRD00000000	PRJNA212909	112, 113
Hemignathus virens	Hawaii amakihi	Passeriformes	Fringillidae			164
MAMMALIA						
Homo sapiens	Human	Primates	Hominidae	NCBI36		165, 166
Mus musculus	House mouse	Rodentia	Muridae			167
Rattus norvegicus	Norway rat	Rodentia	Muridae	AABR00000000	PRJNA10629	168
Canis familiaris	Domestic dog	Carnivora	Canidae	AAEX00000000	PRJNA13179	169
Pan troglodytes	Chimpanzee	Primates	Hominidae	AADA01000000	PRJNA13184	170
Felis catus	Domestic cat	Carnivora	Felidae	AANG00000000	PRJNA16726	171
Macaca mulatta	Rhesus macaque	Primates	Cercopithecidae	AANU00000000; AEHK00000000	PRJNA12537; PRJNA51409	172, 173
Monodelphis domestica	Gray short-tailed opossum	Didelphimorphia	Didelphidae	AAFR00000000	PRJNA12561	174

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION	BIOPROJECT ID	REFERENCE
Ornithorhynchus anatinus	Platypus	Monotremata	Ornithorhynchidae	AAPN00000000	PRJNA12885	19
Bos taurus	Cow	Cetartiodactyla	Bovidae	AAFC00000000	PRJNA12555	175, 176
Equus caballus	Horse	Perissodactyla	Equidae	AAWR00000000; ATDM00000000	PRJNA18661; PRJNA200654	177, 178
Ailuropoda melanoleuca	**Giant panda**	**Carnivora**	**Ursidae**	**ACTA00000000**	**PRJNA38683**	13
Ovis aries	Domestic sheep	Cetartiodactyla	Bovidae	AMGL00000000	PRJNA169880	179, 180
Cavia porcellus	Guinea pig	Rodentia	Caviidae	AAKN00000000	PRJNA12583	114
Choloepus hoffmanni	Two-toed sloth	Pilosa	Megalonychidae	ABVD00000000	PRJNA30809	114
Cricetulus griseus	Chinese hamster	Rodentia	Cricetidae	AFTD00000000; APMK00000000; AMDS00000000	PRJNA189319; PRJNA187553	181–183
Dasypus novemicinctus	Nine-banded armadillo	Cingulata	Dasypodidae	AAGV00000000	PRJNA12594	114
Dipodomys ordii	Ord's kangaroo rat	Rodentia	Heteromyidae	ABRO00000000	PRJNA20385	114
Echinops telfairi	Lesser hedgehog tenrec	Afrosoricida	Tenrecidae	AAIY00000000	PRJNA12590	114
Erinaceus europaeus	Western European hedgehog	Eulipotyphla	Erinaceidae	AMDU00000000	PRJNA74585	114
Heterocephalus glaber	**Naked mole rat**	**Rodentia**	**Bathyergidae**	**AFSB00000000**	**PRJNA68323**	184
Ictidomys tridecemlineatus	Thirteen-lined ground squirrel	Rodentia	Sciuridae	AAQQ01000000; AGTP00000000	PRJNA13937; PRJNA61725	114
Loxodonta africana	African savanna elephant	Proboscidea	Elephantidae	AAGU00000000	PRJNA12569	114
Macaca fascicularis	**Crab-eating macaque**	**Primates**	**Cercopithecidae**	**AEHL00000000**	**PRJNA51411**	173, 185
Macropus eugenii	Tammar wallaby	Diprotodontia	Macropodidae	ABQO000000000	PRJNA12587	186
Microcebus murinus	Gray mouse lemur	Primates	Cheirogaleidae	ABDC00000000	PRJNA19967	114
Myotis lucifugus	Little brown bat	Chiroptera	Vespertilionidae	AAPE00000000	PRJNA16951	114
Ochotona princeps	American pika	Lagomorpha	Ochotonidae	AAYZ00000000; ALIT00000000	PRJNA19235; PRJNA74593	114
Odocoileus virginianus	White-tailed deer	Cetartiodactyla	Cervidae	AEGY00000000; AEGZ00000000	PRJNA52611	187
Oryctolagus cuniculus	Rabbit	Lagomorpha	Leporidae	AAGW00000000	PRJNA12819	114
Otolemur garnettii	Bushbaby (small-eared galago)	Primates	Galagidae	AAQR00000000	PRJNA16955	114
Pongo abelii	Sumatran orangutan	Primates	Hominidae	ABGA00000000	PRJNA20869	188
Procavia capensis	Rock hyrax	Hyracoidea	Procaviidae	ABRQ00000000	PRJNA13972	114
Pteropus vampyrus	Large flying fox	Chiroptera	Pteropodidae	ABRP00000000	PRJNA20325	114
Sarcophilus harrisii	Tasmanian devil	Dasyuromorphia	Dasyuridae	AFEY00000000; AEFK00000000	PRJNA65325; PRJNA51853	123, 189
Sorex araneus	European shrew	Eulipotyphla	Soricidae	AALT00000000	PRJNA13689	114
Tarsius syrichta	Philippine tarsier	Primates	Tarsiidae	ABRT000000000	PRJNA20339	114

