Crinoid respiration and the distribution of energetic strategies among marine invertebrates

JAMES SAULSBURY*,

Museum of Paleontology and Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, MI 48109, USA

During the Mesozoic, the radiation of durophagous marine predators caused the ecological and evolutionary diminution of once-successful groups, including stalked, suspension-feeding echinoderms known as crinoids. Featherstars, crinoids that shed the stalk during development and exhibit anti-predatory adaptations such as high motility, defied this trend, and today they are widespread and diverse across ocean depths. As a 'success story' of the Mesozoic Marine Revolution, featherstars could be used to reveal how some marine lineages succeeded in the face of increased predation over geological time. However, current limited understanding of crinoid functional anatomy has inhibited such study. Using microphotography, scanning electron microscopy and computed tomography, I characterize the structure and variation of crinoid circulatory anatomy and explore differences between featherstars and stalked forms. Contrary to previous accounts, I find support for the role of coelomic circulation in crinoid respiration. This includes a previously undocumented case of positive allometry: larger crinoids have more complex circulatory anatomy. Moreover, quantitative analysis of coelomic anatomy shows that the circulatory system is generally more complex in featherstars than in stalked crinoids. The adaptations that allowed featherstars to persist in shallow water apparently entailed an increase in the functional capacity of the circulatory system, possibly due to consistently greater metabolic rates.

ADDITIONAL KEYWORDS: adaptation – comparative anatomy – computed tomography – echinoderms – functional morphology – morphometrics – scanning electron microscopy – skeleton.

INTRODUCTION

During the Jurassic and Cretaceous, the structure of marine ecosystems underwent a profound shift known as the Mesozoic Marine Revolution (MMR), chiefly represented by the rise of the major modern groups of eukaryotic phytoplankton and the concurrent radiations of multiple groups of marine grazers and durophagous predators (Vermeij, 1977; Knoll & Follows, 2016). Evidence from the fossil record indicates that during this time marine animals became on average larger, fleshier, more well defended against predators and more motile, a transition which occurred not across the entire biota but by the success of some groups over others (Finnegan *et al.*, 2011; Heim *et al.*, 2015; Bush, Hunt, & Bambach, 2016). Crinoids (Fig. 1) – passive suspension-feeding echinoderms that dominated benthic ecosystems during much

of the Palaeozoic and Mesozoic – have served as an important case study of a group in which success or failure across the MMR was apparently determined by aspects of life history. As durophagous predators such as teleosts and echinoids radiated in the oceans, sessile or slow-moving stalked crinoids were restricted over the course of the Cretaceous and Palaeogene to deep-water settings in which they encountered fewer predators (Meyer & Macurda, 1977; Bottjer & Jablonski, 1988; Oji, 1996; Baumiller *et al.*, 2010; Whittle *et al.*, 2018). Featherstars (Fig. 1A), crinoids in the order Comatulida that shed their stalk during ontogeny, counterpose this trend: featherstars today are globally distributed in shallow- and deep-water settings, while also making up the majority of crinoid diversity (556/665 species; Appeltans *et al.*, 2012). Their relative ecological and evolutionary success has long been attributed to the enhanced motility afforded by a stalkless lifestyle. Although some stalked crinoids crawl (Baumiller & Messing, 2007), featherstars are the only crinoids that change position
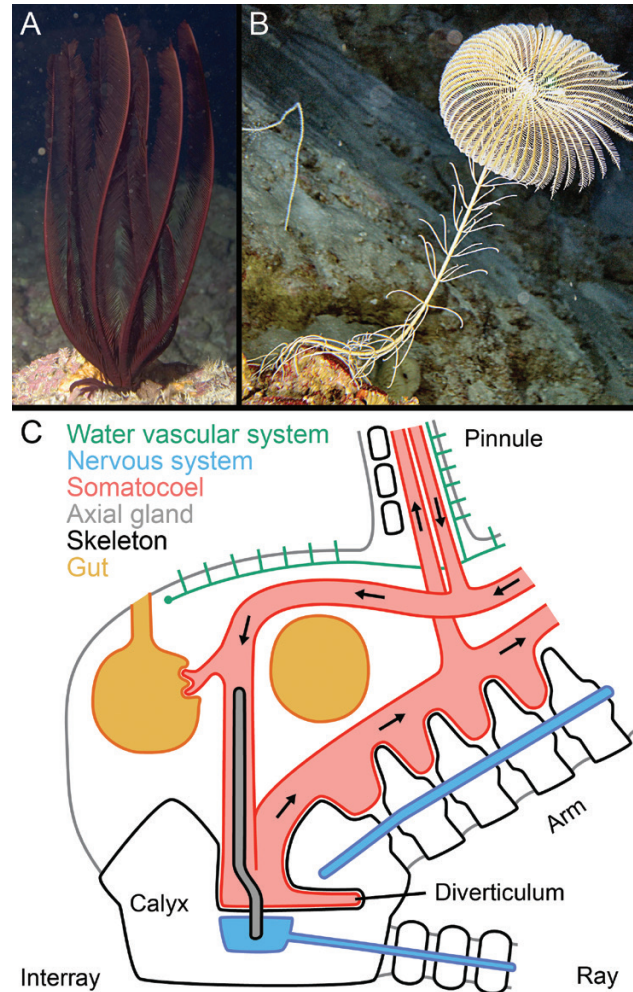
*E-mail: jgsauls@umich.edu

Figure 1. Crinoid life habit and anatomy. A, the featherstar *Tropiometra afra* in life position. Shallow reef, Okinawa Island, Japan. Photo © Gustav Paulay. B, the stalked crinoid *Cenocrinus asterius* in life position. Roatan, Honduras, depth: ~150 m. Photo © Charles G. Messing. C, idealized crinoid internal anatomy: cross-section through the central body with the calyx at the bottom, an arm and cirrus on the right, and a pinnule at top. Black arrows depict the pattern of coelomic fluid flow as described by Grimmer & Holland (1979). Note the lateral projection of the somatocoel in the calyx, referred to here as a coelomic diverticulum. The canals of the water vascular system are much smaller than the somatocoel, and are shown as a single line. The complex interface between the gut and somatocoel is represented by a simple interfingering at left of centre.

diurnally, and many reef species only emerge at night when visual predators are relatively scarce (Meyer *et al.*, 1984; Slattery, 2010). Famously, members of many featherstar subclades have been documented swimming, probably as a response to potential predators (Janevski & Baumiller, 2010; Janevski, 2011). Appropriate for a relatively motile existence, the featherstar skeleton is lighter than that of stalked forms (Baumiller & LaBarbera, 1989). Featherstars may regenerate their arms as much as four times faster than stalked crinoids following autotomy (Amemiya & Oji, 1992; Baumiller & Stevenson, 2018), an ability which might be a result of a difference in metabolic

rates. Importantly, featherstars are apparently paraphyletic: two to four lineages of comatulid crinoids are thought to have secondarily re-acquired sessility by retaining a cemented or rooted stalk into adulthood (Rouse *et al.*, 2013). These stalked comatulids, referred to as bourgueticrinids and guillecrinids, are found exclusively in deep water despite occurring in shallow water in the Mesozoic and Paleogene (Zamora *et al.*, 2018), substantiating the claim that featherstars can persist in shallow water as a result of their unique lifestyle.

