The Global Invertebrate Genomics Alliance (GIGA): Developing Community Resources to Study Diverse Invertebrate Genomes

Supplemental Text

Selection of Taxa

Porifera (sponges) are a diverse taxon of benthic aquatic (marine and limnic) animals, with over 8,500 described species distributed over four main extant lineages: Demospongiae (83% of living species; demosponges, including bath sponges), Hexactinellida (glass sponges), Calcarea (calcareous sponges), and Homoscleromorpha (flesh sponges) (Van Soest et al. 2012) (Fig. 2). Traditionally, sponges were considered the sister group to the rest of Metazoa, and therefore of great significance for the reconstruction of early metazoan evolution. Sponges are now regarded to be monophyletic (reviewed in Wörheide et al. 2012), though further work is needed to unequivocally resolve their placement among the other non-bilaterian animals (i.e., those without bilateral symmetry) (Fig. 1). Although sponges are of great importance ecologically (as filter-feeders, bioeroders, and habitat formers), commercially (e.g., bath sponges) and pharmaceutically (as producers of bioactive secondary metabolites), their internal phylogeny and genomic diversity remains unresolved and understudied (Lavrov et al, 2008; Wörheide et al., 2012; Hill et al 2013). Comparative genomic approaches will not only shed light on the early evolution of metazoan genomes, but also unravel the genomic adaptations that led to the enormous ecological success of sponges over 550 million years. Comparative genomics will advance our understanding of the processes responsible for secondary metabolite production as well as unravel the genetic basis for biosilica synthesis, both of which have enormous potential for biomedical and biomimetic applications. Currently, the genome of only one sponge (Amphimedon queenslandica) has been published (Srivastava et al. 2010), a species not easily amenable to laboratory culture and experimental manipulation.

Ctenophora (comb jellies) are exclusively marine, and are the largest organisms (up to a meter long) that rely on cilia for locomotion. Although historically grouped with Cnidaria in a clade called Coelenterata (or Radiata), most morphological traits uniting the two lineages are now considered convergent (Harbison 1985). Many ctenophore characteristics are unique, including their adhesive cells (colloblasts) and giant locomotory cilia fused into plates along 'ctene rows'. Although ctenophores are ubiquitous in the global pelagic realm, only 242 species have been described. Many species are difficult to collect, especially in the deep sea, leaving much diversity undescribed, even at higher taxonomic levels. Half of the deep-sea species have not been assigned to any family, and the group's phylogenetic placement in the animal tree of life (Figs 1, 2) is controversial (e.g., Dunn et al., 2008; Hejnol et al., 2009; Pick et al., 2010; Philippe et al., 2011; Nosenko et al., 2013; reviewed in Dohrmann & Wörheide, 2013).

Placozoa are small (up to few millimeters across) benthic marine animals that resemble a flat ciliated disc (Fig. 1). Although with a differentiated upper and lower side, they only possess four distinguishable somatic cell types. The recently sequenced genome of *Trichoplax adhaerens* (Srivastava et al. 2008) revealed unexpected genome complexity, but the phylogenetic position of placozoans is currently unresolved (e.g., Nosenko et al. 2013). Although only one species has been formally described, the phylum likely is more speciose (Voigt et al., 2004; Eitel and Schierwater, 2010).

Cnidaria occurs in all aquatic environments and includes more than 12,000 species, which range from inconspicuous but abundant hydroids through the Portuguese man-o-war (*Physalia*), and reef-forming corals, to economically important parasites such as caviar pests and the agent causing fish-whirling disease (Fig. 2). All cnidarians possess cnidae--protein-filled capsular organelles containing eversible tubules. One form of cnida, the nematocyst, consists of a harpoon-like tubule that everts at extraordinarily high speeds when triggered, releasing a venomous cocktail of proteins useful in prey capture and predator avoidance. A number of cnidarians can inflict painful and sometimes life-threatening stings on humans. The group is renowned for life cycle and

colony variation, and many species form symbioses with photosynthetic algae. To date three cnidarian genomes have been sequenced and published, including the reef coral *Acropora digitifera*, the sea anemone *Nematostella vectensis* (both Anthozoa, Hexacorallia), and the hydrozoan model organism *Hydra magnipapillata* (Medusozoa, Hydrozoa) (Putnam et al. 2007; Chapman et al. 2010; Shinzato et al. 2011); several more genome projects are in progress. Comparisons between bilaterian genomes and that of *N. vectensis* have shown that the genome of this sea anemone has maintained many ancestral genomic features (Putnam et al. 2007). Comparative analysis of cnidarian genomes will allow for a deeper understanding of the evolution of toxins, metazoan-algal symbioses, colony formation, luminescence, visual systems and biomineralization.

