SkateBase, an elasmobranch genome project and collection of molecular resources for chondrichthyan fishes [version 1; peer review: 2 approved]

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Abstract

Chondrichthyan fishes are a diverse class of gnathostomes that provide a valuable perspective on fundamental characteristics shared by all jawed and limbed vertebrates. Studies of phylogeny, species diversity, population structure, conservation, and physiology are accelerated by genomic, transcriptomic and protein sequence data. These data are widely available for many sarcopterygii (coelacanth, lungfish and tetrapods) and actinoptergii (ray-finned fish including teleosts) taxa, but limited for chondrichthyan fishes. In this study, we summarize available data for chondrichthyes and describe resources for one of the largest projects to characterize one of these fish, Leucoraja erinacea, the little skate. SkateBase (http://skatebase.org) serves as the skate genome project portal linking data, research tools, and teaching resources.

This article is included in the Bioinformatics gateway.

This article is included in the Elasmobranch biology & conservation collection.
This article is included in the Phylogenetics collection.

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Introduction

Chondrichthyan fishes are composed of two subclasses, Holoccephali and Elasmobranchii. Holoccephalans are the more basal of the pair having first appeared more than 400 million years ago and include a single surviving order, Chimaeriformes, the chimaeras, with 39 extant species. Elasmobranchs appeared approximately 350 million years ago and include more than 1000 species of sharks, skates, and rays. Chondrichthyan fishes occupy a pivotal position at the base of the vertebrate phylogenetic tree. For research that includes an evolutionary component, representation of this diverse class affords a valuable perspective to evaluate all vertebrates.

Chondrichthyan fishes are circumglobal in distribution and occupy a wide range of ecological habitats. Their life history parameters are equally disparate but in general chondrichthyan are slow growing and late maturing fishes with an increased risk of extinction. Fecundity is as few as 1 or 2 for viviparous species such as the sand tiger shark, Carcharias taurus and as high as 300 for the whale shark, Rhincodon typus. They are of economic importance for fisheries as well as ecotourism. Management and assessment of stock is essential to ensure both ecotourism interests and food resources remain sustainable. Management of fish populations has increasingly relied on molecular tools to investigate population structure, properly identify species, and compliance with fishing quotas.

Elasmobranchs have been used as a model for biomedical research for more than 100 years. Elasmobranchs, like other cartilaginous fishes, exhibit many fundamental vertebrate characteristics, including a neural crest, jaws and teeth, an adaptive immune system, and a pressurized circulatory system. The skate is a powerful comparative model to study biological processes shared among jawed and limbed vertebrates such as development, renal physiology, immunology, toxicology, neurobiology, and wound healing and regeneration. They are the most ancient vertebrates to possess an adaptive immune system that generates antibodies using a V(D)J combinatorial mechanism. Phylogenetically, cartilaginous fishes are the first vertebrates to possess a thymus, a central lymphoid organ that provides a microenvironment for the development of T cells. The thymus shares a common organization with more derived vertebrates containing cortical and medullary regions.

In addition to shared physiological characteristics, the diversity of specializations between species allows investigations of evolution within a single clade. For example, elasmobranchs use a plethora of reproductive strategies that span the full range of maternal investment from placental viviparity to strict lecitrophic oviparity. Besides sexual reproduction, captive elasmobranchs are capable of asexual parthenogenesis. Of these reproductive mechanisms, the most tractable for research purposes is oviparity. Approximately 45% of chondrichthyan utilize oviparity including all Chimaeriformes, Heterodontiformes (bullhead sharks), Rajiformes (skates) and Scyliorhinidae (catsharks). Many species can be maintained in captivity and will breed and lay eggs throughout an annual season. Artificial insemination has been reported for two oviparous species, the common skate, Raja eglanteria, and the cloudy catshark, Scyliorhinus torazame. Additionally, sperm storage allows wild caught females to lay eggs for several years without requiring males or captive mating events.

Leucoraja erinacea, the little skate, was chosen for a genome sequencing project to represent this clade of fishes because of their use as a biomedical model, experimental tractability, genome size, existing sequence data, and northeast regional distribution. The sequencing project is an ongoing effort of the North East Bioinformatics Collaborative (NEBC) of the North East Cyberinfrastructure Consortium (NECC), composed of the bioinformatics core facilities from Delaware, Maine, New Hampshire, Rhode Island, and Vermont funded by National Institutes of Health (NIH) Institutional Development Awards (IDeA) and/or National Science Foundation (NSF) Experimental Program to Stimulate Competitive Research (EPSCoR) programs.

Existing resources

There is a single order of holoccephalans and 13 orders of elasmobranchs. The distribution of species in orders, families and genera is shown in Figure 1. The batoids are composed of 4 orders, Rajiformes, Myliobatiformes, Torpidiformes, and Rhinopristsiformes, and contain 54% of extant chondrichthyan species. Sharks are broadly divided into two super orders, Galeomorphi and Squalomorphi that together account for 43% of extant chondrichthyan species. The galean sharks include 4 orders: Heterodontiformes, Orectolobiformes, Lamniformes and Carcharhiniformes, and represent 30% of extant chondrichthyan species. Squalean sharks are composed of 4 orders: Squaliformes, Squatiniformes, Pristiphoridae, and Hexanchiformes, comprising 13% of extant chondrichthyan species. Among individual orders, Rajiformes, the skates, have the most species (345) followed by Carcharhiniformes, the ground sharks (283) and Myliobatiformes (226). These ‘big three’ orders contain 854 species, 72% of extant chondrichthyan species.

Chondrichthyan conservation, management, and research all benefit from easily accessible and well-documented molecular resources. The organization of data and metadata in archival databases is critically important for efficient use of large and complex datasets. The International Nucleotide Sequence Database Collaboration (INSDC) is composed of three large public nucleotide repositories, DNA Data Bank of Japan (DDBJ), European Molecular Biology Laboratory-European Bioinformatics Institute (EMBL-EBI), and GenBank at the National Center for Biotechnology Information (NCBI). Recently, two new NCBI database projects were initiated to collect details of samples, BioSample, and project data, BioProject, and propagate the metadata to all associated database entries in an effort to expand the use of already existing and rapidly expanding molecular resources. Figure 2 illustrates the relationship between BioProject, BioSample and the sequence data for SkateBase. Because the BioProject and BioSample databases were established in 2012, not all existing datasets have metadata or details of the biological source to populate a BioSample and BioProject entry. When available, BioProject and BioSample hyperlinks are included for Sequence Read Archive (SRA), Expresseed Sequence Tag (EST) and Genome Survey Sequence (GSS) datasets in the tables below.

Table 1 is a summary of chondrichthyan sequence data in NCBI databases, UniProtKB, and the Protein Data Bank (PDB) with L. erinacea, Callorhinichus mili and Scyliorhinus canicula, the three species featured at SkateBase listed individually. The distribution of holoccephalans and elasmobranchs in public databases
is illustrated in Figure 3. Despite the majority of species belonging to Elasmobranchi, the GenBank, UniProtKB/TrEMBL, and Gene databases are dominated by chimaera data derived from the genome sequence of the elephant shark, *C. milii*. Elasmobranch data predominates in UniProtKB/Swiss-Prot, PDB, BioProject and BioSample databases as well as the number of whole mitochondrial genomes (WMG) in GenBank. The EST and SRA databases are nearly equally split between the two subclasses.