As a group in which ecological and evolutionary success apparently hinged on a relatively energetic

lifestyle, crinoids are an ideal group with which to test ideas about metabolism and the MMR. However, the current picture of crinoid physiology is rudimentary in some important ways, precluding deep comparative study of energetic strategies. For example, the most common account of crinoid respiration holds that these animals absorb oxygen from their surroundings by way of the tube feet and water vascular system (Fig. 1C), and that this plus diffusion through the body wall suffices to meet respiratory demands (Farmanfarmaian, 1966; Schick, 1983). This is the picture given in recent invertebrate zoology textbooks (Ruppert *et al.*, 2004; Schmidt-Rhaesa, 2007; Brusca *et al.*, 2016) and appears to be widely accepted, but a simple theoretical approach suffices to show that it cannot be the only respiratory mechanism at work in crinoids. Harvey (1928) derived a model in which the maximum radius of a spherical body respiring via diffusion is given by the following equation:

$$r = \sqrt{\frac{6C_oD}{A}} \qquad (1)$$

where C_o is the ambient concentration of oxygen (atm), A is respiratory exchange rate (mL O_2/g/min) and D (atm/cm/cm^2) is a diffusion coefficient. This equation can be applied to estimate the maximum possible size of the crinoid calyx (Fig. 1C), one part of the crinoid central body that is large, subspherical and full of respiring tissues (Heinzeller & Welsch, 1994). This feature is isolated from the tube feet (Fig. 1C), so that even though the vast system of tube feet must be an effective absorber of oxygen, the calyx should nevertheless respire entirely by diffusion under the textbook model. Given a respiratory rate of 2.03×10^{-4} mL O_2/g/min (the lowest observed for a crinoid; the highest values are greater by a factor of 7; Baumiller & LaBarbera, 1989), a typical marine oxygen concentration of 0.21 atm, and a diffusion coefficient of 1.1×10^{-5} atm/cm/cm^2 for connective tissue (Krogh, 1941), I calculate a maximum radius of 2.61 mm for the crinoid calyx. This value is similar to Farmanfarmaian's (1966) theoretical maximum for an echinoid, but many living crinoids exceed this liberally estimated maximum: calyces 1 cm or more in diameter are common among featherstars (Rasmussen, 1961) and stalked crinoids (Roux & Pawson, 1999; Hess & Messing, 2011) alike, to say nothing of giant extinct forms such as *Uintacrinus* and *Scyphocrinites* that grew to exceed 6 cm in maximum diameter (Moore & Teichert, 1978; Milsom *et al.*, 1994). Either estimates of respiratory rate in crinoids are too high by one to several orders of magnitude, or crinoid respiration is more complex than is commonly assumed. Diffusion by itself is a viable mode of respiration for small animals, but many crinoids are not small.

The simple model of respiration stated above is not the only one that has been put forward. Grimmer & Holland (1979) demonstrated steady circulation of coelomic fluid at about 1 mm/s in the arms of the featherstar *Florometra serratissima* and suggested that it might play a role in respiration and several other key functions. The authors focused on the somatocoel, a system of mostly continuous coelomic cavities found throughout the arms and central body (Fig. 1C). If their suggestion is correct, then coelomic circulation is not an alternative respiratory mechanism but a complementary one: the somatocoel is closely associated with the water vascular system, apparently separated by about 5 μm of tissue along the length of the arms (Grimmer & Holland, 1979) – about the thickness of the blood–water barrier in fish gills (Hughes, 1972). Thus, coelomic circulation could serve to transport the oxygen absorbed by the tube feet throughout the body. This possibility is worth exploring not just as an intrinsically interesting aspect of organismal biology, but also as a key to comparative work. The somatocoel is a large, morphologically complex and physiologically important organ that is amenable to study across a variety of taxa. Any differences that may exist in the average metabolic rates of featherstars and stalked crinoids might be reflected in their circulatory anatomy. Moreover, a functional hypothesis for the somatocoel could be expected to furnish adaptive explanations for previously enigmatic aspects of morphology.

In this paper I demonstrate the probable role of coelomic circulation in key physiological processes in crinoids, including respiration and nutrient and hormone transport. I show that the coelomic circulatory system in featherstars has a greater surface area relative to body size than it does in stalked crinoids, and in larger taxa includes morphological features that are hypothesized to be respiratory adaptations. This work highlights the metabolic aspect of the evolutionary and ecological success of featherstars, and underlines the importance of the MMR for understanding the distribution of energetic lifestyles among modern organisms.

MATERIAL AND METHODS

QUALITATIVE STUDY

I used microphotography, scanning electron microscopy (SEM) and X-ray micro-computed tomography (μCT) to study the structure and variation of the crinoid somatocoel. This approach included multifaceted study of the somatocoel within the crinoid calyx, SEM characterization of skeletal structures associated with the coelom, complete three-dimensional reconstruction of the somatocoel across several distantly related taxa,

and characterization of morphological variation in the context of crinoid phylogeny. In the multifaceted approach, µCT, microphotography and SEM were used to reveal the structure of the coelom in the same specimen. SEM imagery of the skeleton focused on two aspects of skeletal morphology that are known to taxonomists but whose functional significance has not been previously remarked on: the 'coelomic furrows' and 'radial pits' (Rasmussen, 1961; Hess & Messing, 2011) that characterize the inner surfaces of the calyx ossicles of some featherstars, and the rows of pits observed on the oral surfaces of some pinnule ossicles. Finally, I used µCT to reconstruct the entire coelomic circulatory pathway in several distantly related taxa. This can be facilitated by iodine staining, but even in untreated specimens the course of coelomic cavities can be visualized with µCT if those cavities have not collapsed due to drying or been filled with clotted coelomic fluid (Boolootian & Giese, 1959). The layout of soft tissues in the crinoid tegmen is exceptionally complex (Balser & Ruppert, 1993), and I did not attempt to isolate the morphology or position of features such as the axial gland (Fig. 1C; sometimes referred to as the axial organ). Specimens were scanned at the University of Michigan CTEES facility with a Nikon 62 XT H 225ST industrial µCT system using a tungsten reflection target. Optimal scan settings were found to be 70–110 kV and 100–200 µA, with lower values for very small specimens. Some specimens were stained in 1% Lugol's iodine stock solution for 24 h before scanning to improve contrast in µCT, following Gignac et al. (2016). Three-dimensional surfaces based on reconstructions of µCT scans were generated using the medical imaging software Materialise Mimics (Materialise NV, Leuven, Belgium). The use of CT for studying echinoderm anatomy has been reviewed by Ziegler (2012) and Aschauer et al. (2010). SEM imaging was accomplished on the JEOL JSM-7800FLV Scanning Electron Microscope at the University of Michigan EMAL facility. To visualize details of the crinoid skeleton, specimens were soaked in dilute bleach to dissolve soft tissues and to allow ossicles of the crinoid skeleton to be easily dissociated from one another. Microphotography was carried out with a Leica M165 C digital stereo microscope. Details of all specimens studied are given in the Supporting Information, Tables S2 and S3.