Xenacoelomorpha is composed of three major lineages or phyla, each with relatively few species. These are Acoela (~380 species), Nemertodermatida (8 species), and Xenoturbellida (2 described species). The former two were traditionally treated as flatworms. These animals lack some of the typical morphological features of other bilaterian groups such as excretory organs, but most retain bilateral symmetry, true mesoderm, and a centralized nervous system.

The relationship of Xenacoleomorpha to other animals is among the most controversial in animal phylogeny (Fig. 1). Two currently conflicting hypotheses treat it as the sister group to Nephrozoa (Ruiz-Trillo et al. 1999; Dunn et al. 2008; Hejnol et al. 2009) or nest it within Deuterostomia as the sister clade to Ambulacraria (hemichordates and echinoderms) (Philippe et al. 2011). Resolution between these two scenarios has major implications for the interpretation of their morphology. The former scenario would provide a clearer understanding of the origin of a complete gut, mesoderm and centralized nervous system, while the latter would allow insights into the evolutionary reduction of genomic and morphological complexity within Deuterostomia. In addition, some acoels are invasive species that can form large blooms (Rivest et al. 1999) with severe impacts on native fauna (McCoy 2003). Currently, no genome has been sequenced for any Xenacoelomorpha.

Ecdysozoa subgroups

Tardigrada

Tardigrades (Fig. 1) are best known for their ability to undergo cryptobiosis (anhydrobiosis), slowing their metabolism (by a factor of 10,000). Tardigrades have become an interesting invertebrate model species due to their extreme capacities for withstanding not only desiccation and freezing, but also for being able to survive interplanetary vacuum, ionizing solar and galactic radiation, extreme temperatures (-150 °C to 150 °C), and large changes in osmolarity (e.g., Persson et al. 2011; Welnicz et al. 2011). Understanding the genomes of tardigrades is important not only to understand anhydrobiosis, miniaturization and DNA repair (Förster et al. 2012), but also to obtain insights into the evolution of the clade that leads to the enormous diversity of arthropods. To date, no whole genome sequences of a tardigrade species has been published. Onychophora (Fig. 1) is also important for understanding the evolution of early arthropods, and for being the only exclusively terrestrial animal phylum.

Arthropoda (Fig. 3). The largest group within Ecdysozoa is Arthropoda, which contains Pancrustacea (Crustacea + Hexapoda [=insects and entognaths]) and groups such as horsehoe crabs, sea spiders, spiders and relatives (Chelicerata), as well as centipedes, millipedes and relatives (Myriapoda) (Fig. 3).

Chelicerata evolved in the oceans, and two major lineages remain completely marine: Pycnogonida (sea spiders; 1323 species) and Xiphosura (horseshoe crabs; 4 extant species). The other major chelicerate clade, Arachnida, diversified mostly on land during the Silurian/Devonian, although mites (Acari) have several aquatic lineages (both marine and limnic), and palpigrades are known from meiofaunal shallow marine environments (Giere 2009). Several arachnid lineages are being sequenced as part of the i5K initiative, and thus we will direct our effort to the marine lineages Pycnogonida and Xiphosura.

Myriapods most probably constitute the sister group of Pancrustacea (Fig. 3), which together constitute the clade Mandibulata (Giribet and Edgecombe 2013). Myriapods include four mostly terrestrial lineages: Chilopoda (centipedes), Diplopoda (millipedes), Symphyla and Pauropoda. As in the case of arachnids, some myriapods are being sequenced as part of the i5K initiative, but others may be included in the GIGA initiative.