Annu Rev Anim Biosci. Author manuscript; available in PMC 2018 March 05.

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION	BIOPROJECT ID	REFERENCE
Tupaia belangeri	Northern tree shrew	Scandentia	Tupaiidae	AAPY00000000	PRJNA13971	114
Tursiops truncatus	Bottle-nosed dolphin	Cetartiodactyla	Delphinidae	ABRN00000000	PRJNA20367	114
Vicugna pacos	Alpaca	Cetartiodactyla	Camelidae	ABRR00000000 JEMW00000000	PRJNA30567 PRJNA233565	114, 190
Bos indicus	Zebu	Cetartiodactyla	Bovidae	AGFL00000000	PRJNA72827	191
Bos grunniens mutus	**Yak**	**Cetartiodactyla**	**Bovidae**	**AGSK00000000**	**PRJNA74739**	116
Camelus bactrianus ferus	**Bactrian camel**	**Cetartiodactyla**	**Camelidae**	AGVR00000000 **JARL00000000**	PRJNA76177 **PRJNA183605**	190, 192
Capra hircus	**Goat**	**Cetartiodactyla**	**Bovidae**	**AJPT00000000**	**PRJNA158393**	37
Daubentonia madagascariensis	Aye-aye	Primates	Daubentoniidae	AGTM000000000	PRJNA74997	193, 194
Gorilla gorilla	Gorilla	Primates	Hominidae	CABD00000000	PRJEA31265	195
Myotis davidii	**David's myotis**	**Chiroptera**	**Vespertilionidae**	**ALWT00000000**	**PRJNA171994**	196
Pteropus alecto	**Black flying fox**	**Chiroptera**	**Pteropodidae**	**ALWS00000000**	**PRJNA171993**	196
Pan paniscus	Bonobo	Primates	Hominidae	AJFE00000000	PRJNA49285	197
Sus scrofa	Domestic pig	Cetartiodactyla	Suidae	AJKK00000000	PRJNA13421; PRJNA144099	198, 199
Eidolon helvum	Straw-colored fruit bat	Chiroptera	Pteropodidae	AWHC00000000	PRJNA209406	200
Megaderma lyra	Indian false vampire bat	Chiroptera	Megadermatidae	AWHB00000000	PRJNA209407	200
Pteronotus parnellii	Parnell's mustached bat	Chiroptera	Mormoopidae	AWGZ00000000	PRJNA209408	200
Rhinolophus ferrumequinum	Greater horseshoe bat	Chiroptera	Rhinolophidae	AWHA00000000	PRJNA209409	200
Myotis brandtii	**Brandt's bat**	**Chiroptera**	**Vespertilionidae**	**ANKR00000000**	**PRJNA218631**	120
Lipotes vexillifer	**Yangtze river dolphin**	**Cetartiodactyla**	**Lipotidae**	**AUPI00000000**	**PRJNA174066**	201
Panthera tigris	**Amur tiger**	**Carnivora**	**Felidae**	**ATCQ00000000**	**PRJNA182708**	202
Pantholops hodgsonii	**Chiru**	**Cetartiodactyla**	**Bovidae**	**AGTT00000000**	**PRJNA72465**	203
Tupaia chinensis	**Chinese tree shrew**	**Scandentia**	**Tupaiidae**	**ALAR00000000**	**PRJNA169406**	204
Balaenoptera acutorostrata	**Minke whale**	**Cetartiodactyla**	**Balaenopteridae**	**ATDI00000000**	**PRJNA72723**	15
Callithrix jacchus	Common marmoset	Primates	Cebidae	ACFV00000000	PRJNA20401	205
Macaca thibetana	Tibetan macaque	Primates	Cercopithecidae		PRJNA226187	206
Spalax galili	Blind mole rat	Rodentia	Spalacidae	AXCS00000000	PRJNA213569	207
Ursus maritimus	Polar bear	Carnivora	Ursidae	AVOR00000000	PRJNA210951	208
Nomascus leucogenys	White-cheeked gibbon	Primates	Hylobatidae	ADFV00000000	PRJNA13975	209
Camelus dromedarius	**Dromedary**	**Cetartiodactyla**	**Camelidae**	**JDVD00000000**	**PRJNA234474**	190