MORPHOMETRY OF COELOMIC ANATOMY

I used digital 3-D models of crinoid coelomic and skeletal anatomy to test for allometric scaling of the crinoid somatocoel, and to test for differences in the morphological complexity of the coelom between featherstars and stalked crinoids. The premise of the first test is as follows: if coelomic anatomy is totally unimportant for respiration, then the coelom should scale isometrically – that is, with geometric similarity across sizes. Following LaBarbera (1986), a reduced major axis (RMA) regression of coelomic surface area against the biovolume of a relevant anatomical region would have a slope of 2/3 in log–log space. Conversely, if coelomic circulation does play an important role in crinoid physiology, then isometric scaling would result in deleterious effects such as suffocation at larger sizes (Haldane, 1926). In this scenario, the surface area of the coelomic lining should scale with positive allometry to 'keep up' with metabolic demand, which scales with volume.

An RMA linear regression of log metabolic rate against log wet mass, using the 15 crinoid data points from Baumiller & LaBarbera (1989), returns a slope of 0.928 (95% confidence interval: 0.715–1.206); this is the slope expected in a regression of coelomic surface area against biovolume if coelomic circulation is important for respiration. I tested for allometry within featherstars, within stalked crinoids and across the entire dataset by comparing the slopes of RMA regressions, implemented in R with the *lmodel2* package (Legendre, 2018). I also tentatively evaluated within-species scaling for the handful of species that spanned at least a two-fold range of body sizes (calyx volume).

I tested for a difference in the complexity of coelomic morphology between featherstars and stalked crinoids in a model selection framework. Ordinary least squares (OLS) regression assumes that predictor variables are known without error and are controlled by the investigator, and tends to underestimate slopes relative to RMA regression, which makes it undesirable for allometry studies (LaBarbera, 1986). However, no readily accessible implementations of RMA or other model II regressions include calculations of likelihood. Thus, RMA cannot be used in model selection with the Akaike information criterion (AIC), which discriminates among competing models based on likelihood and the number of estimated parameters. For this reason I used OLS regression for model selection. AIC scores were used to compare linear regressions for two models: in one, estimated coelomic surface area was regressed against both calyx volume and a binary variable indicating the presence or absence of a stalk; in the other, only calyx volume was included as a predictor. Model selection was implemented in R.

In generating 3-D models for morphometry, coelomic surface area is estimated as the surface of the interface between the skeleton and the coelomic cavities, with the model ending at the oralmost extent of the calyx. This definition underestimates the true surface area of the coelom within the calyx because some coelomic tissue within the calyx is uncalcified. However, it

allows for consistent measurement across specimens whose soft tissues may not appear clearly in μCT scans, and provides a reasonable estimate of the surface available for diffusion of oxygen, nutrients, etc., from the coelomic fluid into the surrounding tissue. This definition also assumes that the radial cavity is fully lined by coelomic lining, which Heinzeller & Welsch (1994) found to be true in the few crinoids examined histologically. I generated and measured the volume of 3-D models of the calyx, including any cavities in the skeleton occupied by nervous tissue. Delimiting the calyx is straightforward in featherstars, in which it includes the centrodorsal, basal and radial ossicles, but it is less straightforward in stalked crinoids, in which the calyx grades smoothly into the stalk in some taxa (e.g. in *Democrinus*). In cases in which such a distal cutoff was not straightforward to define, I chose the most conservative (smallest) estimate of calyx volume, as this approach has the greatest tendency to refute the hypothesis that featherstars have more coelomic surface area for a given calyx volume. For isocrinids, this definition encompassed the radials and basals only; for other stalked crinoids (*Phrynocrinus* and *Democrinus*) the position of the aboral nerve centre along the crinoid axis served as the aboral cutoff.

Following Mandelbrot (1967), the measured perimeter of a statistically self-similar shape increases non-asymptotically with increasing resolution of measurement. It is not clear whether crinoid coelomic anatomy is fractal-like in this way, but changing the resolution of 3-D models of complex objects clearly changes their measured surface area. Indeed, if 3-D models of larger specimens tended to have greater resolution, larger specimens might spuriously appear to have more complex internal anatomy. For this reason, I recorded the file size of 3-D models in kilobytes to test for the effect of model quality on scaling patterns.

Finally, individuals (not species) in the scaling study were scored for the presence or absence or coelomic diverticula, extensions of the somatocoel from the axis (centre) of the calyx outward. Diverticula were marked as 'present' if they extended laterally at least halfway between the axis and the outer margin of the radials.

RESULTS

Qualitative study

I integrated microphotography, SEM and μCT data to establish a detailed picture of crinoid coelomic morphology and its variation across crinoid phylogeny, building on previous histological and physiological studies (Hyman, 1955; Grimmer & Holland, 1979; Balser & Ruppert, 1993; Heinzeller & Welsch, 1994; Mozzi *et al.*, 2006; Engle, 2012). μCT-based reconstructions of the course of the somatocoel through the arms, tegmen and calyx of various crinoids (Fig. 2) support the picture of circulatory anatomy given for the featherstar *Florometra serratissima* by Grimmer & Holland (1979) and reveal new insights as well. Each crinoid arm bears two broad canals: an aboral canal in which fluid passes out into the arms, and an oral canal (subtentacular canal) in which fluid is returned to the axis. [Each arm also contains haemal cavities, a genital coelomic canal and the canals of the water vascular system, but these are typically too small or too deformed to visualize with μCT, although Engle (2012) succeeded in reconstructing water vascular features in 3-D from histological slides.] The oral and aboral arm canals each send a single offshoot into each pinnule and communicate with each other, both in the distal parts of the arms and pinnules, and also intermittently along their entire lengths (Grimmer & Holland, 1979; Engle, 2012). The aboral canal in the pinnules bears a row of densely ciliated pits which apparently help drive the flow of coelomic fluid (Grimmer & Holland, 1979). Fluid transport systems driven by ciliary beating are notably rare among animals compared to pump-driven systems, which may explain why the crinoid circulatory system does not obey Murray's law of vessel branching (LaBarbera, 1990). Although ciliated pits do not appear clearly in μCT scans, they correspond to distinctive skeletal signatures visible with SEM (see below).

The bundle of coelomic canals in the calyx, typically referred to as the axial sinus, is linked to the aboral coelomic canal in the arms by an anastomosing network of canals. This network forms the base of the tegmen and constitutes the plane of separation when the tegmen is autotomized in a typical anti-predatory response (Mozzi *et al.*, 2006; Bobrovskaya & Dolmatov, 2014; Kalacheva *et al.*, 2017). Between the point at which the oral coelomic canals enter the tegmen and subsequently enter the calyx, offshoots of the somatocoel arise in some taxa, which interface with the digestive tract in an exceptionally complex way. At these interfaces the linings of the digestive tract and coelom interdigitate extensively, such that they share a relatively large surface area (see below for the possible functional significance of this interface) (Fig. 2A, B). Where the five oral coelomic canals enter the tegmen, they come together in the pattern of 2–1–2 symmetry that defines the bodyplans of crinoids and many extinct echinoderm lineages (Kammer *et al.*, 2013). Importantly, both the oral and the aboral canals enter the calyx, with the aboral canals forming a ring lateral to the oral ones. This indicates that coelomic fluid would flow through the calyx rather than past it, and legitimizes treating the axial sinus as part of the circulatory system.