Pancrustacea (=Tetraconata) is a morphologically diverse clade of arthropods with a rich fossil record dating back approximately 511 million years into the Cambrian (Siveter et al. 2001). With the recent inclusion of Hexapoda (Insecta and Entognatha), the group (Fig. 3) represents a monophyletic taxon with over 800,000 described species, accounting for more than half of described metazoan species biodiversity. Although the monophyly of the group is well supported, relationships among the ~84 orders remain unresolved, and, for the most part, the ordinal diversity is unsampled. Only 26 of the 84 orders of Pancrustacea have been included in past molecular analyses, and most of the functionally diverse and taxonomically challenging groups have remained a phylogenetic mystery with respect to their position in the tree of life. For this initiative we focus on species within Pancrustacea (normally referred to as crustaceans) that are not included in i5K. There are 9 major crustacean lineages (Mystacocarida, Ostracoda, Ichthyostraca, Branchiopoda, Thecostraca, Malacostraca, Copepoda, Remipedia, and Cephalocarida, Fig. 3) and 66,914 species (Zhang 2011b). Despite the rich species diversity, only 1 crustacean genome sequence is currently available (Daphnia pulex, water flea). The group includes both well-known and unfamiliar forms, such as the charismatic king and hermit crabs, enigmatic bioluminescent ostracods, commercially important shrimps, lobsters and barnacles, and parasitic pentastomids that thrive in the respiratory tracts of vertebrates. The morphological disparity among crustaceans is among the most astonishing of all invertebrates, with body sizes ranging on the order of micrometers (parasitic tantulocarid Stygotantulus stocki) to meters (spider crab Macrocheira kaempferi). The ecological diversity is equally as impressive with representatives found in freshwater, terrestrial, marine, cave, and hydrothermal vent habitats. Crustacean distributions in the marine realm extend from the ocean's surface to hadal depths, including abundant amphipods at the bottom of the Mariana Trench. Understanding the morphological and ecological diversity of crustaceans could represent an important economic commodity for major commercial fisheries (Dawson 1989; Lovrich and Vinuesa 1999) and the

aquarium hobbyist trade (Rhyne et al. 2009). Moreover, some species are threatened or endangered due to their rarity (Macpherson et al. 2005), overfishing (Lovrich and Vinuesa 1999), or habitat loss (e.g., Xu et al. 2009), while others are invasive. Crustaceans are often used to study adaptation, speciation, diversification, and embryonic development due to their unique morphological, physiological, ecological and biochemical properties. As such, genomic studies will contribute to a fundamental understanding of evolutionary and ecosystem processes and patterns.

Spiralia subgroups

Mollusca includes 117,358 living described species of mostly marine invertebrates (Fig. 4). Of its eight diverse lineages (currently recognized as "classes": Neomeniomorpha, Chaetodermomorpha, Polyplacophora, Monoplacophora, Scaphopoda, Gastropoda, Bivalvia and Cephalopoda), Bivalvia (clams, mussels, oysters) have invaded freshwaters multiple times (Graf 2013), and only Gastropoda (e.g., snails, slugs) has successfully colonized limnic and terrestrial environments, with multiple radiations. Molluscs are ecologically important as ecosystem architects, invasive species, and intermediate hosts for major tropical diseases such as schistosomiasis (Campbell et al. 2000). Many molluscs (e.g., pulmonate land and freshwater snails, sea hares, nudibranchs and cephalopods) are used as model organisms to study the cellular bases of behavior and memory (Kandel, 2001), genomics of single cells (Moroz et al., 2006) and transcriptomes of cell compartments (Moroz, 2011; Puthanveettil et al., 2013). Their broad diversity is reflected in the unprecedented parallel evolution of their nervous systems (Moroz, 2009, Wollesen et al. 2007). They also include numerous charismatic species, extremophiles, and constitute the dominant animal group in many deep-sea environments.

Molluscan phylogenetics has been debated for centuries, and only recently, with the advent of next generation sequencing techniques, have studies started to converge towards the primary distinction between the monophylyetic Aculifera (including the "worm molluscs," or Aplacophora, and chitons) and Conchifera (the familiar bivalves, gastropods and cephalopods and the lesser known tusk shells [Scaphopoda] and deepsea monoplacophorans) (Fig. 4), and to resolve the interrelationships among some of the conchiferan taxa, such as gastropods, bivalves and scaphopods (Kocot et al. 2011; Smith et al. 2011).

Molluscan diversity is highly asymmetrical, ranging from the roughly 30 species of recent Monoplacophora (Haszprunar and Ruthensteiner 2013) to the megadiverse Gastropoda, with 40,000 to 150,000 living species (Lindberg et al. 2004). Cephalopods (761 species) are charismatic animals of commercial and biomedical importance (Nishiguchi and Mapes 2008), and thus are receiving an enhanced focus for a genomics perspective (Albertin et al. 2012).