**Chondrichthyan genomes**

Currently there are multiple efforts to sequence an elasmobranch genome in various stages of completion (Table 2); however, only

![Figure 1. Species distribution within chondrichthyan orders.](image)

*Figure 1. Species distribution within chondrichthyan orders.* There is a single order of Holocephalans, Chimaeriformes, and 13 orders of elasmobranchs. The distribution of chondrichthyan species in each of the 14 orders is shown relative to the total number of species, genera and families for the clade. The batoids are composed of 4 orders, Rajiformes, Myliobatiformes, Torpidiformes, and Rhinopristiformes, and contain 54% of extant chondrichthyan species. Sharks are broadly divided into two super orders, Galeomorphii and Squalomorphii that together include the remaining 9 orders and 43% of extant chondrichthyan species.
the skate genome project currently has data publically available. Efforts to sequence the whale shark are underway at the Georgia Aquarium and Emory University (personal communication, Alistair Dove, Georgia Aquarium). Genoscope leads a project to sequence the genome of another oviparous elasmobranch, the catshark, *S. canicula*[^2]. The current assembly is described in Table 2. A second version of the catshark genome with 200x coverage, including mate pair sequencing, is in progress (personal communication, Sylvie Mazan, French National Centre for Scientific Research). Among holocephalans, the genome of the elephant shark, *C. milii*, was described in a 1.4x coverage assembly in 2006[^3]. With continued sequencing the assembly coverage is currently 19.25x and data has been made available through the project website (http://esharkgenome.imcb.a-star.edu.sg/) and Genbank[^4].

A powerful resource for characterizing genomes is large-insert clone libraries where each clone contains a large (~100kb) genomic region. Bacterial artificial chromosome (BAC) and P1-derived artificial chromosome (PAC) libraries are DNA constructs within a plasmid used to transform bacteria. As the bacteria grow the inserted DNA is amplified and subsequently isolated and sequenced. BACs are beneficial for genome sequencing projects because the insert size can be very large, nearly 350 kb, facilitating assembly post-sequencing. BAC/PAC libraries were built for several chondrichthyan species.

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### Table 1. Chondrichthyan molecular sequence data in public databases.

| Taxonomy     | GenBank WMG | GenBank EST | GenBank EST lib | GenBank GSS | GenBank GSS lib | WGS (Mbp) | GEO | SRA | Swiss-Prot | TrEMBL | PDB |
|--------------|-------------|-------------|-----------------|-------------|-----------------|-----------|-----|-----|------------|--------|-----|
| Chondrichthytes | 7777        | 16          | 75              | 21069       | 55810           | 72        | 192948 | 33  | 28497      | 5      | 2492.3 | 3   | 22  | 276 | 26485* | 178  |
| Holocephali   | 7863        | 3           | 21              | 20201       | 39512           | 8         | 109965 | 6   | 27944      | 1      | 936.9  | 1   | 13  | 12  | 20170  | 0    |
| *C. miliaris* | 7868        | 3           | 21              | 20110       | 39232           | 1         | 109965 | 6   | 27944      | 1      | 936.9  | 1   | 13  | 3   | 19989   | 0    |
| Elasmobranchii| 7778        | 13          | 54              | 868         | 16273           | 64        | 82983  | 27  | 553        | 4      | 1555.4 | 2   | 9   | 264 | 6299   | 178  |
| *L. erinacea* | 7782        | 3           | 7               | 13          | 284             | 1         | 31167  | 5   | 0          | 0      | 0      | 1555.4 | 1   | 2   | 6   | 123    | 0    |
| *S. canicula* | 7830        | 2           | 8               | 13          | 645             | 1         | 1600   | 7   | 0          | 0      | 0      | 1555.4 | 1   | 1   | 38  | 283    | 1    |

(WMG) whole mitochondrial genome, (EST) Expressed Sequence Tags, (lib) libraries (GSS) Genome Survey Sequences, (GEO) Gene Expression Omnibus, (WGS) Whole Genome Shotgun, (SRA) Sequence Read Archive, (WMG) whole mitochondrial genomes, (PDB) Protein Data Bank. * includes 16 unidentified fin entries.

NCBI databases accessed July 25, 2014, Release 2014_07 of 09-Jul-2014, GEO sample accessions

### Table 2. Chondrichthyan genome sequencing projects.

| Website      | Genome size (Gb) | Coverage | Contigs | N50 (bp) | Platform | Facility | Genbank       | BioProject | BioSample | Date      |
|--------------|------------------|----------|---------|----------|----------|----------|----------------|------------|-----------|-----------|
| *Callorhinus milii* | esharkgenome    | 0.910    | 19.25x  | 21,203   | Sanger   & 454 | IMCB     | AAVX02000000 | PRJNA236996 | SAMN000000800 | 20-Dec-13* |
| Elasmobranchii |      |          |         |          |          |          |                |            |           |           |
| *Leucoraja erinacea* | skatebase.org   | 3.42     | 26x     | 2,62,365 | Illumina PE | NECC     | AESE010000000 | PRJNA60893 | SAMN00189066 | 22-Dec-11  |
| *Scyliorhinus canicula* | -         | 3.5      | 32x     | 3,449,662 | Illumina PE | Genopscope-CEA | -         | -         | -         |
| *Rhinodon typus* | -               | 3.44(est.) | 35x    | 1,292    | Illumina PE | Emory University & Georgia Aquarium | -         | PRJNA255419 | SAMN002918461 & SAMN002918462 | 16-Jul-14 |

* (M) Mega or (G) Giga base pairs; (PE) paired end; (est) estimated; (ICMB) Institute of Molecular and Cell Biology, A*STAR, (NECC) North East Cyberinfrastructure Consortium

* replaced original sequence data GenBank AAVX00000000.1 (1.4x coverage) released 20-DEC-2006
The distribution of data for Holocephalii (chimaeras) and elasmobranchii (sharks and rays) subclasses of chondrichthyan fishes does not always reflect their species distribution. The number of species represented in GenBank is representative of the actual species distribution but the amount of data in GenBank is not. Holocephalan data forms the majority of the NCBI Gene, GenBank, Genome Survey Sequence (GSS) and UniProt TrEMBL databases. The number of Short Reach Archive (SRA) experiments and EST sequences in nearly equal for each subclass and the remaining databases are primarily populated by elasmobranch data.

including the nurse shark, *Ginglymostoma cirratum*; elephant shark, *C. milli*; little skate, *L. erinacea*; horn shark, *Heterodontus francisci*; dogfish shark, *Squalus acanthias*; and catshark, *S. canicula*. These libraries were used to successfully characterize a handful of genomic regions such as little skate *HoxA* cluster, *Hox A and D* clusters, catshark *HoxA, B and D* clusters, *C. mili HoxA-D clusters*, immunoglobulin receptor IgW C regions, and neurohypophysial gene loci.