SEM and microphotography reveal several important new aspects of crinoid circulatory physiology
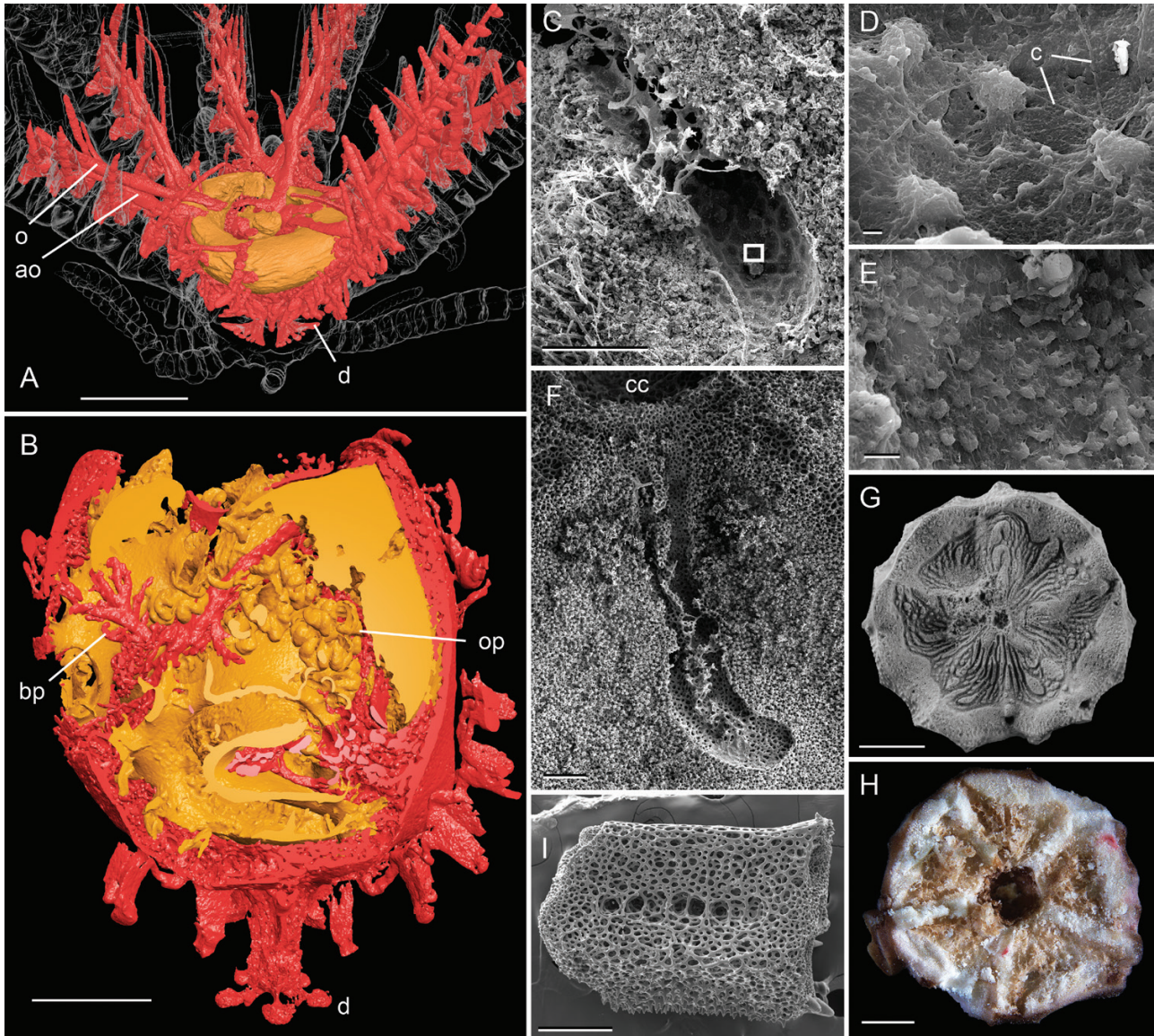
Figure 2. Qualitative characterization of crinoid coelomic anatomy. A, featherstar *Tropiometra carinata*: 3-D model of the internal anatomy generated from µCT scan data, showing general configuration of somatocoel (red) and gut (orange) (skeleton translucent). The oral arm coelom (o) passes over the gut before descending into the axis, while the aboral arm coelom (ao) passes under (aboral to) the gut. B, featherstar *Heliometra glacialis*: cross-section of 3-D models of gut and somatocoel showing complex interface between somatocoel and gut, including branching processes of the somatocoel (bp) that conform to the gut, and thin outpocketings of the gut (op) in the vicinity of the somatocoel. Colour code as in A. C and D, featherstar *Davidaster rubiginosus*: SEM image of the inside of calyx interior, showing coelomic lining of a single diverticulum. Calyx has been sanded down from the side. C, view of entire diverticulum. D, enlargement of region within white rectangle in C. Thin cilia (c) and evenly spaced globular features of unknown affinity cover the coelomic lining. A and F, featherstar *Cenometra bella*. E, SEM image of the coelomic lining in the calyx axis showing the same cilia and globular features. F, SEM image of the inner surface of the centrodorsal, bleached to remove soft tissues and reveal the cavity in the skeleton corresponding to a single coelomic diverticulum. Calyx axis at top. G, Cretaceous featherstar *Decameros ricordeanus*: photograph of inner surface of the centrodorsal revealing a complex system of canals corresponding to coelomic diverticula. H, featherstar *Tropiometra carinata*: photograph of inner surface of unbleached centrodorsal, showing configuration of coelomic lining within cavities in the skeleton. I, featherstar *Florometra serratissima*: SEM image, oral view of single pinnule ossicle. The row of pits along the centre of the pinnular correspond in size, shape and spacing to densely ciliated pits in the somatocoel. Specimens are listed in Supporting Information, Table S2. ao, aboral arm coelom; bp, branching processes; c, cilia; cc, centrodorsal cavity; d, coelomic diverticulum; o, oral arm coelom; op, outpocketings of the gut. Scale bars: (A, B, G), 4 mm; (C, F, I), 200 µm; (D), 1 µm; (E), 5 µm; (H), 1 mm.

and anatomy. SEM images of sectioned crinoid calyces show that the coelomic lining in the calyx generally conforms to the skeleton (Fig. 2C–E), but includes some 'free-standing' tissue as well (Fig. 2H), confirming the prediction stated above that the surface area of the skeletal cavities underestimates true coelomic surface area. The internal surface of the coelom in the calyx is lined by long, whip-like features whose width (~0.3 µm) and length (~10 µm) identifies them as probable cilia. Thus, the axial sinus appears to bear the same general ciliation that Grimmer & Holland (1979) observed in other parts of the somatocoel credited with helping drive circulation. Curiously, the internal surface of the coelom in the calyx also features evenly spaced globules ~2 µm in diameter (Fig. 2D, E). The nature of these structures is unclear but should be amenable to histological study.

SEM reveals a single row of pits in the ambulacrum of pinnule ossicles in most species of crinoids studied (Fig. 2I). These pits are of similar diameter, spacing and position to the ciliated pits that line the coelom in the pinnule, and they are suggested to be receptacles of those ciliated pits. Rows of pits in the pinnule ossicles of the featherstars *Davidaster rubiginosus* and *Comactinia echinoptera* have been observed previously but not remarked on (Macurda & Meyer, 1975). Moreover, histological studies (Grimmer & Holland, 1979; Heinzeller & Welsch, 1994) have described ciliated pits in the stalked isocrinid *Neocrinus decorus* and the featherstar *Florometra serratissima*, and I have observed skeletal correlates of these pits in the pinnule ossicles of both species. The existence of skeletal features that correspond to ciliated pits is especially interesting, because it can be used to infer coelomic circulation in well-preserved fossil crinoids. Not all pinnule ossicles have receptacles for ciliated pits in those taxa that have them, but I detected no pattern in the distribution of ossicles with and without pits around the body. The only taxon in which these pits were not observed was a single specimen of *Holopus rangii* (Cyrtocrinida), a highly derived form in which several major internal organs have apparently been lost (Grimmer & Holland, 1990).

