


Topics in Geobiology 41

Daniel I. Hembree
Brian F. Platt
Jon J. Smith *Editors*

Experimental Approaches to Understanding Fossil Organisms

Lessons from the Living

 Springer

Experimental Approaches to Understanding Fossil Organisms

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Editors

Experimental Approaches to Understanding Fossil Organisms

Lessons from the Living

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Preface

The study of modern organisms is invaluable for understanding ancient life, ecosystems, and environments. In most instances, the only way for paleontologists to address questions related to the life activities of extinct taxa is to investigate their closest living ancestors. Modern-analog studies allow paleontologists and sedimentary geologists to assess a range of questions regarding ancient life, from the behavioral and environmental significance of ichnofossils to the conditions responsible for different modes of fossil preservation, to the biomechanics of animal locomotion. While the application of modern observation and experimentation to assessing the past has been fundamental in the geosciences since the nineteenth century, recently developed techniques have arisen in multiple disciplines that allow new questions about the history of life to be addressed.

Experimental Approaches to Understanding Fossil Organisms is based on a topical session that we organized and held on October 11, 2011 at the Geological Society of America's Annual Meeting in Minneapolis, Minnesota. This session included 24 presentations covering a wide range of topics all focused on studying modern organisms to better understand and interpret ancient life. This was the third time we organized a session with this theme for the Geological Society of America. The first was at the 2007 Joint South-Central and North-Central Section Meeting in Lawrence, Kansas and the second was at the 2008 Annual Meeting in Houston, Texas. Given the diversity of the research presented and the size of the audiences attending these sessions, we felt that this was a topic of great interest and held relevance to the modern paleontological and sedimentary geology communities.

This volume is intended to provide professionals and students in the fields of paleontology and sedimentary geology in academia and industry with specific case studies demonstrating the variety of questions that can be asked, techniques and methodologies that can be employed, and interpretations that can be made using modern analogs to study ancient life. We hope that the work described in this volume will be useful in launching new research questions and methods which will ultimately lead to a better understanding of the history of life on our planet.

Experimental Approaches to Understanding Fossil Organisms is divided into three parts. Part I includes papers that analyze the functional morphology of ancient organisms by conducting experiments with fossil material or by studying the

morphology, physiology, and behavior of similar modern organisms. These studies include the investigation of the function of a unique type of anchor-shaped crinoid holdfasts by directly testing models of well-preserved fossils (Chap. 1), an assessment of the functional role of elongate shells in bivalves (Chap. 2), a test of the morphological features of fossil bivalves thought to suggest chemosymbiosis (Chap. 3), a comparison of the interpreted life habits of eurypterids to those known in modern horseshoe crabs and scorpions (Chap. 4), and an investigation of the feeding behaviors of Eocene whales through comparisons with skull morphologies of extant whales (Chap. 5). Part II incorporates studies of taphonomy and environmental controls on organism distribution. These studies include an investigation of microbialites through time (Chap. 6), the preservation of tropical, shallow marine mollusk assemblages (Chap. 7), the distribution of burrowing organisms on beaches (Chap. 8), the concentration of iron minerals around burrows (Chap. 9), and the preservation of phytoliths in modern, disturbed ecosystems (Chap. 10). Part III broadly covers organism-substrate interactions or neoichnology. While these studies also examine aspects of functional morphology, taphonomy, and environment, the focus is on the production of biogenic structures in the sediment or other media. These studies include the characterization of burrows produced by modern scorpions (Chap. 11), salamanders (Chap. 13), skinks (Chap. 14), and lemmings (Chap. 16) in a variety of media and environmental conditions, surface trails produced by swimming fish (Chap. 12), an array of novel surface traces produced by modern African and Asian elephants (Chap. 15), and a new means of detecting animal burrows and buried tracks and trails in various types of sediment using ground-penetrating radar (Chap. 17).

We are very grateful to our group of expert reviewers who provided insightful, helpful, and timely reviews of the papers included in this volume. Our panel of expert reviewers consisted of 26 researchers from around the world including Emese Bordy (University of Cape town), Danita Brandt (Michigan State University), Joseph Carter (University of North Carolina), Al Curran (Smith College), Shahin Dashtgard (Simon Fraser University), Jason Dunlop (Museum für Naturkunde), Murray Gingras (University of Alberta), Leslie Harbargen (SUNY Oneonta), Gary Haynes (University of Nevada), Daniel Hembree (Ohio University), Jonathan Hendricks (San Jose State), Adiël Klompmaker (Florida Museum of Natural History and University of Florida), Dirk Knaust (Statoil ASA), Matthew Kosnik (Macquarie University), Ricardo Melchor (INCITAP (UNLPam-CONICET)), Radek Mikulas (Academy of Sciences of the Czech Republic), Elizabeth Nesbitt (University of Washington), Renatta Netto (PPGeo Unisinos), Karla Parsons-Hubbard (Oberlin College), Brian Platt (University of Mississippi), Roy Plotnick (University of Illinois at Chicago), Sara Pruss (Smith College), Tami Ransom (Salisbury University), Jon Smith (Kansas Geological Survey), Nigel Trewin (University of Aberdeen), and Andrea Wetzels (University of Basel). We would also like to thank Tamara Welschot, Judith Terpos, and Sherestha Saini at Springer for all their help with putting this volume together.