Although molluscs were primitively marine and benthic, several lineages have colonized the pelagic environment by developing floating devices or by reducing their shells. Many gastropod lineages, most notably the terrestrial and marine sea slugs, have completely lost the shell. Unique adaptations associated with shell loss are observed in many sea slugs, which accumulate toxic products from their prey, or incorporate cnidarian nematocysts. Symbioses are common among bivalves and gastropods, especially those living in hydrothermal vents, and feeding on wood (bacterial symbioses), as well as several species of cardiids (including the giant clams) that supplement their diets with carbon compounds obtained from photosynthetic endosymbionts (dinoflagellate symbioses) (Ishikura et al. 2004; Taylor and Glover 2010; Distel et al. 2011). Genomes of three molluscan species have been sequenced: two gastropods (*Aplysia* and *Lottia*) and the oyster, *Crassostrea* (Zhang et al, 2012; Takeuchi et al, 2012).

Annelida is a group commonly referred to as segmented worms. They are found worldwide from sediments of the deepest marine trenches to the terrestrial soils of farms and forests, where their bioturbation activities make them important ecosystem engineers. The placement of annelids in the tree of life is still unclear, although most recent hypotheses relate them to molluscs, nemerteans, and brachiopods (Dunn et al. 2008; Hejnol et al. 2009) (Fig. 1). Around 18,000 species of annelids are currently recognized (Rouse and Pleijel 2001). Annelida comprises a paraphyletic assemblage of polychaete lineages and a clade termed Clitellata, which contains earthworms and

leeches, among some other forms. The former phyla Echiura, Pogonophora and Vestimentifera have recently become regarded as annelid subgroups (McHugh 1997; Rouse and Fauchald 1997) and Sipuncula (peanut worms) may be the sister group to annelids (Struck et al. 2011) (Fig. 4).

Annelids show a tremendous diversity of reproductive modes and feeding mechanisms and are dominant members of many infaunal communities. Annelids include extraordinary forms such as hydrothermal vent worms, leeches, bone-devouring *Osedax* (Rouse et al, 2004), fireworms, and scaleworms, many of which have medical importance. To date only the leech *Helobdella robusta* and the polychaete *Capitella telata* have had their genomes sequenced.

Platyzoa constitutes a heterogeneous group (Fig. 1) that may or may not be monophyletic (Wey-Fabrizius et al. 2013). They include lineages such as Platyhelminthes (flatworms) (29,285 species), Rotifera (2,775 species, including the parasitic Acanthocephala), and other smaller lineages, such as Gastrotricha (790 species), Gnathostomulida (109 species), and Micrognathozoa (1 species). Platyhelminthes has diversified into marine, freshwater and terrestrial environments; Gastrotricha and Rotifera encompass several marine and freshwater lineages; Gnathostomulida are exclusively marine, and Micrognathozoa is known from a single limnic species from Greenland (Kristensen and Funch 2000), although there is an additional report from a sub-Antarctic island (De Smet 2002).

Platyhelminthes includes free-living forms as well as the parasitic tapeworms and flukes. The group is a key lineage for biomedical studies, as many species are human parasites and several others are leading models of regeneration. Expansion of taxon sampling will provide critical resolution for reconstructing the ancestral states of pathogenicity genes, which are likely to be fast evolving.

Rotifera is a group of minute pseudocoelomate animals characterized by an anterior cilated field used for locomotion and/or food gathering (Wallace 2001). Most rotifers exist in freshwater habitats, but some are found in soil or marine environments, and a large clade, Acanthocephala, formerly a phylum but now recognized as a group of rotifers, is parasitic on vertebrates. Members of the smallest clade, Seisonidea, are

external symbionts of leptostracan crustaceans. Both clades are obligately sexual. In contrast, members of the largest group, Monogononta, are cyclically or facultatively parthenogenetic. Monogononts are key components of fresh and brackish water ecosystems throughout the world. They are cultured extensively to feed fish fry in aquaculture and are used in studies of ecology, ecotoxicology, aging, and speciation. A third group, Bdelloidea, is notable for apparently abandoning sexual reproduction tens of millions of years ago (Mark Welch and Meselson 2000). Bdelloid rotifers are also extraordinarily desiccation tolerant, are resistant to doses of gamma irradiation capable of killing most other animals, and have incorporated hundreds of non-metazoan genes into their genomes. The peculiar reproductive strategies within Rotifera have established this group as a key for understanding the role of sexual reproduction in metazoan evolution.