COELOMIC DIVERTICULA

A coelomic diverticulum is an outward extension, either radial or interradial, of the axial sinus (part of the somatocoel) within the calyx. Radial diverticula may be oriented laterally or aborally (corresponding to the coelomic furrows and radial pits of the taxonomic literature, respectively), whereas interradial diverticula are apparently always lateral. The skeletal cavities that house coelomic diverticula are conspicuous and morphologically complex (Fig. 2G; Fig. 3), and many authors have used them for taxonomy (Clark, 1915a; Rasmussen, 1961; Hess & Messing, 2011; Taylor, 2015). However, to date, the functional and anatomical significance of coelomic diverticula in crinoids has been only minimally remarked on (e.g. Clark, 1915b: 374–376).

In this study, µCT scans revealed a spectacular diversity of coelomic diverticula in the calyces of some featherstars (Fig. 3), ranging from spacious conical pits (*Notocrinus virilis*) to fan-shaped complexes of anastomosing canals (*Amphimetra ensifera*) and to simple nub-like projections (*Analcidometra armata*). In some taxa (e.g. *Pterometra pulcherrima*, Fig. 3), aboral coelomic diverticula open onto the surface of the calyx, although the coelomic cavity probably does not communicate directly with the surrounding seawater. Openings such as these probably constitute the dorsal star described in several extinct taxa [e.g. *Semiometra* (Rasmussen, 1961)]. Almost all featherstars with prominent coelomic diverticula are restricted to a single subclade of featherstars: the smallest clade that includes *Notocrinus*, *Aporometra*, Himerometroidea, some Tropiometroidea and Antedonidae (Hemery *et al.*, 2013; Rouse *et al.*, 2013). The only exception was a very large specimen of *Davidaster rubiginosus*, which belongs to a separate subclade including Comatulidae and Thalassometridae (Fig. 3). The most morphologically complex circulatory apparatus is seen in the giant extinct featherstar *Decameros ricordeanus*, which a recent phylogenetic analysis places close to the Tropiometroidea and Himerometroidea (Saulsbury & Zamora, 2019). The handful of fossil genera attributed to the family Notocrinidae uniformly bear radial pits, but their phylogenetic affinities have not been tested (Hess & Messing, 2011).

Coelomic diverticula must have either arisen several times, been lost several times, or both, as many extant families and some extant genera (e.g. *Davidaster*) include some representatives with this feature and some without it (Fig. 3). The pattern of gains and losses of coelomic diverticula may be clarified as several groups currently considered polyphyletic (e.g. Antedonidae, Tropiometroidea) undergo systematic revision. Importantly, nearly all featherstars that bear coelomic diverticula are large (typically with a calyx > 20 mm³ in volume; Fig. 4) (see below). Regardless of the presence or absence of diverticula, the somatocoel is aborally invaginated into the calyx to some degree in all featherstars, whereas this is not the case in the stalked bourgueticrinids studied here.

SCALING STUDY

Estimated coelomic surface area scales with positive allometry across the entire dataset (Table 1). Among featherstars (40 specimens in 29 species), the natural log of coelomic surface area regresses (RMA) against
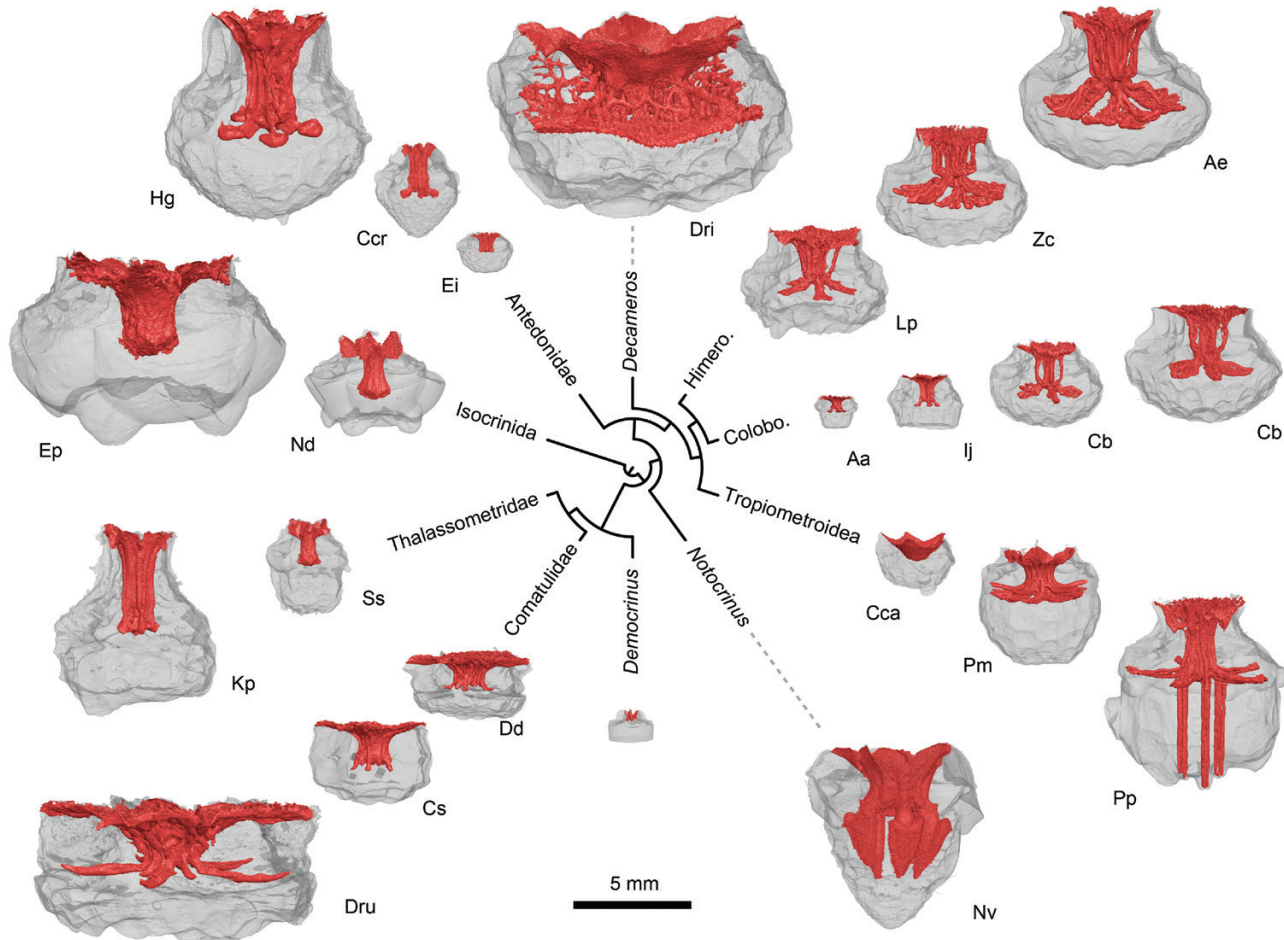
Figure 3. Coelomic morphology in the crinoid calyx across body size and phylogeny. The relationships depicted in the phylogeny at centre are based on those of Hemery *et al.* (2013: fig. 1), Cohen & Pisera (2017) and Rouse *et al.*, 2013: fig. 2). The position of the fossil featherstar *Decameros* is based on Saulsbury & Zamora (2019). 3-D models shown are the same ones used to calculate calyx volume and coelomic surface area. Abbreviations: Aa, *Analcidometra armata*; Ae, *Amphimetra ensifer*; Cca, *Calometra callista*; Cb, *Cenometra bella*; Ccr, *Comatonia cristata*; Cs, *Comaster schlegelii*; Dd, *Davidaster discoideus*; Dri, *Decameros ricordeanus*; Dru, *Davidaster rubiginosus*; Ei, *Eudiocrinus indivisus*; Ep, *Endoxocrinus parrae*; Hg, *Heliometra glacialis*; Ij, *Iconometra japonica*; Kp, *Koehlermetra porrecta*; Lp, *Lamprometra palmata*; Nd, *Neocrinus decorus*; Nv, *Notocrinus virilis*; Pm, *Ptilometra macronema*; Pp, *Pterometra pulcherrima*; Ss, *Stylometra spinifera*; Zc, *Zygometra comata*.