**RNA databases**

Transcriptome sequencing seeks to characterize all genes expressed in a tissue or set of tissues in a sample. Technologies to identify the complete RNA transcript sequence have developed from studies of a small number of transcripts to comprehensive characterizations. The application of large-scale cDNA cloning of Expressed Sequence Tags (ESTs) gave initial characterizations of 5-prime and/or 3-prime ends of transcripts in several elasmobranchs including *L. erinacea* and *S. acanthias* (Table 3). EST sequence data are available in the EST divisions of the GenBank, EMBL and DDBJ databases that make up the INSDC. cDNA clones and their sequences from these EST projects have enabled the complete characterization of the full-length cDNA sequence of several genes. In the last five years, high-throughput RNA sequencing (RNA-Seq) has been applied to comprehensively examine the complete
sequence of transcripts in tissues of cartilaginous fishes. Among the most valuable RNA-Seq datasets are those from whole late-stage embryos following organogenesis. Our project has generated these datasets for L. erinacea, S. canicula and C. milii⁴³. Public RNA-Seq data sets can be found in the NCBI Gene Expression Omnibus and Short Read Archive (SRA) databases or the EBI ArrayExpress and European Nucleic Acid (ENA) archives (Table 3 and Table 4).

### Mitochondrial genomes

Individual mitochondrial genes such as cytochrome c oxidase subunit I (CO1 or COX1) and NADH-ubiquinone oxidoreductase chain 2 (NADH2 or MT-ND2) have been used extensively to construct molecular phylogenies⁴⁴-⁴⁷. The Fish barcode of life (FISH-BOL) a working group of the International Barcode of Life Project (iBOL), has CO1 barcodes for 54% of elasmobranchs and 62% of holocentrodans (http://www.fishbol.org, accessed July 24, 2014). Recently, whole mitochondrial sequences are increasingly popular for their increased granularity when resolving branches of phylogenetic trees⁴⁸. Whole mitochondrial genome sequences currently are available for 72 species of sharks, skates, rays and chimaeras. These sequences are accessible in the GenBank, EMBL and DDBJ databases summarized in Table 5⁴⁹.

### Chondrichthyan Tree of Life

Currently, molecular data for cartilaginous fishes is being collected as part of the Chondrichthyan Tree of Life project (http://sharksrays.org). The project website currently includes 5 elements: 1) an interactive phylogenetic tree⁵₀; 2) scientific illustrations of specimens; 3) range information for all extant species; 4) interactive comparative anatomy through segmented CT scan data; and 5) DNA sequence for 1265 single copy orthologous genes⁵₁. Project data will be available in public databases as well as through the project website once collection and analysis is complete (personal communication, Gavin Naylor, Medical University of South Carolina).

### Protein databases

Given the improved technologies to characterize full-length transcripts using RNA-Seq, there are increasingly more protein sequence data for chondrichthyan. The UniProt Consortium, consists of groups from the European Bioinformatics Institute (EBI), the Swiss Institute of Bioinformatics (SIB) and the Protein Information Resource (PIR). The consortium maintains the UniProt Knowledgebase (UniProtKB), a comprehensive and standardized catalogue of protein sequences and functional annotation knowledgebase⁵₂. Proteins with UniProtKB accessions are first automatically annotated, unreviewed UniProtKB/TrEMBL entries that progress to UniProtKB/TrEMBL entries following curator review. Among Chondrichthyans, there are 12 UniProtKB/Swiss-Prot and 20,170 UniProtKB/TrEMBL entries for holocentrodans and 264 UniProtKB/Swiss-Prot and 6,299 UniProtKB/TrEMBL entries for elasmobranchs in Release 2014_07 of 09-Jul-2014 of the knowledgebase (Table 1). An unidentified fin sample accounts for 16 UniProtKB/TrEMBL entries that are not included in either Holocentrodan or Elasmobranchii. PDB, an archive of protein macromolecular structural data, has 178 entries for Chondrichthyans, all elasmobranchs⁵³. Of these, 76% are derived from 2 species from a single family, Torpediniformes, the electric rays, and in total only 10 species are represented in PDB.

The distribution of data in NCBI databases, PDB, and UniProtKB for chondrichthyan orders is shown in Figure 4. When order Chimaeriformes is included (Figure 4A) the distributions are disproportionate due to the large volume of annotated sequence data from the elephant shark genome. The distributions are repeated exclusively for elasmobranchs. To understand if the data distribution is representative of the number of species in each order, a species distribution is included in each chart. A cladogram (Figure 4B) is linked to the chart legend and illustrates the phylogeny between chondrichthyan orders.

### SkateBase

SkateBase (http://skatebase.org) is the public portal for the little skate genome project and is a valuable collection of data and learning resources. The NEBC little skate genome project team hosted three week-long workshops and a mitochondrial genome annotation jamboree with the goal of using the project data to develop a bioinformatics aware workforce and foster collaborative and distributed big data research. The lecture materials and worked annotation examples are included at SkateBase for educational use (http://skatebase.org/workshops). The project vitae contains an overview and timeline of the genome project effort along with key personnel, project related publications and presentations, the curation team, and citation information for researchers utilizing the resource in their publication. A Gene Table currently represents manually curated genes derived from workshops and curriculum with extensive annotation evidence. The number of gene entries will continue to grow through usage and expansion of the SkateBase educational modules. Plans to update the annotation interface to enable community annotation by domain experts is planned for the future.

SkateBase provides links to web resources with chondrichthyan data including the Chondrichthyan Tree of Life, Elephant Shark Genome Project (http://esharkgenome.imcb.a-star.edu.sg), the first described genome for a chimaera⁵₄, and Vertebrate TimeCapsule, (http://transcriptome.cdb.riken.go.jp/vtcap), a project that aims to develop a gene database to represent evolution and development for vertebrates and currently includes transcriptome data for a hagfish (Eptatretus burgeri), shark (S. torazame) and birchir (Polypterus senegalus)⁵₅. SkateBase data is linked locally as well as from NCBI in the Gene Expression Omnibus (GSE26235), GenBank (AEO010000000) and Sequence Read Archive (SRA026856) to ensure convenient and easy access. A link to the American Elasmobranch Society (http://www.elasmo.org), a non-profit organization with the mission of advancing the scientific study of living and fossil sharks, skates, rays, and chimaeras and promoting education, conservation, and wise utilization of natural resources, connects domain scientists to the little skate genome project.