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION	BIOPROJECT ID	REFERENCE
Rhinopithecus roxellana	Golden snub-nosed monkey	Primates	Cercopithecidae	JABR00000000	PRJNA230020	210

[1] Species are listed chronologically according to year genome was first published. Species in boldface were sequenced through the BGI-G10K collaborative effort.

Table 3

List of 113 vertebrate genomes that either are unpublished or have been targeted for de novo sequencing through the BGI-G10K collaborative effort

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION or BGI-G10K species
CHONDRICHTHYES				
Sphyrna mokarran	Great hammerhead shark	Carcharhiniformes	Sphyrnidae	BGI-G10K
ACTINOPTERYGII				
Acipenser sinensis	Chinese sturgeon	Acipenseriformes	Acipenseridae	BGI-G10K
Amia calva	Bowfin	Amiiformes	Amiidae	BGI-G10K
Polypterus senegalus	Bichir	Polypteriformes	Polypteridae	BGI-G10K
Hoplostethus atlanticus	Orange roughy	Beryciformes	Trachichthyidae	BGI-G10K
Astyanax mexicanus	Blind cave fish	Characiformes	Characidae	BGI-G10K
Carassius auratus gibelio	Prussian carp	Cypriniformes	Cyprinidae	BGI-G10K
Megalobrama amblycephala	Wuchang bream	Cypriniformes	Cyprinidae	BGI-G10K
Hypophthalmichthys molitrix	Silver carp	Cypriniformes	Cyprinidae	BGI-G10K
Gobiocypris rarus	Rare gudgeon	Cypriniformes	Cyprinidae	BGI-G10K
Hippocampus comes	Tiger tail seahorse	Gasterosteiformes	Syngnathidae	BGI-G10K
Scleropages formosus	Golden arowana	Osteoglossiformes	Osteoglossidae	BGI-G10K
Chaenocephalus aceratus	Blackfin icefish	Perciformes	Channichthyidae	BGI-G10K
Eleginops maclovinus	Patagonian blenny	Perciformes	Eleginopidae	BGI-G10K
Boleophthalmus pectinirostris	Mudskipper	Perciformes	Gobiidae	BGI-G10K
Periophthalmus magnuspinnatus	Giant-fin mudskipper	Perciformes	Gobiidae	BGI-G10K
Sinocyclocheilus grahami	Golden Line fish	Cypriniformes	Cyprinidae	BGI-G10K
Dissostichus mawsoni	Antarctic toothfish	Perciformes	Nototheniidae	BGI-G10K
Pseudosciaena crocea	Large yellow croaker	Perciformes	Sciaenidae	BGI-G10K
Sparus aurata	Gilthead sea bream	Perciformes	Sparidae	BGI-G10K
Paralichthys olivaceus	Bastard halibut	Pleuronectiformes	Paralichthyidae	BGI-G10K
Thunnus albacares	Yellowfin tuna	Scombriformes	Scombridae	BGI-G10K
Epinephelus coioides	Grouper	Perciformes	Serranidae	BGI-G10K
Platycephalus bassensis	Sand flathead	Scorpaeniformes	Platycephalidae	BGI-G10K
Siganus oramin	Pearl-spotted spinefoot	Perciforms	Siganidae	BGI-G10K
Monopterus albus	Finless eel	Synbranchiformes	Synbranchidae	BGI-G10K
Mola mola	Ocean sunfish	Tetraodontiformes	Molidae	BGI-G10K
Amphilophus citrinellus	Midas cichlid	Cichliformes	Cichlidae	CCOE00000000
Anguilla anguilla	European eel	Anguilliformes	Anguillidae	AZBK00000000
Anoplopoma fimbria	Sablefish	Perciformes	Anoplopomatidae	AWGY00000000
Astyanax mexicanus	Blind cave fish	Characiformes	Characidae	APWO00000000
Cyprinodon nevadensis	Amargosa pupfish	Cyprinodontiformes	Cyprinodontidae	JSUU00000000
Cyprinodon variegatus	Sheepshead minnow	Cyprinodontiformes	Cyprinodontidae	JPKM01000000

