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Ophiuroid locomotion from fundamental structures to integrated systems

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Abstract

The phylum Echinodermata includes an estimated 7,000 extant and 13,000 extinct species. Each living class represents a separate body plan with a unique mode of movement and locomotion. Brittle stars (Class Ophiuroidea) utilize complex arm musculoskeletal physiology for rapid locomotion, in contrast to the other echinoderm classes, which are typically slow moving. Ophiuroid locomotion and its origins are poorly understood. This paper is a review of the current state of ophiuroid research, with a focus on topics relevant to ophiuroid movement and locomotion, including anatomy, physiology, functional morphology, disparity, ecology, and evolutionary history.

Key words: Ophiuroidea, locomotion, functional morphology

Introduction

The Phyla Echinodermata, Chordata, and Hemichordata comprise a monophyletic group (Deuterostomia) with over 76,000 extant species (Lake 1990; Brusca & Brusca 1990; Halanych 2004; Pawson 2007; Edgecombe *et al*. 2011; Roskov *et al*. 2017). Despite this close relationship, the morphological trajectories of the vertebrate and echinoderm lineages are vastly disparate. Vertebrates evolved the ability to venture into fresh water and on land, grow to large body sizes and ultimately radiate into over 69,000 extant species (Roskov *et al*. 2017), whereas echinoderms have fascinating features and abilities that other deuterostome groups do not, many of which impact the available strategies for movement and locomotion. Echinoderms, for instance, can regenerate entire parts of their anatomy, such as limbs or internal organs (Candia Carnevali 2006; Dupont & Thorndyke 2007). Their collagenous tissue can change tensile strength, an attribute they can use to hold postures while expending minimal energy (Wilkie 1984, 2005). They have derived pentameral symmetry and lack an anterior/posterior axis so that they do not need to turn to change direction (excluding forms with secondarily derived bilateral symmetry, such as holothurians and irregular echinoids) (e.g., Kano *et al*. 2012). Echinoderms have decentralized nervous control yet execute coordinated movements, differing fundamentally from the centralized nervous system found in vertebrates (e.g., Watanabe *et al*. 2012; Kano *et al*. 2012; Kano *et al*. 2017). They also have an internal hydrostatic system with external outpockets that many use for locomotion. The applications of echinoderm morphological research to other fields, including material sciences, regenerative medicine and robotic engineering, prompted by this unique suite of morphological features, are extensive (for instance, see Wilkie 2005; Dupont & Thorndyke 2007; García-Arrarás & Dolmatov 2010; Watanabe *et al*. 2012; Kano *et al*. 2012; Barbaglio *et al*. 2012, 2013; Kano *et al*. 2017).

Brittle stars (Phylum Echinodermata, Class Ophiuroidea) have a distinctive form of rapid musculoskeletal based locomotion in which they coordinate oscillations of their five arms. This strategy distinguishes them from their closest relatives, which primarily rely on tube feet (Smith 1947; Kerkut 1953; Reich *et al*. 2015), and are relatively slow moving. The sudden appearance of the ophiuroid morphology in the Ordovician (Shackleton 2005) creates challenges for resolving the steps underlying the functional evolution of ophiuroid locomotion. Here, we review the current understanding of ophiuroid locomotion and its evolution.

The 2,000 species of extant ophiuroids make them the largest echinoderm class (Stöhr *et al*. 2012, 2018).

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Extant ophiuroids have been split phylogenetically into two groups: the euryalids and the non-euryalids. Non-euryalid ophiuroids include more than 90% of ophiuroid species; euryalids include the remaining 10% (Stöhr *et al*. 2012). The euryalids diverged from the non-euryalids during the Triassic (O'Hara *et al*. 2014). The euryalids include taxa with branched (i.e., basket stars) and unbranched arms (such as *Astrobrachion constrictum*) (Stewart 1998). Several morphological features distinguish them from non-euryalid ophiuroids such as hourglass-shaped vertebral joint articulations (present in only one non-euryalid family, the Hemieuryalida) and the lack of dorsal and ventral plates (Emson & Woodley 1987; O'Hara *et al*. 2014; Thuy 2015). The earliest euryalid fossils to date are mid-Jurassic (Thuy 2015).