SkateBase data includes embryonic transcripts for three chondrichthyan species, a chimaera, C. mili, a shark, S. canicula and the little skate, L. erinaceus as well as the first draft of the little skate genome. The assembled skate genome sequence gave a single high-coverage contiguous sequence that represented the entire length of the mitochondrial genome. The mitochondrial genome was subsequently annotated as part of a Jamboree in 2011⁵₆. The annotated sequence is represented by the NCBI Reference Sequence (RefSeq) project, accession NC_016429, and provides extensive information for each gene.
### Table 3

| BioSample | BioSample Description | Library ID | Organism | Sample age/sex | Sample type | ESTs | Facility | Date |
|-----------|-----------------------|------------|----------|----------------|-------------|------|----------|------|
| 1006673   | Elephant shark full-length cDNA library from gills | 1000673   | Callorhinchus milii | testis | 27944 | IMCB | 2004 |
| 1006674   | Elephant shark full-length cDNA library from intestine | 1000674   | Callorhinchus milii | testis | 29234 | IMCB | 2012 |
| 1006675   | Elephant shark full-length cDNA library from liver | 1000675   | Callorhinchus milii | testis | 16664 | IMCB | 2012 |
| 1006676   | Elephant shark full-length cDNA library from kidney | 1000676   | Callorhinchus milii | testis | 16573 | IMCB | 2012 |
| 1006677   | Elephant shark full-length cDNA library from spleen | 1000677   | Callorhinchus milii | testis | 19246 | IMCB | 2012 |
| 1006678   | Elephant shark full-length cDNA library from intestine | 1000678   | Callorhinchus milii | testis | 12146 | IMCB | 2012 |
| 158310    | Torpedo marmorata electric lobe | 158310    | Torpedo marmorata | - | 8 | CNRS | 2000 |
| 158311    | Torpedo marmorata electric organ | 158311    | Torpedo marmorata | - | 8 | CNRS | 2000 |
| 159482    | Toptedo californica electric organ | 159482    | Toptedo californica | - | 10185 | Children's National Medical Center, USA | 2006 |
| 154386    | Little skate embryo cell line (LEE-1); 5' sequences | 154386    | Leucoraja erinacea | adult, mixed | 5698 | MDIBL | 2004 |
| 154387    | Little skate embryo tissues; 5' sequences | 154387    | Leucoraja erinacea | embryo, stages 19-24 | 5600 | MDIBL | 2006 |
| 222710    | Dogfish testis, round spermatids zone (SSH) | 222710    | Scyliorhinus canicula | adult | 79 | Genoscope-CEA | 2011 |
| 222711    | Dogfish testis - spermatogonia zone (SSH) | 222711    | Scyliorhinus canicula | adult | 79 | Genoscope-CEA | 2011 |
| 222712    | Dogfish testis - round spermatids zone (SSH) | 222712    | Scyliorhinus canicula | adult | 79 | Genoscope-CEA | 2011 |
| 222713    | Dogfish testis - spermatogonia zone (SSH) | 222713    | Scyliorhinus canicula | adult | 79 | Genoscope-CEA | 2011 |
| 222714    | Dogfish testis - round spermatids zone (SSH) | 222714    | Scyliorhinus canicula | adult | 79 | Genoscope-CEA | 2011 |
| 222715    | Dogfish testis - spermatogonia zone (SSH) | 222715    | Scyliorhinus canicula | adult | 79 | Genoscope-CEA | 2011 |
| BioSample   | BioSample Description                           | Library ID  | Sample type | Organism | BioProject   | SRA description                                                                 | SRA   | Facility | Date     |
|-------------|------------------------------------------------|-------------|-------------|----------|-------------|--------------------------------------------------------------------------------|-------|----------|-----------|
| PRJNA18361  | cloudy catshark embryo cDNA library            | SAMN0000800 | EST: LIBEST| Scyliorhinus torazame | adult      | Scyliorhinus torazame embryo with external yolk sac                          | SRX001870 | IMCB     | 2008      |
| PRJNA135005 | shark whole genome shotgun library 2          | GSM643959   | GSM: LIBGSS| Ginglymostoma cirratum | adult      | Ginglymostoma cirratum adult red blood cells                                    | SRX036538 | MDIBL    | 2011      |
| PRJNA168475 | shark whole genome shotgun library 1          | EST: LIBEST| EST: LIBEST| Chiloscyllium plagiosum | adult      | Chiloscyllium plagiosum adult thymus RNA                                       | SRX220387 | IMCB     | 2013      |
| PRJNA184342 | shark liver regeneration                      | EST: LIBEST| EST: LIBEST| Chiloscyllium plagiosum | female     | Chiloscyllium plagiosum female liver                                             | SRX001870 | IMCB     | 2008      |
| PRJNA183175 | shark liver regeneration                      | EST: LIBEST| EST: LIBEST| Chiloscyllium plagiosum | female     | Chiloscyllium plagiosum female liver                                             | SRX001870 | IMCB     | 2008      |
| PRJNA184343 | shark whole genome shotgun library 2          | EST: LIBEST| EST: LIBEST| Chiloscyllium plagiosum | female     | Chiloscyllium plagiosum female liver                                             | SRX001870 | IMCB     | 2008      |
| PRJNA192740 | shark whole genome shotgun library 1          | EST: LIBEST| EST: LIBEST| Chiloscyllium plagiosum | female     | Chiloscyllium plagiosum female liver                                             | SRX001870 | IMCB     | 2008      |

**Table 4.** National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) database: Chondrichthyan sequence data. [ssh] suppressive subtractive hybridization; [mixed] liver, kidney, brain, testis, ovary, gill, intestine.
| BioSample | SRA  | BioProject | SRA description | SRA description | Facility | Date |
|-----------|------|------------|----------------|----------------|----------|------|
| PRJNA168475 | SAMN02699938 | SRR154861 | Illumina sequencing of elephant shark testis RNA | Callorhinchus milii - testis | IMCB | 2013 |
| PRJNA168475 | SAMN02699937 | SRR154860 | Illumina sequencing of elephant shark spleen RNA | Callorhinchus milii - spleen | IMCB | 2013 |
| PRJNA168475 | SAMN02699936 | SRR154859 | Illumina sequencing of elephant shark ovary RNA | Callorhinchus milii - ovary | IMCB | 2013 |
| PRJNA168475 | SAMN02699935 | SRR154858 | Illumina sequencing of elephant shark liver RNA | Callorhinchus milii - liver | IMCB | 2013 |
| PRJNA168475 | SAMN02699934 | SRR154857 | Illumina sequencing of elephant shark muscle RNA | Callorhinchus milii - muscle | IMCB | 2013 |
| PRJNA168475 | SAMN02699933 | SRR154856 | Illumina sequencing of elephant shark kidney RNA | Callorhinchus milii - kidney | IMCB | 2013 |
| PRJNA168475 | SAMN02699932 | SRR154855 | Illumina sequencing of elephant shark intestine RNA | Callorhinchus milii - intestine | IMCB | 2013 |
| PRJNA168475 | SAMN02699931 | SRR154854 | Illumina sequencing of elephant shark heart RNA | Callorhinchus milii - heart | IMCB | 2013 |
| PRJNA168475 | SAMN02699930 | SRR154853 | Illumina sequencing of elephant shark brain RNA | Callorhinchus milii - brain | IMCB | 2013 |
| SAMN00188953 | GSM643957 | PRJNA135005 | Leucoraja erinacea pooled Stage 20–29 embryos | Leucoraja erinacea - stage 20–29 | MDIBL | 2011 |
| SAMN00188954 | GSM643958 | PRJNA135005 | Scyliorhinus canicula pooled Stage 24–30 embryos | Scyliorhinus canicula - stage 24–30 | MDIBL | 2011 |
| DRX000491 | DRX000491 | PRJDA61447 | Torazame EST | Ginglymostoma torazame | RIKEN | 2011 |
| SAMN01890966 | SRX036534 | PRJNA177971 | Initial Characterization of Leucoraja erinacea Genome Using 500bp Paired-End Sequencing | Leucoraja erinacea - embryo | NECC | 2011 |
| SAMN01890965 | SRX036535 | PRJNA177971 | Initial Characterization of Leucoraja erinacea Genome Using 500bp Paired-End Sequencing | Leucoraja erinacea - stage 32 | NECC | 2011 |
| SAMN01890964 | SRX036536 | PRJNA177971 | Initial Characterization of Leucoraja erinacea Genome Using 500bp Paired-End Sequencing | Leucoraja erinacea - stage 32 | NECC | 2011 |
| SRR154861 | SRR154860 | PRJNA168475 | Illumina sequencing of elephant shark testis RNA | Callorhinchus milii - testis | IMCB | 2013 |
| SRR154859 | SRR154858 | PRJNA168475 | Illumina sequencing of elephant shark ovary RNA | Callorhinchus milii - ovary | IMCB | 2013 |
| SRR154857 | SRR154856 | PRJNA168475 | Illumina sequencing of elephant shark muscle RNA | Callorhinchus milii - muscle | IMCB | 2013 |
| SRR154855 | SRR154854 | PRJNA168475 | Illumina sequencing of elephant shark intestine RNA | Callorhinchus milii - intestine | IMCB | 2013 |
| SRR154853 | SRR154852 | PRJNA168475 | Illumina sequencing of elephant shark heart RNA | Callorhinchus milii - heart | IMCB | 2013 |
| SRR154851 | SRR154850 | PRJNA168475 | Illumina sequencing of elephant shark brain RNA | Callorhinchus milii - brain | IMCB | 2013 |