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION or BGI-G10K species
Haplochromis burtoni	Burton's mouthbrooder	Cichliformes	Cichlidae	AFNZ00000000
Lepisosteus oculatus	Spotted gar	Semionotiformes	Lepisosteidae	AHAT00000000
Neolamprologus brichardi	Princess cichlid	Cichliformes	Cichlidae	AFNY00000000
Notothenia coriiceps	Black rockcod	Perciformes	Nototheniidae	AZAD01000000
Oreochromis niloticus	Nile tilapia	Cichliformes	Cichlidae	AERX00000000
Pampus argenteus	Silver pomfret	Scombriformes	Stromateidae	JHEK00000000
Pimephales promelas	Fathead minnow	Cypriniformes	Cyprinidae	JNCD01000000
Poecilia formosa	Amazon molly	Cyprinodontiformes	Poeciliidae	AYCK00000000
Poecilia reticulata	Guppy	Cyprinodontiformes	Poeciliidae	AZHG00000000
Pundamilia nyererei	Flame back cichlid	Cichliformes	Cichlidae	AFNX00000000
Salmo salar	Atlantic salmon	Salmoniformes	Salmonidae	AGKD00000000 (275)
Sebastes nigrocinctus	Tiger rockfish	Perciformes	Sebastidae	AUPR00000000
Sebastes rubrivinctus	Flag rockfish	Perciformes	Sebastidae	AUPQ00000000
Stegastes partitus	Bicolor damselfish	Perciformes	Pomacentridae	JMKM00000000
AMPHIBIA				
Xenopus (Silurana) laevis	African clawed frog	Anura	Pipidae	http://www.xenbase.org/entry/
Ascaphus truei	Coastal tailed frog	Anura	Ascaphidae	BGI-G10K
Spea bombifrons	Plains spadefoot toad	Anura	Scaphiopodidae	BGI-G10K
Bufo marinus	Cane toad	Anura	Bufonidae	BGI-G10K
Limnodynastes dumerilii	Eastern banjo frog	Anura	Limnodynastidae	BGI-G10K
Oophaga pumilio	Strawberry dart-poison frog	Anura	Dendrobatidae	BGI-G10K
Physalaemus pustulosus	Tungara frog	Anura	Leiuperidae	BGI-G10K
Eleutherodactylus coqui	Coqui	Anura	Eleutherodactylidae	BGI-G10K
Nanorana parkeri	Tibetan frog	Anura	Dicroglossidae	BGI-G10K
Gastrotheca cornuta	Horned marsupial frog	Anura	Hemiphractidae	BGI-G10K
Ichthyophis bannanicus	Banna caecilian	Gymnophiona	Ichthyophiidae	BGI-G10K
"REPTILIA"				
Sphenodon punctatus	Tuatara	Sphenodontia	Sphenodontidae	AWC-G10K
Eublepharus macularius	Leopard gecko	Squamata	Gekkonidae	BGI-G10K
Heloderma suspectum	Gila monster	Squamata	Helodermatidae	BGI-G10K
Podarcus muralis	Wall lizard	Squamata	Lacertidae	BGI-G10K
Ophisaurus harti	Chinese glass lizard	Squamata	Anguidae	BGI-G10K
Aspidoscelis arizonae	Western whiptail	Squamata	Teiidae	BGI-G10K
Pogona vitticeps	Central bearded dragon	Squamata	Agamidae	BGI-G10K
Shinisaurus crocodilurus	Chinese crocodile lizard	Squamata	Shinisauridae	BGI-G10K
Apalone spinifera	Spiny softshell turtle	Testudines	Trionychidae	APJP00000000
AVES				
Zonotrichia albicollis	White-throated sparrow	Passeriformes	Fringillidae	ARWJ00000000
MAMMALIA				