The morphological differences between euryalids and non-euryalids are thought to be related to their distinctive life modes; euryalids typically sit perpendicular to the substrate and filter feed with their many branched arms, while non-euryalids generally have an epibenthic or infaunal mode of life and spend most of their time with the disk parallel to the ocean floor (O'Hara *et al*. 2014). These differing morphological features are thought to have functional consequences (Hyman 1955; Byrne 1994; LeClair 1996) related to their divergent life strategies, but a more rigorous quantitative biomechanical analysis is necessary in order to evaluate these claims.

Research to resolve the phylogenetic relationships within the Ophiuroidea is ongoing. Recent work has helped to resolve the relationship between extant taxa. A phylogenetic investigation by O'Hara *et al*. sequenced ophiuroid transcriptomes and resolved three major clades, A, B, and C. Euryalids were resolved as a monophyletic group within clade C, diverging from the paraphyletic ophiurida (clade A, B, and part of C) (O'Hara *et al*. 2014; O'Hara *et al*. 2017). Evidence suggests that the major divisions between clades originated in the deep ocean (O'Hara *et al*. 2014), in contrast to traditional hypotheses of speciation in shallower waters (see Wilson & Hessler 1987).

Fundamental structures: the skeletal system, collagenous tissue, and the water vascular system

This section describes several universal facets of echinoderms that are integrated to build structures for motion. The skeletal system, collagenous tissue and the water vascular system are considered here.

Skeletal system

Similar to that of vertebrates, the echinoderm skeleton is internal. Muscles and connective tissues attach to the skeletal elements (ossicles) and are surrounded by a skin. The genes and molecular pathway for forming the skeleton are unique to echinoderms, although many of the extracellular matrix proteins and signaling pathways involved in biomineralization are homologous with those in vertebrates (Bottjer *et al*. 2006).

The ossicles are made of high magnesium calcite crystals organized in a framework known as stereom. Stereom skeletons are a synapomorphy of all echinoderms, and their evolution is used to mark the divergence of the echinoderm lineage from the rest of the deuterostomes (Smith 2005; Rahman *et al*. 2010). The stereom framework is spongy and mesh-like in its texture; the material consists of a network of thin, branching calcium carbonate beams called trabeculae that surround a large network of open pores throughout the ossicle. Trabeculae generally range from about 1–30 microns in thickness, and the pores range from 2–40 microns in diameter (Smith 1990). Trabeculae are composed of calcite nanobrick units around 20–40nm wide (Oaki & Imai 2006).

Based on analyses using extant taxa, the structure of the mesh-like arrangement of the stereom has been shown to be indicative of functional characteristics (Smith 1980; Roux 1975; Macurda & Meyer 1975; Macurda 1976; Smith 1990). Certain proportions of trabeculae to pore space in the outermost stereom layer correlate with soft tissue attachment sites, including collagenous tissue and muscle fibers (Smith 1980, 1990). Smith (1980) formalized a semi-quantitative technique for identifying soft tissue attachment sites by measuring the maximum pore diameter and minimum trabecular thickness of the stereom area in echinoids, and later extended the analysis to include asteroids, crinoids, and ophiuroids (Smith 1990). Eight categories of stereom have been recognized based on thickness and arrangement of the trabeculae, the width of pores, and the presence or absence of the repetition of layers penetrating the ossicle (see Smith 1990). Stereom with small pores and thin trabeculae are generally associated with muscular or collagenous tissue attachments (Smith 1990). Stereom with thicker trabeculae generally provide plate stability and structure (Smith 1990). In ophiuroids, galleried stereom with pore diameters between 5–16 microns and trabecular thickness between 1–

5 microns are associated with connective tissue attachment sites (Smith 1990). Stereom with <1–3micron pore diameters and trabeculae 2.5–6.5 microns thick is associated with muscle attachments.

Occasionally, stereom fabric survives with high fidelity in the fossil record. Fossilized stereom has been found preserved in a variety of ways, including silicification, pyritization, iron oxidization, recalcification, and phosphatization (Brand & Morrison 1987; Gorzelak & Zamora 2013). Stereom is present in the fossil record as early as the Cambrian (Smith 1990), and has been an important tool in establishing affinities of several Paleozoic echinoderms and even their musculature and movement capabilities in some cases (Clausen & Smith 2005; Smith 2005). Chemical analysis of fossilized stereom has been used as a tool for exploring the oscillation in ocean chemistry between calcite and aragonite seas (Dickson 2004). Stereom has been found in fossil ophiuroids, and can be visualized using a scanning electron microscope, high-resolution micro-CT scanners, or synchrotron imaging.