1. SE: single end or (PE) paired end
2. (M): Mega or (G): Giga base pairs
## Table 5. Whole mitochondrial sequences for chondrichthyian fishes.

| Accessions | BioProject | NCBI Ref_seq | GenBank | Organism | bp  | G+C | Date       |
|------------|------------|--------------|---------|----------|-----|-----|------------|
| Holocephali |            |              |         |          |     |     |            |
| Chimaeriformes |            |              |         |          |     |     |            |
| PRJNA50265 | NC_014281.1 | HM147135.1   | CF1     | Callorhinchus callorhinchus | 16758 | 34  | 21-Oct-10 |
| PRJNA50271 | NC_014284.1 | HM147136.1   | CF1     | Callorhinchus capensis      | 16760 | 34.1| 21-Oct-10 |
| PRJNA50273 | NC_014285.1 | HM147137.1   | CF1     | Callorhinchus millii       | 16769 | 33.7| 21-Oct-10 |
| PRJNA11978 | NC_003136.1 | AJ310140.1   | CF1     | Chimaera monstrosa         | 18580 | 38.6| 14-Nov-06 |
| PRJNA50279 | NC_014288.1 | HM147138     | CF1     | Chimaera fulva             | 21336 | 38.2| 19-Oct-10 |
| PRJNA50287 | NC_014292.1 | HM147140.1   | CF1     | Harriotta raleighana       | 18024 | 42.5| 19-Oct-10 |
| PRJNA50283 | NC_014290.1 | HM147139.1   | CF1     | Hydrolagus lemuress        | 21233 | 39.4| 19-Oct-10 |
| PRJNA50289 | NC_014293.1 | HM147141.1   | CF1     | Rhinocimara pacifica       | 24889 | 41.6| 19-Oct-10 |
| Myliobatiformes |            |              |         |          |     |     |            |
| PRJNA247653 | NC_024102.1  | KJ617038.1   | CF1     | Gymnura poecilura          | 17874 | 45.1| 7-May-14  |
| PRJNA239601 | NC_023525.1  | KF751650.1   | CF1     | Himantura granulata        | 17657 | 39.1| 25-Feb-14 |
| PRJNA229016 | NC_022837.1  | KF482070.1   | CF1     | Aetobatus flagellum        | 20201 | 40.9| 3-Nov-13  |
| PRJNA198706 | NC_021132.1  | KS526959.1   | CF1     | Dasyatia akajei            | 17658 | 40.4| 10-Mar-14 |
| PRJNA190131 | NC_020352.2  | KC196067.2   | CF1     | Dasyatia bennetti          | 17668 | 40.2| 22-Jul-13 |
| PRJNA182669 | NC_019634.1  | JX524174.1   | CF1     | Dasyatis zugei             | 18264 | 36.6| 24-May-13 |
| PRJNA15549  | NC_007230.1  | AY597334.1   | CF1     | Plesiobatis davesi         | 17514 | 41.9| 20-Mar-07 |
| PRJNA212605 | NC_021767.1  | KS992792.1   | CF1     | Neotrygon kuhli            | 16905 | 39.5| 17-Jul-13 |
| PRJNA182647 | NC_019641.1  | JX827260.1   | CF1     | Taeniura meyeni            | 17638 | 41.6| 8-Nov-13  |
| Rajiformes  |            |              |         |          |     |     |            |
| PRJNA239623 | NC_023505.2  | JG763823.1   | CF1     | Dipturus kwangtungensis     | 16912 | 41.6| 13-Mar-14 |
| PRJNA81399  | NC_016429.1  | JQ034406.1   | CF1     | Leucoraja erinacea         | 16724 | 40.3| 28-Nov-11 |
| PRJNA13984  | NC_007173.1  | AY525783.1   | CF1     | Okamejei kenojei           | 16972 | 42.4| 15-Jun-05 |
| PRJNA111977 | NC_000893.1  | AF106038.1   | CF1     | Amblyraja radiata          | 16783 | 40.3| 22-Apr-09 |
| PRJNA214404 | NC_021946.1  | KC914434.1   | CF1     | Raja rhina                 | 16910 | 41.4| 11-Sep-13 |
| PRJNA214407 | NC_021963.1  | KC914433.1   | CF1     | Hongeo koreana             | 16905 | 42.2| 17-Sep-13 |
| PRJNA244226 | NC_023944.1  | KF648508.1   | CF1     | Zearaja chilensis          | 16990 | 41.1| 1-May-14  |
| Rhinopristiformes |              |              |         |          |     |     |            |
| PRJNA228994 | NC_022821.1  | KF381507.1   | CF1     | Pristis clavata            | 16804 | 39.8| 13-Nov-13 |
| PRJNA229000 | NC_022841.1  | KF534708.1   | CF1     | Rhinobatos hynnicephalus   | 16776 | 40.3| 13-Nov-13 |
| PRJNA244205 | NC_023951.1  | KJ140136.1   | CF1     | Rhinobatos schlegeli       | 16780 | 39.6| 6-Apr-14  |
| Elasmobranchii: Selachii (sharks) |            |              |         |          |     |     |            |
| Carcharhiniformes |            |              |         |          |     |     |            |
| PRJNA246074 | NC_024055.1  | KJ728380.1   | CF1     | Carcharhinus acronotus      | 16719 | 38.4| 29-Apr-14 |
| PRJNA244183 | NC_023948.1  | KF956523.1   | CF1     | Carcharhinus amblyrynchoides| 16705 | 38.2| 6-Apr-14  |
| PRJNA239607 | NC_023522.1  | KF646785.1   | CF1     | Carcharhinus leucas        | 16704 | 37.4| 25-Feb-14 |
| PRJNA252486 | NC_024284.1  | KJ720818.1   | CF1     | Carcharhinus melanosulmus   | 16706 | 38.6| 7-Jun-14  |
| PRJNA193929 | NC_020611.1  | KC470543.1   | CF1     | Carcharhinus obscurus       | 16706 | 38.6| 8-Nov-13  |
| PRJNA239626 | NC_023521.1  | KF612341.1   | CF1     | Carcharhinus sorrah         | 16707 | 38.9| 25-Feb-14 |
| Accessions | BioProject | NCBI Ref_seq | GenBank | Organism | bp | *G+C | Date   |
|------------|------------|--------------|---------|----------|----|-------|--------|