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION or BGI-G10K species
Acinonyx jubatus	Cheetah	Carnivora	Felidae	BGI-G10K
Panthera leo	Lion	Carnivora	Felidae	BGI-G10K
Puma concolor coryi	Puma	Carnivora	Felidae	BGI-G10K
Crocuta crocuta	Spotted hyena	Carnivora	Hyaenidae	BGI-G10K
Vulpes vulpes	Red fox	Carnivora	Canidae	BGI-G10K
Connochaetes taurinus	Blue wildebeest	Cetartiodactyla	Bovidae	BGI-G10K
Elaphurus davidianus	Pere David's deer	Cetartiodactyla	Cervidae	BGI-G10K
Sousa chinensis	Chinese white dolphin	Cetartiodactyla	Delphinidae	BGI-G10K
Giraffa camelopardalis	Giraffe	Cetartiodactyla	Giraffidae	BGI-G10K
Tragulus napu	Greater Malayan chevrotain	Cetartiodactyla	Tragulidae	BGI-G10K
Oryx gazella	Gemsbok	Cetartiodactyla	Bovidae	BGI-G10K
Muntiacus reevesi	Chinese muntjac	Cetartiodactyla	Cervidae	BGI-G10K
Muntiacus muntjak	Indian muntjac	Cetartiodactyla	Cervidae	BGI-G10K
Desmodus rotundus	Common vampire bat	Chiroptera	Phyllostomidae	BGI-G10K
Dromiciops gliroides	Monito del monte	Microbiotheria	Microbiotheriidae	BGI-G10K
Tachyglossus aculeatus	Short-beaked echidna	Monotremata	Tachyglossidae	BGI-G10K
Equus przewalskii	Mongolian horse	Perissodactyla	Equidae	BGI-G10K
Fukomys damarensis	Damaraland mole rat	Rodentia	Bathyergidae	BGI-G10K
Spermophilus dauricus	Daurian souslik ground squirrel	Rodentia	Sciuridae	BGI-G10K
Bison bison	American bison	Cetartiodactyla	Bovidae	JPYT00000000
Bubalus bubalis	Water buffalo	Cetartiodactyla	Bovidae	AWWX00000000
Cavia aperea	Brazilian guinea pig	Rodentia	Caviidae	AVPZ00000000
Ceratotherium simum simum	Southern white rhinoceros	Perissodactyla	Rhinocerotidae	AKZM00000000
Chinchilla lanigera	Long-tailed chinchilla	Rodentia	Chinchillidae	AGCD00000000
Chlorocebus sabaeus	Green monkey	Primates	Cercopithecidae	AQIB00000000
Chrysochloris asiatica	Cape golden mole	Afrosoricida	Chrysochloridae	AMDV00000000
Condylura cristata	Star-nosed mole	Eulipotyphla	Talpidae	AJFV00000000
Elephantulus edwardii	Cape elephant shrew	Macroscelidae	Macroscelididae	AMGZ00000000
Eptesicus fuscus	Big brown bat	Chiroptera	Vespertilionidae	ALEH00000000
Galeopterus variegatus	Sunda flying lemur	Dermoptera	Cynocephalidae	JMZW00000000
Jaculus jaculus	Lesser Egyptian jerboa	Rodentia	Dipodidae	AKZC00000000
Leptonychotes weddellii	Weddell seal	Carnivora	Phocidae	APMU00000000
Manis pentadactyla	Chinese pangolin	Pholidota	Manidae	JPTV00000000
Mesocricetus auratus	Golden hamster	Rodentia	Cricetidae	APMT00000000
Microtus ochrogaster	Prairie vole	Rodentia	Cricetidae	AHZW00000000
Mustela putorius furo	Domestic ferret	Carnivora	Mustelidae	AEYP00000000
Octodon degus	Degu	Rodentia	Octodontidae	AJSA00000000
Odobenus rosmarus divergens	Pacific walrus	Carnivora	Odobenidae	ANOP00000000