the natural log of calyx volume with a slope of 0.932 (Fig. 4). The 95% confidence interval on the slope of the regression (0.824–1.055) includes unity and the scaling exponent for mass metabolic rate (0.928) but not isometry (0.667). All featherstars with calyces larger than 6 mm³ (maximum observed: 416.12 mm³) have coelomic diverticula. Small featherstars generally lack this feature, with *Analcidometra armata* the single exception. Specimens of this species nevertheless fall on the regression line and have markedly less complex coelomic features than other members of the same family (Colobometridae; Fig. 3). Coelomic surface area therefore scales with positive allometry, and in larger featherstars this manifests as coelomic diverticula.

Positive allometry is observed in stalked crinoids (14 specimens in seven species), although with less clarity than in featherstars and with an interesting caveat. An RMA regression including all stalked crinoids returned a slope of 0.916 (Table 1), and the confidence interval on the slope (0.665–1.262) barely includes isometry at its lower end. The genus *Democrinus* is a conspicuous exception, as it exhibits isometric scaling of coelomic morphology (RMA regression slope: 0.675; Table 1). As such, the 3-D surfaces isolated for analysis in this taxon might not have the same functional significance as those of the other taxa studied. However, because the calyx of *Democrinus* contains no other plausible respiratory surfaces, these data points probably overestimate respiratory surface area.
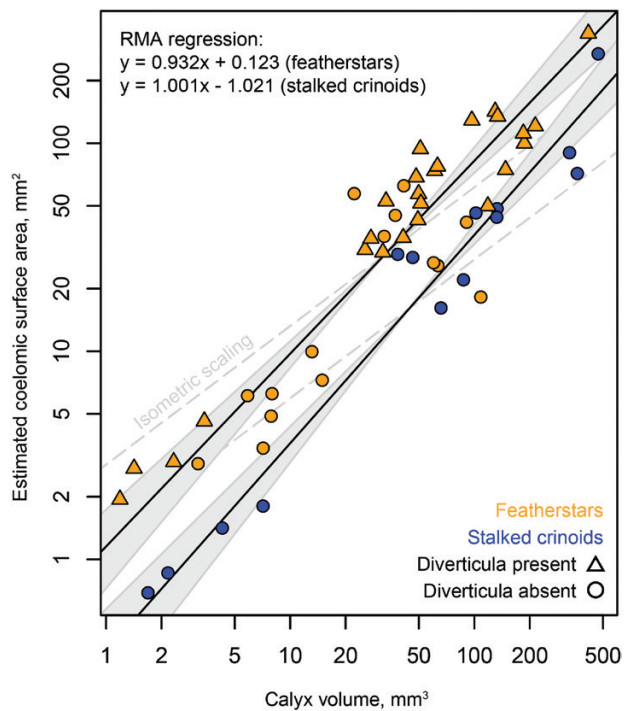
Figure 4. Coelomic scaling in featherstars and stalked crinoids. Regression lines are shown for featherstars and stalked crinoids, along with 95% confidence intervals on the slopes. Isometric scaling lines (2/3 slope) are shown for comparison. See text for definitions of surfaces and volumes isolated for analysis. All shapefiles used in this analysis are available in the Supporting Information.

RMA regression slopes exceed isometry in all four species whose sampling encompasses a broad range of body sizes (the stalked crinoids *Endoxocrinus parrae* and *Neocrinus decorus* and the featherstars *Analcidometra armata* and *Cenometra bella*), but sample sizes are low and confidence intervals on all slopes are very broad (Table 1). Curiously, two species (*Cenometra bella* and *Neocrinus decorus*) exhibit very weak relationships between calyx volume and coelomic surface area, despite each encompassing a roughly 2.5-fold range of body size (Fig. 4). In fact, the largest *C. bella* specimen studied has the lowest coelomic surface area within the species.

I recover a weak but positive correlation between body size and 3-D model quality in log–log space ($R^2 = 0.122$, $P = 0.0096$) (Supporting Information, Table S1; Fig. S1): the limits of the μCT scanner used in this study prevented the acquisition of very high-quality 3-D models of very small crinoids. However, excluding the smallest crinoids (calyx volume <20 mm³) causes this correlation to disappear, and positive allometry is still observed among featherstars (RMA regression slope = 0.877) and among stalked crinoids

Table 1. Reduced major axis (RMA) regressions of coelomic surface area against calyx volume for different subsets of the dataset. *N* is sample size.

Data subset	N	RMA slope (95% confidence interval)	RMA intercept (95% confidence interval)	r^2	Angle between ordinary least squares regressions
Entire dataset	54	0.969 (0.865–1.086)	−0.238 (−0.655 to 0.134)	0.912	5.283
Featherstars	40	0.932 (0.824–1.055)	0.123 (−0.305 to 0.501)	0.857	4.407
Stalked crinoids	14	1.001 (0.880–1.139)	−1.021 (−1.543 to −0.562)	0.958	1.234
Featherstars >20 mm³	29	0.877 (0.654–1.176)	0.390 (−0.871 to 1.331)	0.432	23.176
Stalked crinoids >20 mm³	10	0.927 (0.618–1.392)	−0.641 (−2.889 to 0.856)	0.738	8.649
Democrinus	4	0.675 (0.492–0.926)	−0.693 (−0.989 to −0.477)	0.988	0.299
Cenometra bella	7	1.041 (0.409–2.649)	−0.116 (−6.013 to 2.203)	0.125	51.041
Analcidometra armata	4	0.742 (0.294–1.867)	0.587 (−0.145 to 0.877)	0.879	3.545
Endoxocrinus parrae	3	0.740 (0.222–2.462)	0.217 (−8.723 to 2.902)	0.986	0.392
Neocrinus decorus	4	1.000 (0.170–5.875)	−0.741 (−20.601 to 2.639)	0.121	51.69

(slope = 0.927) when the smallest specimens are excluded in this way (Table 1).