| PRJNA217222 | NC_022193.1 | KF111728.1 | Galeocerdo cuvier | 16703 | 36.9 | 31-Oct-13 |
| PRJNA236275 | NC_023361.1 | KF646786.1 | Glyphis garricki | 16702 | 39.2 | 13-Jan-14 |
| PRJNA212606 | NC_021768.2 | KF006312.2 | Glyphis glyphis | 16701 | 39 | 25-Jul-14 |
| PRJNA239588 | NC_023527.1 | KF899325.1 | Mustelus griseus | 16754 | 39 | 25-Feb-14 |
| PRJNA11875 | NC_000890.1 | AB015962.1 | Mustelus manazo | 16707 | 38.3 | 8-Apr-00 |
| PRJNA228986 | NC_022819.1 | KF356249.1 | Prionace glauca | 16705 | 37.5 | 13-Nov-13 |
| PRJNA222618 | NC_022735.1 | AB560493.1 | Pseudotriakis microdon | 16700 | 36.4 | 29-Oct-13 |
| PRJNA168394 | NC_018052.1 | JQ693102.1 | Scoliodon macrorhynchos | 16693 | 37 | 31-Mar-14 |
| PRJNA11849 | NC_001950.1 | Y16067.1 | Scyllorhinus canicula | 16697 | 38 | 18-Apr-05 |
| PRJNA226138 | NC_022679.1 | JX827259.1 | Sphyra lewini | 16726 | 39.5 | 8-Nov-13 |
| **Orectolobiformes** | | | | | | |
| PRJNA165947 | NC_017882.1 | JQ434458.1 | Chiloscyllium griseum | 16755 | 36.1 | 6-Mar-12 |
| PRJNA37667 | NC_012570.1 | JX162601.1 | Chiloscyllium plagiosum | 16725 | 37.4 | 25-Jul-12 |
| PRJNA81281 | NC_016686.1 | JQ082337.1 | Chiloscyllium punctatum | 16703 | 36.8 | 31-Mar-14 |
| PRJNA217221 | NC_022148.1 | KF111729.1 | Orectolobus japonicus | 16676 | 37.3 | 19-Sep-13 |
| PRJNA238093 | NC_023455.1 | KF679782.1 | Rhinodon typus | 16875 | 37.1 | 19-Mar-14 |
| | | KC633221 | Rhinodon typus | 16928 | 37.1 | 31-Mar-14 |
| **Lamniformes** | | | | | | |
| PRJNA239610 | NC_023520.1 | KF569943.1 | Carcharias taurus | 16773 | 39.5 | 5-Feb-14 |
| PRJNA221185 | NC_024215.1 | KC914387.1 | Carcharodon carcharias | 16744 | 40.8 | 31-Oct-13 |
| PRJNA232870 | NC_023266.1 | KF597303.1 | Cetorhinus maximus | 16670 | 40.6 | 14-Jan-14 |
| PRJNA2266140 | NC_022691.1 | KF361861.1 | Isurus oxyrinchus | 16701 | 43.2 | 28-Sep-13 |
| PRJNA247657 | NC_024101.1 | KJ616742.1 | Isurus paucus | 16704 | 43.8 | 7-May-14 |
| PRJNA252473 | NC_024269.1 | KF962053.1 | Lamna ditropis | 16699 | 41.8 | 30-May-14 |
| PRJNA207613 | NC_021442.1 | KC702506.1 | Megachasma pelagios | 16694 | 36.7 | 13-May-13 |
| PRJNA33525 | NC_011825.1 | EU528659.1 | Mitsukurina owstoni | 17743 | 38.8 | 29-Dec-08 |
| PRJNA228992 | NC_022822.1 | KF412639.1 | Alopias pelagicus | 16692 | 38.6 | 18-Dec-13 |
| PRJNA207614 | NC_021443.1 | KC757415.1 | Alopias superciliosus | 16719 | 39.3 | 26-Jun-13 |
| **Heterodontiformes** | | | | | | |
| PRJNA111979 | NC_003137.1 | AJ310141.1 | Heterodontus francisci | 16708 | 39.9 | 14-Nov-06 |
| PRJNA209901 | NC_021615.1 | KC845548.1 | Heterodontus zebra | 16720 | 40 | 18-Jun-13 |
| **Squaliformes** | | | | | | |
| PRJNA246067 | NC_024059.1 | KJ128289.1 | Cirrhitagaleus australis | 16543 | 38.8 | 29-Apr-14 |
| PRJNA226141 | NC_022734.1 | AB560492.1 | Somniosus pacificus | 16730 | 39.3 | 29-Oct-13 |
| PRJNA11856 | NC_002012.1 | Y18134.1 | Squalus acanthias | 16738 | 38.8 | 18-Apr-05 |
| **Squatinaformes** | | | | | | |
| PRJNA252467 | NC_024276.1 | KJ619663.1 | Squatina plana | 16689 | 37.9 | 4-Jun-14 |
| **Pristiophoriformes** | | | | | | |
| PRJNA247682 | NC_024110.1 | AB721306.1 | Pristionchus japonicus | 18430 | 44.5 | 10-May-14 |
| **Hexanchiformes** | | | | | | |
| PRJNA226134 | NC_022732.1 | AB560490.1 | Hexanchus griseus | 17223 | 36.3 | 29-Oct-13 |
| PRJNA226149 | NC_022733.1 | AB560491.1 | Hexanchus nakamura | 18605 | 36.3 | 29-Oct-13 |
| PRJNA226155 | NC_022730.1 | AB560488.1 | Heptanchias perlo | 18909 | 35.9 | 29-Oct-13 |
| PRJNA226147 | NC_022729.1 | AB560487.1 | Chlamydoselachus anguineus | 17314 | 35 | 29-Oct-13 |
| PRJNA226123 | NC_022731.1 | AB560489.1 | Notorynchus cepedianus | 16990 | 38.2 | 29-Oct-13 |

*Metazoan Mitochondrial Genomes Accessible dataset Metamiga ([http://amiga.cbmeg.unicamp.br/](http://amiga.cbmeg.unicamp.br/))
Figure 4. A survey of public data and phylogeny for chondrichthyan orders. A. The 14 orders of chondrichthyan fish and their relative distribution in public nucleotide and protein databases for Chondrichthyes and Elasmobranchii are shown individually. The species distribution for each Order and GenBank are similar indicating sequence data has been collected for a broad range of chondrichthyans. For Chondrichthyes, the elephant shark genome project data contributes the majority of the data in NCBI Gene, GenBank, Genome Survey Sequence (GSS), and the Short Reach Archive (SRA) databases. The NCBI GSS, GSS libraries, and Protein Data Bank (PDB) are the least diverse with representation of 1–6 of the 14 Orders. The color of each Order as represented in the bar chart is included in the cladogram key with left to right in the bar chart corresponding with top to bottom in the cladogram. B. A cladogram of Chondrichthyes illustrates the phylogeny relationship between the 14 Orders. The color code associated with each Order appears consecutively in the bar chart.