The wealth and breadth of active modern-analog research featured in this volume demonstrates that the solutions to many unanswered questions may be achieved

by honoring the founding geological principle of uniformitarianism. Far from being stifled or replaced by technological advances in modeling simulations, digital resources, and statistical analyses, we anticipate that modern-analog studies will remain relevant to the geosciences and will, indeed, thrive as researchers find new creative applications for empirical, experimental approaches. As geoscientists continue to look to the world around us for perspectives on the history of life, new opportunities for interdisciplinary collaborations and the integration of new technologies promise to expand the range of paleontological problems that can be addressed through modern-analog experiments.

Daniel I. Hembree
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Part I
Functional Morphology

Chapter 1

Crinoids Aweigh: Experimental Biomechanics of *Ancyrocrinus* Holdfasts

Roy E. Plotnick and Jennifer Bauer

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Abstract Immobile suspension feeders living on soft substrates, although rare in modern marine habitats, were relatively common in the Paleozoic. Numerous Paleozoic taxa have been interpreted as dwelling on soft unconsolidated sediments and possessing morphologic features that either prevented them from sinking (e.g., strophomenid brachiopods) or anchored them to the sea floor (e.g., crinoid holdfasts). The quantitative expression of the static stresses for forms living on soft, muddy bottoms developed by Thayer (1975) can be easily modified to describe the forces involved in anchoring. One of the more unusual putative anchoring structures is the “grapnel” holdfast of the Devonian crinoid *Ancyrocrinus*. This form does not match the paradigm for most typical current anchoring structures, lacking

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recurved, pointed, and flattened lateral processes. Its form is suggestive, however, of the modern, nautical mushroom anchors deployed on muddy bottoms. Plaster casts of the *Ancyrocrinus* holdfast were used to quantify the actual forces involved in penetrating, being pulled out of, or dragged across soft substrates. The forces were measured using a digital force gauge mounted on a motorized test stand. Substrates used included fine quartz sand, pure kaolin mud, and coarse carbonate sand. The holdfasts readily penetrated soft mud, but encountered much greater resistance in fine sand. They did, however, readily penetrate the latter substrate when rocked, supporting the comparison with mushroom anchors. Holdfasts do not penetrate the sediment when dragged across it, suggesting a minimal ability to passively anchor in this way. Simple calculations of the sinking velocity of *Ancyrocrinus* suggest that when dislodged, they would have easily reimplanted in soft substrates.

Keywords Holdfasts · Crinoids · Biomechanics · Functional morphology

1.1 Introduction

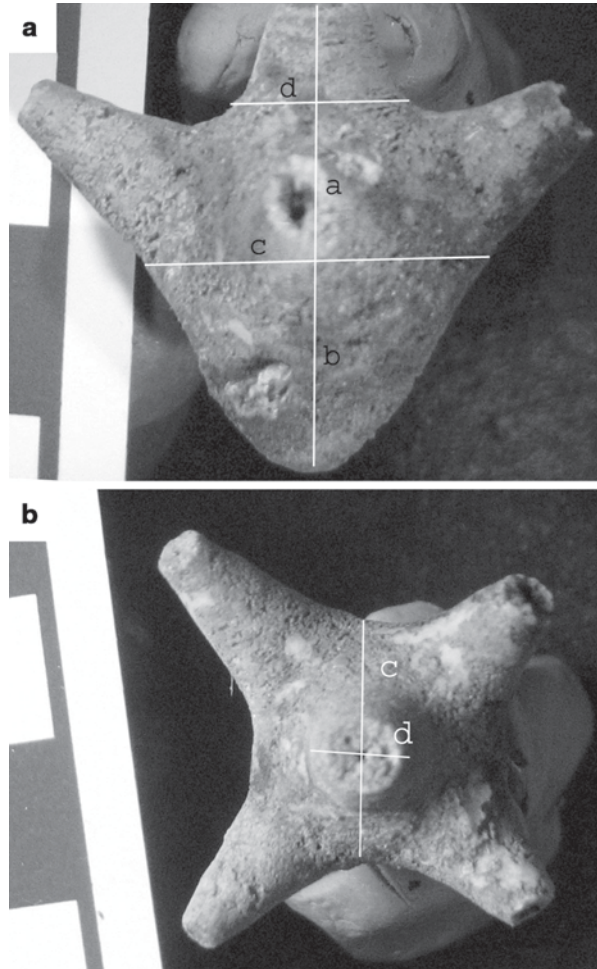
A number of fossil groups have structures identified as adaptations for living on soft substrates. Of these, crinoids and other stalked echinoderms have the best fossil record and have been studied in the greatest detail, although as pointed out by Donovan et al. (2007) as well as Seilacher and MacClintock (2005), the attachment structures (holdfasts) of crinoids are relatively rare as fossils and are far less studied than crown structures. Even well-preserved crinoids often lack the distal part of the stem, the dististele.