SPECIES	COMMON NAME	ORDER	FAMILY	GENBANK ACCESSION or BGI-G10K species
Orcinus orca	Killer whale	Cetartiodactyla	Delphinidae	ANOL00000000
Orycteropus afer	Aardvark	Tubulidentata	Orycteropodidae	ALYB00000000
Papio anubis	Olive baboon	Primates	Cercopithecidae	AHZZ00000000
Peromyscus maniculatus	North American deer mouse	Rodentia	Cricetidae	AYHN00000000
Physeter catodon	Sperm whale	Cetartiodactyla	Physeteridae	AWZP00000000
Saimiri boliviensis	Bolivian squirrel monkey	Primates	Cebidae	AGCE00000000
Trichechus manatus latirostris	Florida manatee	Sirenia	Trichechidae	AHIN00000000

Table 4

Long-read and mapping technologies that promise to improve genome assemblies

Platform or method	Technology	URL/more information
Pacific Biosciences	Single-molecule, real-time sequencing	http://www.pacificbiosciences.com
Illumina Moleculo	Long molecular reads	http://www.illumina.com/technology/next-generation-sequencing/long-read-sequencing-technology.html
Oxford Nanopore	Nanopore sensing	https://www.nanoporetech.com/
BGI Complete Genomics	Self-assembling DNA nanoarrays	http://www.completegenomics.com/
OpGen	Whole genome mapping	http://www.opgen.com/
BioNano Genomics	Single-molecule imaging/nanochannel arrays	http://www.bionanogenomics.com/
Nabsys	Single-molecule sequencing with nanodetectors	http://www.nabsys.com/
Stratos Genomics	Single-molecule sequencing by Sequencing by Expansion (SBX)	http://www.stratosgenomics.com/
Electronic BioSciences	Nanopore single-molecule sequencing	http://electronicbio.com/
GenapSys	Gene Electronic Nano-Integrated Ultra-Sensitive (GENIUS)	http://genapsys.com/
Genia	Single-molecule sequencing with nanopores	http://www.geniachip.com/
Lasergen	Lightning terminator technology	http://lasergen.com/
Noblegen	Single-molecule sequencing with nanopores and optical reading	http://www.noblegenbio.com/
QuantuMDx	Single-molecule sequencing (Q-SEQ)	http://www.quantumdx.com/
Sperm haplotyping	Whole genome haplotyping	34–36
Radiation hybrid maps	Whole chromosome mapping	279
Trios	Whole genome haplotyping	280

Table 5

Example tools used for genome assembly, annotation of genome features, and mapping