Whole embryos were used to build the transcriptome libraries available at SkateBase. Two C. milii embryos, stage 32, were combined and used to build a chimera library. The transcriptome library for S. canicula was assembled from six pooled embryos, stages 24–30. The embryonic skate transcriptome library was assembled using six pooled embryos ranging in stage from 20–29. This combination of stages encompasses a large portion of the developmental period for these fishes and represents a catalog of genes important for organogenesis of all or part of every physiological system. Early developmental events are similar for nearly all elasmobranchs regardless of reproductive mode or adult body form enabling the data to be useful for more than just the specific species from where it was derived. Since all three embryonic transcriptomes contain a similar stage embryo direct comparison for temporal expression patterns is possible. Skatebase includes tools for data investigation, SkateBLAST, a sequence retrieval tool, Skate Contig Lookup, and genome browsers for three skate whole mitochondrial sequences, L. erinacea, the thorny skate, Amblyraja radiata, and, the ocellate spot skate, Okamejei kenojei. Skatebase contains resources that can be used for teaching and research purposes. As an example, two use cases follow, one for sequence or homology based research and the other for education.

SkateBLAST
A common task for researchers is searching for genes of interest in a genome or transcriptome. Knowledge of the gene sequence at the DNA or RNA level is needed for many different studies, including phylogenetic analysis or designing primers for quantitative PCR gene expression studies. Here we describe the major steps necessary to identify relevant sequences for a gene of interest using the BLAST sequence similarity tool at SkateBase. SkateBase features a web interface to BLAST, named SkateBLAST, that builds upon the ViroBLAST package version 2.2, with custom modifications allowing parallel cluster-based execution of queries and enhanced display of results. The overall workflow consists of a) entering a query sequence and selecting the database to search; b) evaluating the alignments returned; c) retrieving the sequence from one of the SkateBLAST databases; and d) checking to make sure that the retrieved sequence aligns best to the query sequence. The following description provides a brief tutorial on the overall workflow while describing tools at SkateBase.

Figure 5 demonstrates the use of SkateBLAST to find expressed sequences for the gene, suppressor of cytokine signaling 6 (SOCS6). SOCS6 is an E3 ubiquitin ligase that interacts with c-KIT to suppress
### Detailed Instructions

#### Step 1: Enter Protein Sequence to Search

1. **Enter Query Parameters**
   - **Query Sequence**: Paste your protein sequence.
   - **Expect**: 10
   - **E Value**: 0.0001

#### Step 2: Select tblastn as Program

- **Program Selection**
  - Select tblastn from the list of available programs.

#### Step 3: Select Skate Transcriptome Contigs

- **Subject Database**
  - Choose the database containing Skate transcriptome contigs.

#### Step 4: Run Search

- **Search Parameters**
  - **Word size**: 11
  - **Max target sequences**: 100
  - **Max hits per target sequence**: 10

- **Click on 'Raw BLAST Output Report' to view alignments**

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### Example Output

| Query | Subject | e-value | Query Cover | Subject Cover |
|-------|---------|---------|-------------|--------------|
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |
| g00138 | g00138  | 1.00E-09| 100.00%     | 100.00%      |

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**Note:**
- The above table is an example of search results. Actual results may vary depending on the input sequence and database selection.
- The **e-value** indicates the statistical significance of the alignment.
- **Query Cover** and **Subject Cover** show the percentage of query and subject sequences that are aligned.

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**F1000Research 2014, 3:191 Last updated: 21 APR 2022**
Length of Query Protein is 535 aa

Length of Subject Sequence (bp)

Score, Expect Value and Percent Identity

Alignment Coordinates and Reading Frame

SkateBase Contig Lookup

Enter a transcriptome contig number OR a genome contig number

Little Skate Transcriptome Contig Result
cellular proliferation through its SH2 domain\(^6\). The first step to identify SOCS6 in the skate transcriptome begins with entering the protein sequence for human SOCS6 that was obtained from UniProt and searching this sequence against the skate transcriptome using the tblastn program. The next step is to evaluate the alignments to determine which transcriptome sequences best represent SOCS6. When interpreting the pairwise alignments from SkateBlast as in any BLAST tool, it is important to examine: a) alignment statistics; b) alignment coverage; and c) presence of protein domains that you may expect to be conserved. The alignment statistics are reported to ascertain whether you would expect the given alignment by chance or not. There are three key alignment statistics, the expectation (E)-value, percent identity and alignment length. The E-value represents the probability that you would expect an alignment with that alignment score or better by random chance, thus the lower the E-value, the better the alignment. Conversely, the greater the percent identity (percent identical sequence) and alignment length, the more similar the two sequences are assumed to be. Alignment coverage with respect to the query or subject sequence (alignment length divided by the length of the query or subject sequence) can also be an important consideration, as low coverage suggests that important regions of one or both sequences may not be represented in the alignment. Finally, there may be particular sequence features, such as protein domains, that you would expect to find in the alignment. If those domains are missing, then it suggests that you have a partial or misleading alignment.

Once a transcriptome sequence of interest, such as contig15542, is identified in the SkateBLAST results, you must do a reciprocal search of that sequence against a database of protein sequences to confirm that the sequence aligns best to your gene of interest. You can retrieve the full sequence directly from the BLAST tool or using the Skate Contig Lookup tool (Figure 5D): a) specify the transcriptome that you had originally searched using SkateBLAST; b) enter the sequence identification or contig number is entered into the query box; and c) select the ‘GO’ button. The user can copy the
returned sequence and use it for further exploration of sequence homology at NCBI or similar databases.

**SkateBase classroom use case: teach concepts of gene and protein annotation**

SkateBase includes valuable teaching resources derived from the project workshops on gene and protein annotation. Infrastructure for sequence annotation was developed and modules for use in teaching are available. Access to the teaching modules is through the Curator Access link from the homepage and permission is granted by request using the email link at the bottom of each page, info@SkateBase.org. Once successfully logged into the site, access to pre-computed blast results, guides and examples, annotation forms, and links to external tools helpful for sequence analysis are available. Gene annotation begins with a transcriptome contig identified through a SkateBlast search as illustrated above. The portion of the transcript that codes for protein is identified using an open reading frame or ORF finder tool. Annotation follows a workflow where complimentary sequences from the transcriptome and genome are aligned allowing annotation of both sequences using Sequence Ontology vocabulary\(^67\). The evidence is recorded in an annotation form that records information about the annotator and sequences and includes a comment box for questions and comments between students and teachers or curators and annotators. The annotation form records the pairwise alignment of the transcriptome and genome contigs, notes concerning mismatches or gaps, as well as output from the ORF tool. The untranslated regions (UTR) at the beginning and end of each sequence, 5'UTR and 3' UTR regions, as well as the intron/exon structure for the genomic contig and CDS for the transcriptomic contig are recorded in the Gene Annotation Form. When completing the Gene Annotation Form, the appropriate activity must be selected and can be customized to specify the user’s course ID, institution or workshop title to track annotation history. Protein annotation uses the rapid annotation interface for proteins, RACE-P, developed by the PIR. A UniProt accession number is required to initiate a new annotation form. The form is composed of 6 blocks of information, protein information, gene information, a bibliography, Gene Ontology (GO), computational analysis using tools such as Pfam\(^68\), TMHMM\(^69\), SignalP\(^70\), COILS\(^71\), NetPhos\(^72\) and EMBOSS\(^73\), and protein family evidence.