There is great morphologic disparity among fossil crinoid holdfasts, certainly greater than that among living forms (Brett 1981; Donovan et al. 2007). One of the most distinctive holdfast morphologies is the so-called grapnel of the Devonian inadunate *Ancyrocrinus* Hall 1862 (Fig. 1.1). Specimens of *Ancyrocrinus* are one of the most common crinoid holdfasts in US museum collections, represented by hundreds of specimens. Since their original description (Hall 1862), their morphology and function have been discussed by Ehrenberg (1929), Goldring (1942), Lowenstam (1942), McIntosh and Schreiber (1971), Brett (1981), and Seilacher and MacClintock (2005). In this chapter, we will apply the methods of paleobiomechanics (Plotnick and Baumiller 2000) to test alternative hypotheses of function of these unique forms, such as whether the structure functioned as a surface drag (Ubahgs 1953) or was instead embedded in the sediment (Seilacher and MacClintock 2005).

1.1.1 *Ancyrocrinus*

The morphology, stratigraphic, environmental distribution, ontogeny, and history of the study of *Ancyrocrinus* were reviewed in detail by McIntosh and Schreiber (1971) and will be only briefly summarized here. The genus is known from a num-

Fig. 1.1 Typical example of an *Ancyrocrinus* holdfast (University of Cincinnati Mus. 26158; Middle Devonian (Givetian), Beechwood Limestone, Louisville Cement Quarry, Speed, Indiana). **a** Lateral view. **b** Top view. *Lines* show the measurements taken on specimens used as models in the experiments (Table 1.1); *a* total height of grapnel; *b* height of arms above base; *c* width at the base of radices; *d* width at the top of radices. Scale bars = 1 cm



ber of localities in Hamilton Group (Middle Devonian) strata from New York, Pennsylvania, Michigan, Indiana, Ontario, and France (Le Menn and Jaouen 2003). Lithologies include both limestone and shale.

Ancyrocrinus was originally named by Hall (1862) for isolated holdfast structures and the holotype single specimen with an attached 7 in. portion of the column. The generic name derives from the anchor-like shape of the holdfast. Hall named two species, *Ancyrocrinus bulbosus* and *Ancyrocrinus spinosus*, the latter being synonymized with the former by subsequent authors. The crown was unknown until the description of several specimens by Goldring (1942), which revealed a cup not much wider than the stem, as well as a large anal tube and relatively small and sparsely pinnulate arms. This provided sufficient information to assign the genus to the inadunate family Botryocrinidae (Cladida: Dendrocrinina). Although the crown of *Ancyrocrinus* is not unusual, it is the dististele that makes it unique. First, al-

though it does occur rarely in other forms (Donovan 2006), the distal part of the stem is quadrangular. This terminates in mature forms in the “grapnel,” a term used as far back as Bather (1900). Brett (1981) classified these structures as “grapnel radices.” In the remainder of this chapter, we will use grapnel as a general term to refer to the holdfast structure, rather than in a functional sense.

The external form of the grapnel is quite variable (Ehrenberg 1929; Lowenstam 1942; McIntosh and Schreiber 1971). The most common form (Fig. 1.1) has a rounded bottom and a single level of four equally spaced spurs, arising just proximal to the bottom. Measurements of nine individuals show a mean angle of 60° ($s=5.4^\circ$) between the spurs and the central axis of the grapnel. Measurements were made from photographs using ImageJ (Schneider et al. 2012). The spurs are rounded in cross section and are usually rounded at the tip, although many are broken off. Interestingly, Hall (1862) illustrated the holotype specimens as having spurs ending in sharp points. This formed the basis for reconstructions in Ubaghs (1953) and Autsch et al. (1999). An illustration of this specimen by Goldring (1923) and a photo in McIntosh and Schreiber (1971, Pl. 1, Fig. 18), however, clearly show that the spurs in this specimen were broken off and showed no signs of terminating as points.