Collagenous tissue

Collagenous connective tissue is a structural material present in almost all multicellular organisms (Wilkie 2005). Echinoderm collagenous tissue can be found subepidermally in the integument, surrounding organs, and comprising some ligaments and tendons (Wilkie 1984). Mutable collagenous tissue (MCT), a type of collagenous tissue found in all echinoderms (Wilkie 1984) can change its stiffness; MCT can hold muscle in a contracted state with the exertion of minimal energy, allowing the echinoderm to hold certain postures for extended periods of time energetically-efficiently (Wilkie 1984). MCT is also involved in other processes such as executing arm autotomy in ophiuroids (Wilkie 1984, 2005). The properties of echinoderm MCT, although remarkably utilitarian, are not found in any other phylum (Wilkie 1984). The mechanical properties of MCT have been considered for their direct application to connective tissue improvement in humans and the development of novel biomaterials (Wilkie 2005; Barbaglio *et al*. 2012, 2013; Ferrario *et al*. 2017; Goh & Holmes 2017).

Echinoderm muscle is connected to the skeletal structures via tendons, as in vertebrates. The structure of the attachment of muscle to skeleton varies between echinoderm classes (Stauber & Märkel 1988). In ophiuroids, the tendon invaginates the outermost stereom pore space and loops around the trabeculae of the stereom (Stauber & Märkel 1988).

The water vascular system

Echinoderms have a unique network of internal fluid-filled canals called the water vascular system (WVS). Functions include locomotion, feeding, and sensing (Nichols 1972). The water vascular system in ophiuroids and asteroids consists of five main parts. The first is a small zone that connects the WVS to the sea water. In extant ophiuroids, this function is performed by one or more openings (the "hydropores") on the oral surface of the disk. In asteroids sea water is accessed through a sieve-like calcified plate on the dorsal surface (the "madreporite") (Stöhr *et al*. 2012); a madreporite plate is present in some fossil ophiuroids (Dean 1999). It is thought that the hydropore in ophiuroids has minimal functional significance, as experimental evidence suggests that most of the water in the ophiuroid WVS is recruited from internal fluid instead of the sea (Ferguson 1995). The stone canal connects the madreporite/hydropore to the WVS network within the rest of the body. The proximal end of the stone canal connects to the ring canal, a circular hoop of WVS tissue inside the main body area. The WVS extends from the ring canal into each arm in what is known as the peripheral system. The peripheral system includes the radial canal, a channel extending linearly along the arm, and the tube feet, external projections of the WVS along the arms (Nichols 1972). Tube feet in ophiuroids are used primarily for feeding. Some ophiuroids suspension feed by trapping small food particles with aerosol filtration or mucus secreted by the tube feet, and use the tube feet to pass small mucus boluses to the mouth (LaBarbera 1978). Ophiuroids also have oral tube feet around the mouth, which play a role in manipulating food items and also discriminating between edible and non-edible items, unlike the tube feet of the arm (Fontaine 1965). Ophiuroid tube feet (Glass & Blake 2004; Glass 2006) and the internal morphology of the water vascular system (Clark *et al*. 2017) have been discovered in the fossil record, and provide valuable insights into how this system operated in the past and has changed over time.

Integrated systems: arm segments, joints, locomotion strategies, and nervous control

Using the ubiquitous echinoderm building blocks, ophiuroids have evolved a unique, complex form of movement to execute fast-paced coordinated locomotion, in contrast to the generally slow-moving organisms of the other four extant echinoderm classes. This section describes the anatomy and physiology of the arm, and how its components work synchronously to effect movement.