Feature	Example software	URL	Reference
1. Genome assembly (*de novo*)	ALLPATHS_LG	http://www.broadinstitute.org/software/allpaths-lg/blog/	211
	SOAPdenovo2	http://soap.genomics.org.cn/soapdenovo.html	212
2. Assembly statistics	FASTQC	www.bioinformatics.babraham.ac.uk/projects/fastqc/	
3. Gene annotation[a]	GENSCAN	http://genes.mit.edu/GENSCAN.html	213
	AUGUSTUS	http://bioinf.uni-greifswald.de/augustus/	214
	Gnomon	http://www.ncbi.nlm.nih.gov/genome/guide/gnomon.shtml	
	Genewise	http://www.ebi.ac.uk/~birney/wise2/	216
	Exonerate	http://www.ebi.ac.uk/~guy/exonerate/	217
	Splign	http://www.ncbi.nlm.nih.gov/sutils/splign/splign.cgi	218
4. DNA variants			
a. SNPs	SAMtools	http://samtools.github.io/	219
	VCFtools	http://vcftools.sourceforge.net/	220
	GATK	https://www.broadinstitute.org/gatk/	221
b. Indels	BreakDancer	http://breakdancer.sourceforge.net/	222
	VariationHunter	http://compbio.cs.sfu.ca/software-variation-hunter	223
	Picard	http://sourceforge.net/projects/picard/	
c. Copy number variation[b]	Cortex assembler	http://cortexassembler.sourceforge.net/index_cortex_var.html	224
	Magnolya	http://sourceforge.net/projects/magnolya/	225
	mrCaNaVaR	http://mrcanavar.sourceforge.net	226
	cn.MOPS	http://www.bioinf.jku.at/software/cnmops/	227
5. Repetitive element content			
a. Interspersed repeats	RepeatMasker	http://www.repeatmasker.org	
	WindowMasker	http://www.ncbi.nlm.nih.gov/IEB/ToolBox/CPP_DOC/lxr/source/src/app/winmasker/	228
b. Tandem repeats[c]	Tandem Repeats Finder	http://tandem.bu.edu/trf/trf.html	229
c. Microsatellites	Misa	http://pgrc.ipk-gatersleben.de/misa/	232
	GMATo	http://sourceforge.net/projects/gmato/files/	233
d. Low-complexity regions	DustMasker	http://www.ncbi.nlm.nih.gov/IEB/ToolBox/CPP_DOC/lxr/source/src/app/dustmasker/	230
6. Endogenous retrovirus-like elements	RetroTector	http://retrotector.neuro.uu.se/	234
	LTR_STRUC	http://www.mcdonaldlab.biology.gatech.edu/ltr_struc.htm	235
	LTR-FINDER	http://tlife.fudan.edu.cn/ltr_finder/	236
	LTRharvest	http://www.zbh.uni-hamburg.de/?id5206	237
7. Segmental duplications	Dupmasker	http://www.repeatmasker.org/DupMaskerDownload.html	238
8. MicroRNAs	MiRFinder	http://www.bioinformatics.org/mirfinder/	240
	miRBase	http://www.mirbase.org/	241
	ViennaRNA	http://www.tbi.univie.ac.at/RNA/index.html	242
9. Methylation sites	Bismark	http://www.bioinformatics.babraham.ac.uk/projects/bismark/	244

Feature	Example software	URL	Reference
	BS Seeker	http://pellegrini.mcdb.ucla.edu/BS_Seeker/BS_Seeker.html	245, 246
	FadE	https://code.google.com/p/fade/	247
10. Gene family expansion and contraction	CAFÉ	http://sites.bio.indiana.edu/~hahnlab/Software.html	250, 251
11. Evolutionary constrained elements	phastCons	http://compgen.bscb.cornell.edu/phast/phastCons-HOWTO.html	252
	SiPhy	http://www.broadinstitute.org/genome_bio/siphy/index.html	254
12. Signature of Selection[d]			
a. Ds/Dn ratios	PAML 4	http://abacus.gene.ucl.ac.uk/software/paml.html	255
b. Fst outliers	LOSITAN	http://popgen.net/soft/lositan/	256
c. Homozygous tracks	PLINK	http://pngu.mgh.harvard.edu/~purcell/plink/	257
d. Extended haplotypes	rehh	http://cran.r-project.org/web/packages/rehh/index.html	258
13. Transcriptome mapping			
a. Assembler	Trinity	http://trinityrnaseq.sourceforge.net/	259
b. Aligner	TopHat	http://ccb.jhu.edu/software/tophat/index.shtml	260
	STAR	https://code.google.com/p/rna-star/	261
14. Comparative assessment; HSBs, EBRs	Evolution Highway	http://eh-demo.ncsa.uiuc.edu/	262, 263
	Satsuma	http://sourceforge.net/projects/satsuma/	264
	SyMAP	http://www.agcol.arizona.edu/software/symap/	265
	RACA	http://bioen-compbio.bioen.illinois.edu/RACA/	270
15. Genome alignment	MultiZ	http://www.bx.psu.edu/miller_lab/dis....012109.tar.gz	52
	LASTZ	http://www.bx.psu.edu/~rsharris/lastz/	266
16. Genome browsers	GBrowse	http://gmod.org/wiki/GBrowse	132
	JBrowse	http://jbrowse.org/	133
	UCSC Genome Browser	http://genome.ucsc.edu	134, 267
	Integrative Genomics Viewer (IGV)	https://www.broadinstitute.org/igv/home	268, 269

[a] See review by Yandell & Ence (6).

[b] See review by Zhao et al. (270).

[c] See reviews by Merkel & Gemmell (271) and Lim et al. (272).

[d] See reviews by Oleksyk et al. (273) and Scheinfeldt & Tishkoff (274).