Grapnel forms show a significant variability which is apparently ecophenotypic (Ehrenberg 1929; Lowenstam 1942; McIntosh and Schreiber 1971). Variations include multiple levels of spurs, sometimes two and rarely three; fewer than four spurs in a level; an extended section distal to the spurs, so that the spurs are well above the base; longitudinally bent grapnels; and extended sections proximal to the spurs, apparently incorporating a section of the stem. Isolated spurs were labeled as “mistakes” by Seilacher and MacClintock (2005, Fig. 10). Some small individuals also possess relatively long spurs (McIntosh and Schreiber 1971) or show evidence of attachment to shell debris at the base.

The formation of the grapnel was studied by Lowenstam (1942), who examined several hundred specimens including thin sections. Additional ontogenetic data were provided by a nearly complete juvenile specimen described by McIntosh and Schreiber (1971). Juvenile organisms began life attached to shell debris, as is typical for many other crinoids. They then developed four stem radices, which grew upwards at about 60° from the stem (following Donovan (2006), we use radices in preference to cirri, since these articulate symplectically). Secretion of secondary stereom then began at the base and from the junction of the radices on the stem. Secondary stereom did not cover the entire length of the radix. At some point, the unit breaks free from the original attachment, either directly below the radices or further down the stem. In some cases, parts of the primary attachment may be retained, including shell fragments. Additional stereom then forms over the broken base. Some of the variation in grapnel form clearly comes from differences in the location of the break from the original attachment relative to that of the stem radices and the extent to which growth and secondary stereom secretion occurred prior to the break (McIntosh and Schreiber 1971). Brett (1981) classified such structures as composite holdfasts.

Lowenstam (1942) noted that well-preserved specimens showed surficial wrinkles in the stereom. He described these (p. 25) as a “wrinkled fold series arranged

peripherally around the spur bases and the proximal body portion, overlapping at the junctions of the body and spurs. Fold-like stereom masses were observed on the body and on the spurs. The folds follow each other at equal distances, the axes being vertical to that of the covered skeletal elements.... In a few specimens the folds consisted of several series of close lying tubercles.” These folds were also observed by McIntosh and Schreiber (1971) and drawn by Seilacher and MacClintock (2005, Fig. 10).

1.1.2 *Functional Interpretations*

Hall (1862) proposed that *Ancyrocrinus* began life as attached and then became free floating, with the holdfast acting as a lower balance for the rest of the animal. This interpretation was expanded by Kirk (1911, p. 46), who suggested that the grapnel functioned “rather as a drag and ballast than as a true anchor,” implying that the structure lay on the bottom rather than being buried. Kirk (1911) further suggested that the holdfast acted to maintain stability in quiet waters, but would have been dragged along the bottom by waves or currents. This interpretation was implicit in the reconstruction of *Ancyrocrinus* in Ubaghs (1953, Fig. 120), which was redrawn in Ausich et al. (1999, Fig. 20). The latter reconstruction shows drag marks on the sediment surface produced by the spurs and base. These reconstructions also show the crown in the rheophobic “tulip flower” orientation (Donovan 2011); a more realistic rheophilic orientation was favored by Breimer (1969) and McIntosh and Schreiber (1971). Breimer (1969) speculated that *Ancyrocrinus* was able to reanchor after being passively transported by currents and that this would in some way be advantageous. The idea that the holdfast rested on the sea floor was also supported by Lowenstam (1942) who suggested it was used to regain a stable resting position after detachment from the original distal root.

McIntosh and Schreiber (1971) strongly disagreed with the concept that the holdfast acted as a drag and that the organism would benefit from being moved by currents, since the chance of being relocated to a more favorable setting is low. They suggested two potential functions of the grapnel structure. First, in cases where the spurs are long, they could have prevented sinking deep into the soft muds by either becoming entangled with plants or being partially buried (“iceberg strategy” of Thayer 1975). This is similar to the suggested function of spines in some brachiopods (Leighton 2000). Second, the secretion of stereom to form the grapnel would have moved the center of mass downward away from the crown. Both of these functions were proposed to form a secure base for the crinoid (McIntosh and Schreiber 1971), so that it would have been able to maintain an upright rheophilic posture.

An alternative reconstruction was put forward by Seilacher and MacClintock (2005). Although they also showed the tulip flower crown, the holdfast was shown as being completely buried in sediment. They hypothesized that the wrinkled surface originally described by Lowenstam (1942) was produced by a tough “cuticular sock,” comparable to tight clothing, that protected the underlying epidermis of the

holdfast from both chemical (from reduced pore waters) and physical attacks. The wrinkles were not functional, but a result of fabrication noise related to the presence of the tight cuticular sock. Seilacher and MacClintock (2005) suggested that burial of the *Ancyrocrinus* holdfast occurred passively as the crinoid dragged it along in currents, perhaps aided by scour on the upcurrent side. They also proposed a similar mechanism, which they termed passive implantation, for the Devonian *Aspidocrinus scutelliformis* Hall and the Ordovician *Oryctoconus lobatus* Colchen and Ubaghs.