**Discussion**

The volume of data in GenBank continues to grow exponentially, doubling nearly every 18 months. The first sequences for chondrichthyes appeared in 1983 and the overall data trend for chondrichthyan is similar to all of GenBank with three exceptions. First, the rate of increase is less than GenBank. Second, the number of sequences deposited during the first decade of the 21\(^{st}\) century was nearly stagnant in comparison. Third, a large spike is observed in late 2012 attributed to the Elephant Shark Genome Project data (Figure 6). Molecular data is increasingly important for all aspects of research utilizing chondrichthyan fishes\(^74\). It can be a forensic tool to understand species when fins are landed without carcass and ensure protected species and quotas are respected\(^75\)–\(^79\). For migrating species molecular data serves as a surrogate to classical tagging data to understand population structure and range\(^80\)–\(^83\). In studies of evolution, molecular data provides estimates of divergence time and supplements morphological and ecological traits as the basis for a phylogeny. The benefits and uses of molecular data for these fishes are limited

![Figure 6. GenBank and WGS data trends for Chondrichthyes and all taxa.](image-url)
only by the amount of data available. SkateBase provides the only genomic data publically available for an elasmobranch in addition to embryonic transcriptomes, data tools, and educational resources.

Sequencing projects require significant funding and personnel commitments but generate a large amount of information that can be translated to knowledge by domain experts. The efficiency of this process is affected most by allowing the scientific community to access the data. The value of data sharing can be measured by the number of publications that result from its distribution. To date, 19 publications in peer-reviewed journals have used data derived from SkateBase (http://skatebase.org/vitae). Molecular data are the means to investigate genes and develop reagents for gene expression studies by PCR or in situ hybridization. Small scale sequencing efforts that generate limited or fragmented data often get deposited to hard disks and remain ‘buried’ and out of reach. Efforts to deposit this data at public sequence repositories are encouraged to build the foundation of data required to describe this dynamic and ancient clade of fishes. We invite investigators to contact the authors in an effort to survey the volume of private data available for potential distribution through SkateBase.

The transcriptome data at SkateBase serves as a platform to teach molecular techniques, technologies, and bioinformatics in the context of studying elasmobranchs. As next generation sequencing (NGS) technologies evolve it is important for scientists and students to understand how the sequence was generated and caveats of workflow for each data type in order to recognize errors and customize analysis algorithms. The educational materials and infrastructure at SkateBase have been used by University of Delaware, Georgetown University, MDI Biological Laboratory, University of Maine at Machias, University of Rhode Island, and most recently the Virginia Institute of Marine Science to teach gene and protein annotation concepts. We invite and look forward to continued expansion of the SkateBase educational platform as we refine the infrastructure and expand the data available for investigation through continued sequencing efforts.

Author contributions

The little skate genome project is a collaborative effort with participation from all authors. JTW and BLK prepared the first draft of the manuscript. SWP oversaw the design and implementation of the SkateBase web portal and SkateBLAST tool. All authors were involved with the revision of the draft manuscript and have agreed to the final content.

Competing interests

The authors declare to have no competing interests.

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Ed Heist
Department of Zoology, Southern Illinois University, Carbondale, IL, USA

This manuscript has two components: a description of current genomic, proteomic, and transcriptomic resources for chondrichthyan fishes and a description of the SkateBase project. Of the two, I would rather have seen more emphasis on SkateBase since the rate at which new data are being generated will make the survey data presented in the manuscript increasingly incomplete. Nevertheless I think it is a good paper worthy of publication and SkateBase seems to be a valuable resource.

Specific comments include:

Abstract – capitalize Sarcopterygii, Actinopterygii misspelled. Throughout the manuscript there are numerous inconsistencies in capitalization, e.g. “order Chimaeriformes” and “Fish barcode of life (FISH-BOL) a working group of the International Barcode of Life Project (iBOL)” both on page 8.

Introduction – In the first sentence replace “Chondrichthyan fishes” with “Living chondrichthyan fishes.”

Paragraph 2 – The text implies that the only benefits of chondrichthyans are ecotourism and fisheries. Perhaps a mention of ecological services (e.g. food-web dynamics) or other benefits of chondrichthyan conservation would be appropriate here.

Paragraph 4 – “asexual” parthenogenesis seems redundant.

Paragraph 5 – perhaps some more details on the distribution, life history, reproductive mode, genome size etc. of little skate is in order. Why is the geographic location of the species relevant?

Figure 1 is hard for me to decipher. I can't figure out what the two separate outer rings indicate and why the spacing between them is different for the orders vs. the families, genera, and species. I really think this figure is too complex and tries to cram too much information that is peripheral to the goals of the paper into a single figure. I may be old fashioned, but I think a table that listed...
the numbers of families, genera, and species would have been sufficient. There also needs to be a citation on the source of the information as the taxonomy and number of recognized species of chondrichthyans is changing.

Figure 4B – A citation is needed for the cladogram.

**Competing Interests:** No competing interests were disclosed.

**I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.**
Page 8: change “SkateBase data is linked” to “SkateBase data are linked” and “SkateBase data includes” to “SkateBase data include”.

Page 19, 1st column: change “this data” to “these data”.

Figures and Tables:

- In the figure 1 legend — most of this information is stated in the text. I suggest keeping the sentence: “The distribution of chondrichthyan species in each of the 14 orders is shown relative to the total number of species, genera and families for the clade.” I also suggest explaining the figure in a little more detail. What do the numbers mean? Do the colors represent anything?

- Figure 2 legend: “is” should not be italicized.

- Table 1: What do the numbers in the columns mean? Are these numbers of entries?

- Table 2: Contigs for *L. erinacea* is 2,62,265. Also, under N50, change 1466 to 1,466.

- Figure 4: It is difficult to tell apart colors for the following pairs:
  - Squatiniformes and Carcharhiniformes
  - Lamniformes and Myliobatiformes
  - Chimaeriformes and Rajiformes

  This can be rectified by using black, white and yellow for three of the above orders in the figure.

- Figure 5 legend: I suggest changing “Four important fields in the output should be examined carefully to interpret the alignments and determine which returned alignment best represents the skate ortholog to SOCS6. First, the alignment score, E-value, alignment length and percent identity can be used to interpret the overall alignment significance.” to “Four important fields in the output should be examined carefully to interpret the alignments: the alignment score, E-value, alignment length and percent identity.”

**Competing Interests:** No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.
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