All 14 data points for stalked crinoids fall below the regression line for featherstars. The intercept of the RMA regression line for stalked crinoids is roughly one log unit below that for featherstars (Table 1). More compellingly, the OLS regression model for the entire dataset in which a binary variable specifying stalk presence/absence is included as a predictor along with calyx volume is overwhelmingly supported over the model including only calyx volume (Table 2). Thus, by the metrics used in this study, coelomic anatomy is more complex in featherstars than in stalked crinoids of similar body size. Importantly, the stalked crinoids used in this analysis comprise several distantly related lineages, including two families of bourgueticrinids, which secondarily acquired a sessile habit.

DISCUSSION AND CONCLUSIONS

FUNCTION AND EVOLUTION OF COELOMIC CIRCULATION IN CRINOIDS

Qualitative and quantitative investigations support a role for coelomic circulation in crucial physiological functions. Most notable among these is respiration, as the range of body sizes observed among crinoids is satisfactorily explained by the model proposed here but not by the explanation given in textbooks on invertebrate zoology. The tube feet and the rest of the water vascular system are no doubt effective oxygen absorbers, but because the water vascular system is restricted to the oral side of the body and has no ability to circulate fluid, it cannot deliver oxygen to the rest of the body. Following the theoretical approach developed above, a crinoid with a roughly spherical calyx much larger than 2 or 3 mm in diameter would suffocate if oxygen were supplied to it only by diffusion from the outside. Conversely, continual replenishment of the coelomic canals in the centre of the calyx with oxygenated coelomic fluid, as argued for here, would permit a substantial increase in the maximum calyx diameter possible and, hence, the maximum possible

body size. To follow this logic further, diffusion of oxygen from outside and from coelomic canals in the axis might not suffice for an even larger crinoid, or one with a higher metabolic rate. In this light, coelomic diverticula in featherstars can be interpreted as respiratory adaptations: a sufficiently large featherstar would suffocate without them. Perhaps most importantly, the role of coelomic circulation in surface area-limited physiological functions such as gas exchange explains the allometric scaling observed in this study, of which coelomic diverticula are an expression. This scaling pattern is not a spurious result of phylogenetic autocorrelation – for example, the concentration of all large featherstars in a single clade that happened to have a complex circulatory layout. Rather, positive allometry is observed within many clades, with large forms often bearing coelomic diverticula and small forms lacking them (Fig. 3). These diverticula take on disparate and clade-specific forms. In other words, featherstars achieve positive allometry in many different ways. Positive allometry is also observed independently in stalked crinoids, although stalked forms have less complex coelomic morphology than featherstars of equal size (Fig. 4; see below). Notably, a respiratory role for coelomic circulation in crinoids brings the group in line with the four other living classes of echinoderms, all of which are thought to incorporate coelomic circulation into their respiration in some way (Hyman, 1955; Farmanfarmaian, 1966; Schick, 1983; Brusca *et al.*, 2016). Crinoids also share a propensity to record their circulatory anatomy in detail as skeletal impressions with inarticulate brachiopods, blastoids, rhombiferans and stromatoporoids (Boardman *et al.*, 1987; LaBarbera & Boyajian, 1991).

Some species exhibit quite weak relationships between calyx volume and coelomic surface area, in part because the range of body sizes within a species is much less than the 500-fold range of body sizes in the whole dataset. Three non-mutually exclusive explanations could explain the poor fit within some species, and the somewhat wide spread around the regression line more generally. First, the morphological–functional system studied here may not

Table 2. Model selection results for the test for a difference in coelomic surface area between stalked crinoids and featherstars, indicating overwhelming support for a linear model in which stalk presence is included as a predictor (in bold)

Model	Ln(Likelihood)	ΔAIC	Akaike weight	m	b	a
$y = mx + b$	−11.238	22.542	1.27×10^{-5}	0.7396	0.2445	
$y = mx + aS + b$	**1.033**	**0**	**0.9999**	**0.843**	**0.189**	**−0.439**

Log likelihoods, ΔAIC scores, Akaike weights and parameter estimates are given. The response variable y is the natural log of coelomic surface area, and the predictor variable is the natural log of calyx volume. S is a Boolean variable indicating presence (1) or absence (0) of a stalk.

exhibit a high degree of symmorphosis, the condition characterized by a close fit between structural design and functional demand (Weibel *et al.*, 1991). In other words, the functional capacity of the crinoid circulatory system may greatly exceed the demands placed on it during the life of a typical individual. Alternatively, if the 3-D surfaces isolated for morphometry are noisy proxies for functional capacity, that noise could obscure a truly close relationship between metabolic demand and functional capacity. A third possibility is that metabolic demand might vary widely among individuals of the same species, such that an individual that was especially active, lived at relatively high temperatures, or that lived in stagnant or oxygen-poor water would need a more extensive circulatory apparatus than conspecifics of the same body size. This final option is especially interesting as it relates to phenotypic plasticity, and should be amenable to testing.

Two simple theoretical exercises can test and potentially refute a role for coelomic circulation in respiration. First, the total volume of oxygen delivered by internal circulation to the crinoid calyx (the body part isolated for much of this study's analyses) can be compared to the calyx's oxygen demands. If the respiring calyx requires much more oxygen than circulation delivers, internal circulation would have a negligible impact on respiratory biology. In fact, a generous estimate of oxygen consumption represents only 15% of the estimated total volume of oxygen delivered to the calyx by coelomic circulation (Supporting Information, Theoretical Exercises). This is probably an overestimate because some of the calyx is made up of non-respiring stereom. As a second test, one can ask whether the cost of driving coelomic circulation is much less than the amount of oxygen consumed by the entire animal. If not, the utility of coelomic circulation would be questionable. The power required to drive coelomic circulation with perfect efficiency through the coelomic vasculature of a typical featherstar (*Tropiometra carinata*) turns out to be about three orders of magnitude less than the lowest recorded metabolic rate of any featherstar. Even if coelomic circulation is very inefficient, its cost probably represents a small fraction of total metabolic rate.

A theoretical consideration of the diffusion of oxygen in the body indicates that the somatocoel is probably a respiratory organ, but coelomic circulation probably plays a role in nutrient transport, hormone transport and regeneration of autotomized body parts as well, not least because metazoan circulatory systems are typically 'for' more than one thing (Schmidt-Rhaesa, 2007). Circulation of coelomic fluid probably serves to transport nutrients throughout the body, especially in light of the discovery reported here that the digestive tract and axial sinus interface via highly branched outpocketings in at least some taxa (Fig. 2B). The somatocoel might also play a role in hormone transport: the axial gland, a feature of probable endocrine function (Holland, 1970), is situated axially within the somatocoel (Fig. 1C), and coelomic circulation would be an appropriate mechanism for distributing hormones throughout the body. Lastly, investigations into arm regeneration in crinoids reveal that growth of a developing arm bud recruits coelomocytes from the somatocoel in the arm (Candia Carnevali & Bonasoro, 2001; Kondo & Akasaka, 2010). This process is probably facilitated at least in part by coelomic circulation.

CT, microphotography and SEM have considerable power to reveal the morphology and variation of anatomical features but are limited in their resolution. In particular, experimental physiology and the fine structure of soft tissues are outside the scope of this study. Histological work on echinoderms is challenging because of their dense and extensive skeletons, and is doubly so when studying features that are closely associated with the skeleton. Nevertheless, decalcification methods have been successfully used to prepare echinoderm tissues for transmission electron microscopy (Dietrich & Fontaine, 1975). Likewise, the difficulties of crinoid husbandry are not insurmountable. Future histological and experimental physiological work on the crinoid circulatory system and its associated organs will facilitate important tests of the functional hypotheses explored in this paper.