The main alternative functional interpretation of the *Ancyrocrinus* grapnel, therefore, is that it was either a “drag” lying on the sediment surface, or that it was an “anchor” buried within the sediment. Although, technically both of these are types of anchors, we will use the terms drag and anchor to designate the two options. The paradigm method and experimental paleobiomechanics will be used to assess these alternative reconstructions (Plotnick and Baumiller 2000).

1.2 Functional Morphology of Holdfasts in Soft Sediments

1.2.1 Anchoring Structures in Modern Organisms

The most detailed studies on the biomechanics of anchoring structures have been carried out on terrestrial plants, using a combination of model and living organisms to examine the forces needed to uproot plants and/or to break them free of the anchorage. Plant roots must transfer the forces experienced by the aboveground portions of the plant (shoots) to the soil system (Ennos 1993). The nature of this force transmission depends on whether or not the stem is used to hold the plant upright. In the latter case (recumbent plants), a flexible stem transmits only tensional forces to the roots and soil. This should also be the case where there is a flexible connection between the stem and the anchoring structure. In the case of a stiff stem attached via a stiff connection to the roots, the anchoring system must also be able to resist rotational forces produced by movement of the stem due to wind. This is the case with most trees (Vogel 2003), in which most of the rotational resistance is produced by the weight of the tree.

Ennos (1993) identified three idealized plant anchoring systems. For plants with flexible stems, the roots should radiate out from the base of the stem. This produces a large surface area over which tension can be distributed. For plants with stiff stems, there can either be a stake-like extension (tap root) going deeper into the soil, stabilized by smaller roots spreading laterally, or rigid roots spreading horizontally (plate), with smaller roots spreading laterally and down (see also Vogel 2003).

Following Ennos (1993), Stokes et al. (1996) experimentally examined the resistance to uprooting on model root systems with different geometries. They constructed model root systems out of stiff steel wire. The models differed in the number,

length, and angle of “lateral roots” distributed around a central horizontal structure. They then measured the amount of tensional force required to pull the system out of a container of wet sand. Based on their results and a resulting conceptual model, they concluded that uprooting was best resisted by a design that placed more lateral roots at greater depths, with the lateral roots being perpendicular to the main axis. Similarly, Mickovski et al. (2007) compared pull-out resistance of model root systems differing in geometry and stiffness. Their results confirmed that models with deeper lateral roots were more difficult to remove and that stiffer roots had greater resistance.

The pull-out resistance of bulbs was investigated by Mickovski and Ennos (2003). They compared equal length model bulbs of different geometries (cylinders, cones, bulbous, and spheres) and orientations (apex up or down) to real bulbs (garlic and onion). The greatest resistance to uprooting was produced by a cone, with the apex pointed upward, with a model resembling an actual bulb (wider at the bottom than top) being second best. The greater resistance of the cones was attributed to their greater surface area and to the maximum diameter being most deeply buried. The latter factor increases shear resistance in sandy soils or the area of overlying material to be sheared in cohesive soils. They suggested that the bulb shape was actually superior to the cone, because it lacked sharp edges and would also allow downward movement of the bulb, being pulled by small roots at the base.

The holdfasts of marine coenocytic green algae, such as *Halimeda* and *Udotea*, were studied by Anderson et al. (2006). All of these taxa had similar holdfast morphology: a hemispherical-to-cylindrical mass formed by fine roots (rhizoids) encompassing a mass of sand. This form is thus broadly similar to the bulbs examined by Mickovski and Ennos (2003). Anderson et al. (2006) found that when these algae were subjected to upward tensile stress, they were removed whole from the substrate and did not break. This was in contrast to the forms on hard substrates which mostly break before being dislodged.

In contrast, anchoring mechanisms of modern animals in soft substrates have not been well studied. Modern pennatulacean anthozoans, such as sea pens, sea whips, and sea pansys, are anchored to the bottom by a single polyp, the peduncle. Kastendiek (1976) examined the relationship of rachis and peduncle morphology of the sea pansy *Renilla* to flow velocity. This form is common in shallow turbulent settings with sandy bottoms. The peduncle is flexible and extensible and can be used to reanchor the colony if it is uprooted. Kastendiek (1976) found that the length of the peduncle increased proportional to flow velocity. He also determined that larger colonies were more prone to uprooting.