Arm construction

The arms of living ophiuroids, the primary units involved in locomotion, are made of repeating segments. Most extant ophiuroid arm segments consist of five main ossicles: the vertebra, a dorsal plate, a ventral plate, and two laterals (Clark *et al*. 2018, Figure 1). The vertebra lies in the center flanked by the other plates. Spines extend from the laterals. The vertebral ossicles incorporate the intervertebral muscle attachments and joint interface. The vertebral ossicles tend to follow "Jackson's Law," smaller vertebrae of adults tend to have similar proportions to larger vertebrae in juveniles of the same species, suggesting that interspecific vertebral variation reflects ontogenetic stages (LeClair 1996). Four intervertebral muscles attach to the proximal and distal sides of each vertebra. The muscles surround a central intervertebral joint and an intervertebral ligament. Contraction of the intervertebral muscle pivots the distal segment around the joint (LeClair 1996). Range of motion of the arm segments is thought to be determined by angle of bending permitted by joint architecture, the shape of ossicles surrounding the vertebrae, and the nature of the integument surrounding the arm (Litvinova 1994). There has been debate over whether or not the shape of the vertebrae is significant functionally (Litvinova 1994; LeClair & LaBarbera 1997). A novel framework utilizing 3D imaging and digital modeling has been developed to analyze the relationship between morphology and function of the skeletal elements of the ophiuroid arm (Clark *et al*. 2018). Unlike scanning electron microscopy, the most widely used method for imaging ophiuroid ossicles, micro-CT imaging is non-destructive and allows for visualization of the ossicle in three dimensions, the surface structure in 360°, and the articulations between successive ossicles. In the Clark *et al*. 2018 investigation, ophiuroid arms were micro-CT scanned in multiple positions to visualize the inner workings of the arm during flexion. This novel strategy revealed several important findings, including that non-vertebral arm plates were not found to inhibit arm flexion and that the position of the joint center can vary between different segments along the length of the same arm. Disparate arm morphologies were not always found to have differences in range of motion, which challenges traditional assumptions of functional consequences that had been based on ossicle morphology alone. A wider application of this methodology is necessary to determine the broad-scale relationship between form and function.

Locomotion strategies

Almost all motile animals have bilateral symmetry which delineates a forward direction for movement. Movement in this single direction can be optimized with the adaptation of morphological features. Bilaterally symmetrical organisms have a complex centralized nervous system that is responsible for decision-making and coordination of the two halves of the body.

As the phylum Echinodermata is within the Bilateria clade, the echinoderm lineage is assumed to have been, at one time, bilaterally symmetrical. Echinoderms subsequently derived pentaradial symmetry, a synapomorphy of the crown. Thus, there is no single forward direction of motion. This is beneficial for movement across the benthos; as stimuli can be encountered from all sides, equity in movement direction optimizes reaction time by eliminating the need to change orientation.

When a stimulus is encountered, arms are allocated one of several roles each with a specific set of actions. Arms take on one of three roles: as center limb, forelimb, or hind limb. The forelimbs are typically the primary drivers of motion. The forelimbs are positioned on either side of the body roughly perpendicular to the desired direction of motion and engage in repetitive oscillations that push the body forward. They oscillate by driving posteriorly and pressing against the substrate during the effective stroke to act as a lever that drives the rest of the body forward, and move anteriorly during the recovery stroke which can include partially or fully lifting off the substrate. The center limb and hindlimbs actively oscillate or rest. Two gaits are typical of five-armed brittle stars: "rowing" and "reverse rowing." During "rowing," the center limb is anterior to the direction of motion and is flanked by the forelimbs on either side, with the hindlimbs posterior to the direction of motion. In "reverse rowing" the two forelimbs are anterior to the direction of motion, with the center limb posterior. The center limb is beneficial for sensory feedback particularly when it is anterior to the direction of motion. To change direction of motion, the animal simply reassigns the roles of the arms so that disk rotation is not necessary (Astley 2012). The organism can move in every direction with equal facility without rotating the body, in contrast to a bilateral organism. Taking advantage of pentaradial symmetry, ophiuroids operate with a functional plane of bilateral symmetry during movement through the transient nature of roles for the arms (Astley 2012). Ophiuroids are incredibly resilient to damage; they can immediately adapt their locomotion strategy upon incurring damage to the nerve ring or loss of arms (Matsuzaka *et al.* 2017; Kano *et al.* 2017; Clark *et al.* 2019).

The tube feet in ophiuroids play a minor role in locomotion but can be used as the main driver of locomotion in ophiuroids which have lost the arms (Arshavskii *et al.* 1976c; Pomory *et al.* 2011). It has been observed that the tube feet take a more significant role in locomotion if multiple arms are amputated (Arshavskii *et al.* 1976a). One species, *Amphicutis stygobita*, has been found to utilize podial walking as its primary form of locomotion (Pomory *et al.* 2011), and some research suggests that tube feet may play a more active role in ophiuroid locomotion in certain circumstances (Arshavskii *et al.* 1976c). Systematic investigation is necessary to determine the ubiquity and importance of the tube feet in ophiuroid locomotion.