Among platyzoans, the genomes of four tapeworm species were recently sequenced, revealing important insights into their adaptations to parasitism (Tsai et al. 2013), and several other genomes of parasitic flatworms are nearly complete (Olson et al. 2012). Genomes for other free-living (Robb et al. 2008) and parasitic (Consortium TSjGS 2009; Protasio et al. 2012) platyhelminths have likewise provided insight into aspects of regeneration and disease. The first genome of a bdelloid rotifer (*Adineta vaga*) was recently published (Flot et al. 2013).

Bryozoa (moss animals) is an important phylum with about 5500 Recent species distinguished by colonial, aquatic lifestyles, often with high degres of polymorphism within colonies, and the ability to inhabit tropical to arctic environments (Winston 2010) (Fig. 1). Each module of a colony is represented by small (< 2 mm) zooids. Zooids have a chitinous or calcified outer cuticle, internal organs called polypides, consisting of gut and a funnel of ciliated tentacles, the lophophore which can be everted through hydrostatic muscular action. Many cheilostome bryozoans, the dominant group in geologically Recent oceans (such as the Atlantic), produce structural and defensive zooids, as well as zooids modified for brooding embryos. One very unusual characteristic of the group is the inability to form a permanent individual; polypides degenerate and regenerate several times within zooids. Another is the ecdysozoan-like

ability of at least some species to molt the outer cuticle, after forming a new one beneath it. Over 15,000 fossil species are known, with some dating to the early Paleozic. The phylogenetic placement and affinities of bryozoans remain under debate (Waeschenbach et al, 2006). They were formerly placed with Brachiopoda and Phoronida as lophophorates based on the common possession of a ring or horseshoe of ciliated feeding tentacles. All are now recognized as protostome spiralians, but recent molecular data link them either to the superficially similar Entoprocta (as Polyzoa), another smaller group of tentacular suspension feeders (Helmkampf et al. 2008) or place them near the brachiopods (Jang and Hwang 2009). The production of the potent bryostatin compounds, a family of protein kinase C modulators, by the species, *Bugula neritina*, reflects the productive synergism that can occur between the different fields of invertebrate biology, microbial symbiosis, genomics, biotechnology and natural products research (Trindade-Silva et al, 2010).

Genomics can possibly provide sufficient supplies of therapeutic compounds without the need to collect vast quantities of organisms.

Deuterostomia subgroups

Echinodermata includes familiar seashore sea stars and sea urchins, but the group as a whole—over 7,200 extant species—represents one of the most bizarre radiations of animal life. Though nested well within the Bilateria, echinoderms transition from a twosided larval symmetry to a five-sided radial adult symmetry, the origins of which remain unresolved. Although lacking any centralized nervous system, many have no difficulty, either individually or en masse, with directed movement. A system of unique mesodermal canals and pouches, the water vascular system, functions in various combinations of locomotion, respiration, circulation, excretion and gonad storage.

Echinoderms include five major extant clades, traditionally treated as classes. They are exclusively marine, occurring in all oceans at all depths, often in enormous abundance. Crinoidea, the sea lilies and feather stars, are the sister group to the remaining echinoderms, which are referred to as Eleutherozoa (Fig. 5). Extant crinoids are descended from a previously more diverse lineage which has left vast ancient limestone deposits possibly spanning tens of thousands of square kilometers and reaching hundreds of meters in thickness. Today dense and sometimes diverse crinoid assemblages still occur in habitats ranging from coral reefs to the Antarctic (Rouse et al. 2013).

Despite their familiarity, evolutionary relationships among the four remaining echinoderm clades are not fully resolved (Janies et al. 2011). Asteroidea, the sea stars, are well known as important predators of prey including commercial bivalves and coral polyps, but they also feed on sediment, detritus and plankton. Ophiuroidea, (brittle stars and allies) sometimes reach densities of several thousand per square meter, often controlling sedimentary environments and affecting ecosystem function and nutrient recycling. Sea and brittle stars also have self-healing and limb regeneration capacities that may be of biomedical interest. Sea urchins (Echinoidea) have long been used as models in embryology and are major marine herbivores that control the growth and distribution of kelp forests and other macroalgal communities. Sea cucumbers (Holothuroidea) are major components of sediment communities, particularly in the deep sea. Both sea cucumbers and urchins include important commercial fishery species, and overfishing of both has altered entire marine habitats (Eriksson et al, 2012). The genome of the sea urchins Strongylocentrotus purpuratus, a developmental model for understanding many gene pathways, and Lytechinus variegatus have been sequenced (Sodergren et al. 2006).