1.2.2 Forces Acting on Anchors

As is the case with plants, the forces acting on the holdfast will be dependent on the nature of its attachment to the above substrate portion of the organism (e.g., the stem or stalk). If the connection or the above substrate structure is flexible, then the

forces will be tensional. If the structure and connection are rigid, then there will also be rotational forces. The magnitude of these forces will depend on the size and morphology of the above substrate structure and wave velocity (Denny et al. 1985), i.e., on the drag, lift, and acceleration reactions due to eddying experienced by the organism.

Thayer (1975) reviewed the morphologic adaptations of forms living on soft-muddy bottoms, in particular those that would prevent sinking into the sediments. He summarized the static stress σ exerted downward by an organism on the sediment as:

$$\sigma = (\rho_{\text{org}} - \rho_w) \frac{S_2}{nS_1} r_{\text{org}} g,$$

where p_{org} is the density of the organism; p_w is the density of the fluid; r_{org} is a characteristic linear dimension of the organism; S_1 is a shape factor that relates r_{org} to the organism's total surface area A_{org} ($A_{\text{org}} = S_1 r^2$); n is the fraction of that surface area that is in contact with the surface (the bearing area); S_2 is a shape factor that relates r_{org} to the volume and thus the mass; and g is the acceleration due to gravity. As discussed by Thayer (1975), this equation predicts that an organism can reduce its downward stress by reducing its density. This can be achieved by becoming smaller or by increasing nS_1 relative to S_2 ; the latter occurs by either making the organism flatter ("snowshoe" strategy) or by partially burying it ("iceberg" strategy).

In case of an anchoring structure, we need to be concerned with stress acting upward, rather than downward. The formula of Thayer (1975) is still applicable, except that the concern is maximizing, rather than minimizing, downward force. In general, an attachment should thus be as dense as possible, maximize its overall size, and maximize S_2 relative to nS_1 . The first two of these clearly represent a significant cost in terms of material needed. The third increases downward force per unit area and is the basic idea behind a piling, which may be a useful analog for a sediment sticker (Seilacher 1999; Dornbos 2006).

The success of a particular design and corresponding value of σ depends upon the nature of the substrate. The bearing capacity of the sediment is its ability to support the load without failure. As is the case with terrestrial soils, marine sediments are multicomponent systems of water, solids, gases, and organisms (Jumars et al. 2007). Depending on factors such as water content and particle size, physical properties including bearing capacities can vary dramatically (Bokuniewicz et al. 1974). A major control is the cohesion of the sediment; this drops strongly as water content increases and clay content decreases. Highly fluid sediments have virtually no bearing capacity.

Assuming only upward tension is acting, for an organism not to be removed from the sediment, the upward removing force F_t must be less than some downward anchoring force F_A . Conceptually, F_A should be a function of:

- The weight of the structure

- The weight of the sediment overlying the structure and thus the depth of the burial and the surface area of the structure. Increasing this factor increases downward force without a significant increase in metabolic cost of construction.
- Friction, cohesion, and adhesion between the anchor and the sediment: These will be the functions of the composition of the sediment and the geometry and surface properties of the structure, including the possible presence of biological adhesives (Vogel 2003; Parsley and Prokop 2004). For example, those forms interpreted as sediment stickers can be treated as tapered piles (Sowers and Sowers 1970), in which most of the resistance to motion is produced by skin friction.
- The friction and cohesion within the sediment: These control how the sediment will fail and how forces are distributed with the sediment. Sediments with no cohesion will provide very little resistance to uprooting. Highly cohesive sediments will come up as a relatively massive “root ball.”

In the case of a stiff stalk, we will also need to factor in the relative behavior of the sediments under both compression and tension, produced as the anchoring structure is subject to rotational forces.

1.2.3 *Paradigms for Anchors*

There are a wide variety of nautical anchors; their use depends on such factors as the size of the moored structure, the nature of the substrate, and whether the mooring is permanent or temporary. The simplest anchor is a heavy weight. More sophisticated designs, however, are constructed to interact with the substrate to increase the anchoring force. In particular, they dig in if pulled horizontally (Taylor 2004). One of these designs is the grapnel anchor (Fig. 1.2a), from which the *Ancyrocrinus* structure gets its name. The basic parts of an anchor include the shank or stem, to which the anchor chain or rope attaches, and arms at the base of the shank which curve upward and terminate in flat, triangular flukes. The shape of the flukes allows them to penetrate the seafloor as they are being dragged. The grapnel anchor is distinguished from other types by having equally spaced arms. This allows it to set into the bottom no matter which arm is in contact; the other arms remain above the substrate. It is often also used in bottoms with rocks or coral where it can hook firmly into debris, i.e., it acts like a grappling hook. The arms of grappling hooks also recurve toward the shank so they do not become dislodged.