Nervous control of coordinated locomotion

Ophiuroids are distinctive in that they execute coordinated movements despite a lack of centralized control, an unusual feature among complex animals. A centralized nervous system does not exist, in contrast to other bilaterians; nevertheless, ophiuroid arms are capable of executing both independent and synchronous, periodic, coordinated movements (Arshavskii *et al* 1976a,b; Watanabe *et al.* 2012; Astley 2012; Kano *et al.* 2012). Ophiuroids have a circumoral nerve ring within the disk that connects to a radial nerve within each arm. Experimental evidence suggests that the nerve ring is not analogous to a centralized control center (Cobb & Stubbs 1982; Cobb 1987; Clark *et al.* 2019) but is nevertheless necessary for coordinated locomotion between the arms (Matsuzaka *et al.* 2017; Clark *et al.* 2019).

The nervous control setup underlying ophiuroid locomotion has been studied extensively for its application to robotic engineering. As coordinated movement with non-hierarchical decentralized control is advantageous to robotic agents, particularly those susceptible to damage (Watanabe *et al.* 2012; Kano *et al.* 2012; Kano *et al.* 2017), the complex behavior of ophiuroids has been considered in order to improve coordinated multifaceted robotic devices. Ophiuroid models have been used to build robots with "behavioral versatility," i.e., with decentralized control systems that assign fluctuating roles to the separate parts of the robot and execute periodic and non-periodic arm movements in response to varying external stimuli (Watanabe *et al.* 2012; Kano *et al.* 2012). A model has also been constructed to emulate the mechanism with which ophiuroids shift the roles of the arms in response to damage (Kano *et al.* 2017); after one or multiple arms become damaged, the robot is able to immediately adapt to continue moving in the same direction with limited loss in capability (Kano *et al.* 2017). Future work will incorporate a more accurate understanding of the role of the nerve ring into the robotic models based on recent experiments (Clark *et al.* 2019).

Ophiuroid ecology and mode of life

Ophiuroids can be found from Antarctica to the tropics, from intertidal to hadal depths, and in all major oceans (Stöhr *et al.* 2012). Species in shallower seas are known to hide within rocky substrates, as many ophiuroid taxa are light sensitive (Allee & Fowler 1927; Fell 1966; Sumner-Rooney *et al.* 2017). In deeper regions, they can blanket the ocean floor; densities of 10^7 individuals per km^2 have been noted (Fell 1966). Some species live buried in the substrate with their arms emerging from the sand (Buchanan 1964). Others can live on or in other animals such as corals (Stewart 1998), jellyfish (Kanagaraj *et al.* 2008), and echinoids (Tominaga *et al.* 2017). Ophiuroids exhibit the greatest variety in feeding strategy of any echinoderm group (LeClair & LaBarbera 1997). As they have no anus, they must be selective about ingestion in order to optimize the efficiency of the digestive tract, unlike asteroids and holothurians which can obtain nourishment from consuming large quantities of mud (Stöhr *et al.* 2012). Ophiuroids can feed by holding their arms in the water column and suspension feeding (LaBarbera 1978). They capture food particles with mucus and/or the tube feet, which pass the bolus to the mouth (LaBarbera 1978). Other ophiuroids move across the substrate to acquire food. They can eat different types of food such as detritus, algae, and swimming prey (Warner 1982).

Many use the “arm-loop method,” to grasp and ingest food: the arm surrounds the item and draws it to the mouth (Fontaine 1965). Some species have been observed to employ multiple feeding strategies (Fontaine 1965; Warner 1982). Ophiuroid predators include asteroids, fishes, crustaceans, polychaetes, and other ophiuroids (Fell 1966; Aronson 1987). Ophiuroids have been observed to live at least up to four years (Buchanan 1964); it is estimated that they can live on average 15 years and up to 30 years (Fell 1966). They can reproduce sexually, via viviparity or oviparity, or asexually (Fell 1966).

Future research directions

Although much work has been done, many questions remain regarding the evolutionary history and physiology of the ophiuroid's distinctive form of locomotion. The proliferation of micro-CT scanning holds potential for the visualization of the morphology of the water vascular system of extant ophiuroids and discovery of additional instances of its preservation in the fossil record. Novel 3D imaging and modeling techniques provide a platform for evaluating the influence of morphological disparity on function within the skeletal system of the arm and how this impacts the organisms’ mode of life. This method also has the potential to be applied to model range of motion in fossil taxa as well to begin constraining possible strategies used for locomotion. Behavioral experiments coupled with robotic modeling has shown to be an effective strategy for analyzing aspects of the decentralized control setup underlying ophiuroid locomotion. Muscle physiology and force application capabilities is a major area of research left to be explored.

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