Hemichordata is the sister group of echinoderms (Figs 1, 5) and shares with members of that phylum several important deuterostome features including a three-part coelom that originates from the larval gut. All are marine and occur from shallow water to great depths. An unpaired foregut diverticulum that projects into the anterior coelomic cavity was long considered homologous with the chordate notochord and contributed to the long interest in this group as a source of insight into the origins of the chordate body plan. Hemichordates have traditionally been divided into two main groups, enteropneusts and pterobranchs, though this is no longer phylogenetically correct (Worsaae et al. 2012). Enteropneusts, or acorn worms, are soft, fragile, benthic marine

worms, up to a meter long, with three body divisions that reflect their internal coelomic organization. The anterior region of the trunk bears a series of gill pores that corresponds with internal gill slits. These pharyngeal structures exhibit strong functional, morphological and molecular similarities with those of cephalochordates and chordates, and a recent investigation of conserved transcription factors expressed during early development supports the homology of gill pouches throughout Deuterostomia (Gillis et al. 2012). Pterobranchs share with acorn worms the three body divisions but are colonial, with individual zooids up to 5 mm long. Pterobranchs now seem to be closest relatives to one of the acorn worm groups (Fig. 5). As bilateral deuterostomes, hemichordates are critical for understanding ancestral deuterostome strategies. The presence of both direct- and indirect-developing species within the same group offers opportunities for greater insight into the evolution of larvae and invertebrate life histories (Röttinger and Lowe 2012). The genomes of two hemichordates, *Saccoglossus kowalevskii* and *Ptychodera flava*, have been sequenced, and a high-quality assembly of the S. *kowalevskii* genome is available in GenBank (Röttinger and Lowe 2012).

Chordata are best known as the clade that includes the vertebrates, the focus of Genome10K (G10KCOS 2009). However, the clade also includes two extant invertebrate taxa—Tunicata and Cephalochordata (Figs. 1, 5)—which provide important insights into the origin of vertebrates and connect them to the rest of the animal kingdom. Despite their lack of a backbone, these two groups share with vertebrates a dorsal hollow nerve cord, a flexible rod-shaped notochord that provides axial support, a pharynx perforated with pores or slits and a ventral food-gathering groove (endostyle), and a post-anal tail. However many distinguishing chordate features appear only during embryonic stages (Swalla and Jefferey, 1996; Ruppert et al. 2004).

Tunicata (Urochordata) are sac-like marine filter feeders with either a sessile or planktonic lifestyle. The name derives from the complex tunic secreted by the epidermis, which ranges from thin and delicate to thick and cartilaginous, and consists largely of cellulose. Benthic solitary species are commonly known as sea squirts (ascidians), but colonial benthic ascidians are also common. Planktonic forms include gelatinous forms such as salps, doliolids, pyrosomes and larvaceans (Fig. 5). Although long considered the sister group to the chordates, recent research has shown that, despite their highly modified organization, tunicates are sister to the craniates (Figs 1, 5); and thus more closely related to fish than the morphologically fish-like Cephalochordata, the other clade of invertebrate chordates (Delsuc et al. 2006). In ascidians (benthic tunicates), cilia lining a large pharyngeal basket generate a feeding and respiratory current that enters through an inhalant siphon and exits via a surrounding atrial chamber through an exhalant siphon. In most planktonic species, the feeding and respiratory current is generated instead either by muscle bands or an undulating tail. Due to its phylogenetic position and regeneration powers, the genome of *Ciona intestinalis* was among the first animal genomes to be sequenced (Dehal, et al. 2002), and the genome of the larvacean *Oikoplaura dioca* is also available (Denoeud, et al. 2010).

Cephalochordata is a small clade of marine filter-feeding deuterostomes often referred to as lancelets or amphioxus. Cephalochordates are unique in having a notochord that persists throughout life, and they have been said to resemble the first chordates (Northcutt 2005), with Cambrian fossils such as Cathaymyrus being interpreted as a cephalochordate (Shu et al. 1996). They share with the vertebrates the pharyngeal gill slits and muscles arranged in myomeres. The genome of *Branchiostoma floridae* has been sequenced and supports this placement (Delsuc et al. 2006; Dunn et al. 2008). Cephalochordates were recently shown to express green fluorescent protein (Deheyn et al. 2007), otherwise only known in cnidarians and some copepod crustaceans.

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