If we use these nautical anchors as a paradigm for the function of the *Ancyrocrinus* grapnel, sensu Rudwick (1964), then the design should include spurs that are distally flattened in cross section, end in points, and are recurved toward the stem. The observed geometry of the structure fails on all three of these criteria: The spurs are rounded, terminate bluntly, and are not curved. Similarly, if we assume that it functioned as a grappling hook to catch on debris, then the shape of the spurs does not match the predicted design.

One intriguing alternative anchor design is the mushroom anchor (Fig. 1.2b–d). Usually used for permanent anchors, it is also sometimes used in small boats for

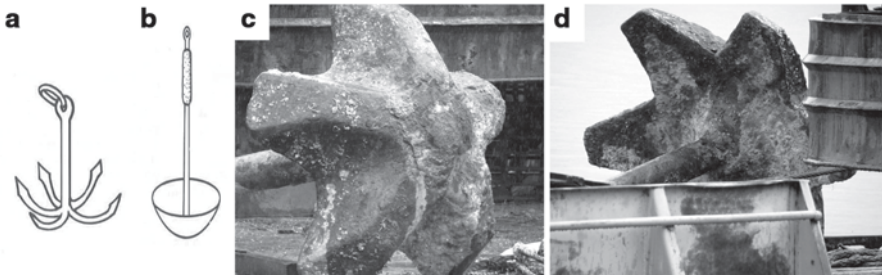


Fig. 1.2 Modern nautical anchors. **a** Grapnel anchor—*pointed* and *flattened flukes*. **b** Mushroom anchor for small boats—*rounded bottom*. **c, d** Large mushroom-type anchor on a US Navy barge, Ketchikan, Alaska

anchoring in muddy bottoms (Hinze 1986). As the anchor oscillates on a soft seabed, it buries itself. This, in turn, greatly increases the holding power. This anchor design might thus be an appropriate paradigm for *Aspidocrinus* and *Oryctoconus*, which were reconstructed by Seilacher and MacClintock (2005) as having bowl-shaped nodal anchors. It is also possible that the rounded bottom of *Ancyrocrinus* served the same purpose.

In order to directly test the ability of the *Ancyrocrinus* grapnel to act as an anchor, we performed a series of experiments on their ability to set and hold in various bottom sediments. We measured forces needed to pull the structures vertically out of sediments, as well as those required to drag them along the sediment surface. In addition, we determined the forces necessary for the structure to penetrate sediments, assuming the holdfasts reimplanted in some manner after dislodgement. These results also led us to measure the drag coefficients of an *Ancyrocrinus* holdfast moving through water. This was also prompted by the qualitative observation that the lateral view of some grapnels closely approximated a streamlined shape. Finally, we conducted qualitative experiments on whether oscillations of the structure on the sediment surface led to deeper penetration of the grapnel.

1.3 Materials and Methods

Specimens of *Ancyrocrinus* were provided by the Cincinnati Museum Center. All specimens were collected in Speed, Indiana, from the Beechwood Member of the North Vernon Limestone (Middle Devonian, Givetian; Goldstein et al. 2009). Latex molds were made of four of the specimens and from these, plaster (Hydrocal) casts were produced (Fig. 1.1; Table 1.1). A pipe cleaner was embedded in the plaster for horizontal tension experiments and a brass rod was hot glued to the apex of the structure for vertical tension and compression studies.

Forces were measured using a Chatillon DFIS-10 digital force gauge, mounted on a Chatillon TCM-200 motorized test stand. The motorized test stand allows ten-

Table 1.1 *Ancyrocrinus* dimensions (Fig. 1.1) and experimental results. Plaster casts were made of the first four specimens (bold type), which were used in experiments. Experimental averages were based on four trials per model, except for specimen 62124a results for penetration in sand ($n=3$). Dimensions are in centimeters, mass in grams. Forces are in newtons, with negative values for compression and positive values for tension. Specimens are from the Cincinnati Museum Center, Ohio, USA

Specimen number	Total height (a)	Height of radices above base (b)	Width at base of radices (c)	Width at top of radices (d)	Mass	Average force penetration in 1 cm sand	Average force penetration in 1 cm mud	Average maximum pullout force in sand	Average maximum pullout force in mud	Average drag force in sand
62124a	2.4	0.9	1.6	0.8	10.6	-4.14	-0.04	4.83	0.20	1.31
26158	4.7	1.5	2.5	1.9	15.9	-4.28	-0.07	7.74	0.23	1.00
26158	6.4	1.8	2.5	1.8	20.4	-4.43	-0.06	7.43	0.21	0.81
26158	4.1	2.0	2.0	1.5	12.8	-5.85	0.07	4.45	0.15	
26158	2.4	1.1	1.4	1.1	3.3	-	-	-		
62124b	2.5	0.8	1.4	1.2	3.7	-	-	-		
62124c	1.9	0.7	1.7	1.2	4.6	-	-	-		
62123a	2.6	1.2	1.6	1.1	6.5	-	-	-		
62123b	3.5	1.4	2.0	1.3	9.5	-	-	-		

sion or compression to be measured over a constant range of velocities. Most runs were done at a vertical velocity of 2.54 cm/min. Data were recorded using Chatillon Nexygen DF software and uploaded into SYSTAT (version 13) for analysis. Forces were applied vertically by pulling or pushing parallel to the direction of movement of the gauge on the test stand (Fig. 1.3a). Horizontal forces were measured by attaching a length of fishing line to model, which ran horizontally to an Erector set pulley and then vertically to the moving gauge (Fig. 1.3b).

Experiments were performed with a soft-mud substrate prepared from kaolin and water or with wet, fine sand. Due to evaporation, consistent water content of the sediment between runs was difficult to maintain. As a result, we standardized among runs by measuring the forces on a brass disc at both the beginning and end of the experiments.

Forces required to penetrate the substrate were measured by attaching the model directly to the force gauge with a metal rod. The model then penetrated the sediment vertically at a constant velocity (usually 2.54 cm/min) until it completely entered the substrate. The software recorded compressive forces (recorded as negative values) experienced as a function of time; we converted time to the depth of penetration. The model was then withdrawn, and the tension (recorded as positive values) was similarly recorded. Both tension and compression measurements were repeated four times at different locations on the substrate for each of the four models.

Resistance encountered while being dragged across a fine sand surface was determined by using models attached via a pipe cleaner and fishing line to the gauge. Specimens were placed with the flanges level with the sediment surface. During the drag, forces were continuously measured and recorded; the peak tension value was

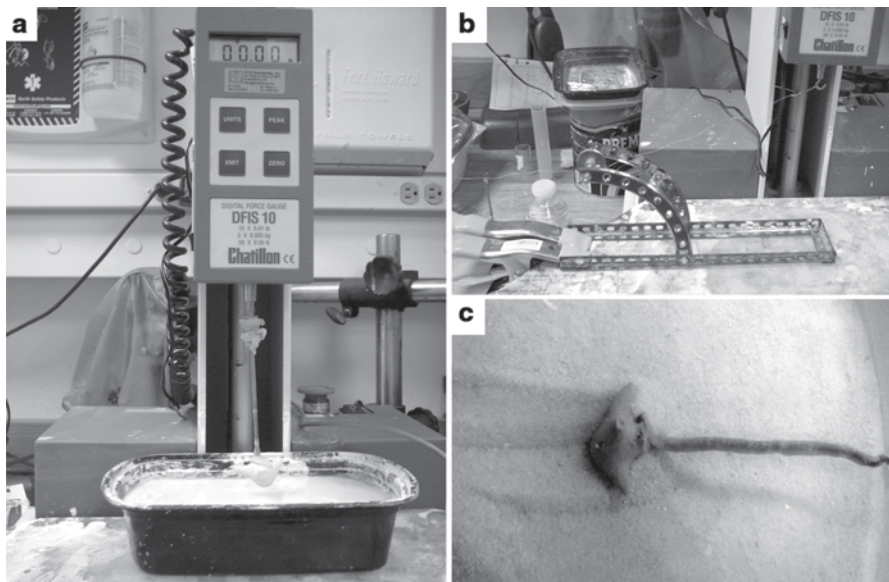


Fig. 1.3 Experimental setups. **a** Arrangement for measuring compressional and tensional forces perpendicular to the substrate surface. Models were attached to a stiff brass rod and moved vertically. **b** Arrangement for measuring forces for grapnels dragged across sediment surface. Models were attached by a pipe cleaner and fishing line around a pulley to the force gauge; **c** *Furrow and sand push pile* produced by dragging

recorded at the end of the run. The experiments were also repeated four times for each model. The sand was smoothed out between each run and the container was rotated after every two runs.

The drag coefficients in water of the grapnels were measured using the method described in Plotnick and Baumiller (1988) and Singer et al. (2012). Two models were placed in a recirculating flow tank with flows ranging from 0.013 to 0.255 m/s. The models were attached via a metal rod to a metal plate equipped with strain gauges, which allowed the direct measurement of drag force for each velocity. The models were oriented with the bottom of the grapnel pointing into the flow. The frontal areas of the models were measured and used with the drag measurements to calculate the dimensionless drag coefficients (C_d), using the formula:

$$C_d = \frac{2D}{U^2 A_c \rho_w},$$

where D is the measured drag force in newtons, U is the water velocity, A_c is the frontal surface area of the crinoid exposed to current, and ρ_w is the density of water (we used the approximate density value of tap water of 998 kg/m³).