FEATHERSTARS, ENERGETICS AND THE MMR

Morphometry of crinoid internal anatomy reveals that a greater surface area of the coelom is exposed to the calyx in featherstars than in stalked crinoids of the same calyx size. The distance over which oxygen diffuses in the calyx is lower in featherstars, and larger featherstars have morphological adaptations that keep this distance low. These findings imply that featherstars have generally higher metabolic rates than their stalked relatives. Such insight is interesting in light of the considerable differences in the life history and evolutionary histories of the two groups, and is worth pursuing experimentally. In particular, estimating metabolic rates for co-occurring assemblages of stalked crinoids and featherstars would circumvent issues that have dogged past attempts at interspecific comparison of metabolic rates (Baumiller & LaBarbera, 1989), although considerable difficulties are associated with estimating standard metabolic rate among deep-sea crinoids. More germane to the present investigation, the use of coelomic surface area as a rough proxy for metabolic rate should be scrutinized in

a laboratory setting. The extent of coelomic diverticula varies substantially within some featherstar species, hinting that this feature may be subject to adaptive phenotypic plasticity.

Importantly, this study does not examine metabolic rate directly. Comparative study of metabolism across Crinoidea has been frustrated by the difficulties of maintaining crinoids in captivity and the challenges of taking standardized and reliable measurements from stalked crinoids, all of which inhabit deep waters (Baumiller & LaBarbera, 1989). Nevertheless, approaches to measuring metabolic rate in deep-sea organisms have become far more sophisticated in recent years (McClain *et al.*, 2012). Seibel & Dranzen (2007) found that motility corresponds closely to metabolic rate among marine animals after taking body mass and temperature into account, suggesting that experimental physiological work on crinoids should support the metabolic hypothesis laid out here. An interesting corollary hypothesis is that variation in metabolic rates among different kinds of stalked crinoids should correspond to differences in life history as well. Specifically, isocrinids – motile stalked crinoids – can crawl away from urchin predators (Baumiller *et al.*, 2008) and might be expected to be energetically intermediate between featherstars and truly sessile crinoids.

Featherstars have long been considered emblematic of the mesozoic marine revolution (MMR) and the changes in the marine biota during this time. Like gastropods, bivalves, irregular echinoids (Vermeij, 1977) and coralline algae (Steneck, 1983), featherstars possess a suite of anti-predatory adaptations that are thought to have promoted their evolutionary and ecological success across the MMR. These include greater motility, toxic flesh and rapid regeneration (Meyer & Macurda, 1977; Slattery, 2010; Baumiller & Stevenson, 2018). Today featherstars are present throughout most of the world's oceans and are some of the most conspicuous and abundant organisms on many coral reefs, while their stalked relatives are relatively species-poor and restricted to the deep sea. In addition to shedding light on circulatory physiology, the present work illuminates the energetic aspects of the persistence of featherstars in shallow water: their suite of anti-predatory adaptations appears to have been facilitated in part by enhanced respiratory capabilities, and potentially by greater metabolic rates.

ACKNOWLEDGEMENTS

REFERENCES

Amemiya S, **Oji T. 1992.** Regeneration in sea lilies. *Nature* **357:** 546–547.

Appeltans W, **Ahyong ST**, **Anderson G**, **Angel MV**, **Artois T**, **Bailly N**, **Bamber R**, **Barber A**, **Bartsch I**, **Berta A**, **Błazewicz-Paszkowycz M**, **Bock P**, **Boxshall G**, **Boyko CB**, **Brandão SN**, **Bray RA**, **Bruce NL**, **Cairns SD**, **Chan TY**, **Cheng L**, **Collins AG**, **Cribb T**, **Curini-Galletti M**, **Dahdouh-Guebas F**, **Davie PJF**, **Dawson MN**, **De Clerck O**, **Decock W**, **De Grave S**, **De Voogd NJ**, **Domning DP**, **Emig CC**, **Erséus C**, **Eschmeyer W**, **Fauchald K**, **Fautin DG**, **Feist SW**, **Fransen CHJM**, **Furuya H**, **Garcia-Alvarez O**, **Gerken S**, **Gibson D**, **Gittenberger A**, **Gofas S**, **Gómez-Daglio L**, **Gordon DP**, **Guiry MD**, **Hernandez F**, **Hoeksema BW**, **Hopcroft RR**, **Jaume D**, **Kirk P**, **Koedam N**, **Koenemann S**, **Kolb JB**, **Kristensen RM**, **Kroh A**, **Lambert G**, **Lazarus DB**, **Lemaitre R**, **Longshaw M**, **Lowry J**, **MacPherson E**, **Madin LP**, **Mah C**, **Mapstone G**, **McLaughlin PA**, **Mees J**, **Meland K**, **Messing CG**, **Mills CE**, **Molodtsova TN**, **Mooi R**, **Neuhaus B**, **Ng PKL**, **Nielsen C**, **Norenburg J**, **Opresko DM**, **Osawa M**, **Paulay G**, **Perrin W**, **Pilger JF**, **Poore GCB**, **Pugh P**, **Read GB**, **Reimer JD**, **Rius M**, **Rocha RM**, **Saiz-Salinas JI**, **Scarabino V**, **Schierwater B**, **Schmidt-Rhaesa A**, **Schnabel KE**, **Schotte M**, **Schuchert P**, **Schwabe E**, **Segers H**, **Self-Sullivan C**, **Shenkar N**, **Siegel V**, **Sterrer W**, **Stöhr S**, **Swalla B**, **Tasker ML**, **Thuesen EV**, **Timm T**, **Todaro MA**, **Turon X**, **Tyler S**, **Uetz P**, **Van Der Land J**, **Vanhoorne B**, **Van Ofwegen LP**, **Van Soest RWM**, **Vanaverbeke J**, **Walker-Smith G**, **Walter TC**, **Warren A**, **Williams GC**, **Wilson SP**, **Costello MJ. 2012.** The magnitude of global marine species diversity. *Current Biology* **22:** 2189–2202.

Aschauer B, **Heinzeller T**, **Weinert P. 2010.** Almost within grasp: crinoid organs rendered 3-dimensionally. In: Harris LG, Böttger SA, Walker CW & Lesser MP, eds. Echinoderms: Durham. Proceedings of the 12th International Echinoderm Conference, Durham, New Hampshire, USA, 7–11 August 2006. Leiden/London/New York/Philadelphia/Singapore: A.A. Balkema Publishers, 9–14.

Balser EJ, **Ruppert EE. 1993.** Ultrastructure of axial vascular and coelomic organs in comasterid featherstars (Echinodermata: Crinoidea). *Acta Zoologica* **74:** 87–101.

Baumiller TK, **LaBarbera M. 1989.** Metabolic rates of Caribbean crinoids (Echinodermata), with special reference to deep-water stalked and stalkless taxa. *Comparative Biochemistry and Physiology -- Part A: Physiology* **93:** 391–394.

Baumiller TK, **Messing CG. 2007.** Stalked crinoid locomotion, and its ecological and evolutionary implications. *Palaeontologia Electronica* **10:** 1–10.

Baumiller TK, **Mooi R**, **Messing CG. 2008.** Urchins in the meadow: paleobiological and evolutionary implications of cidaroid predation on crinoids. *Paleobiology* **34:** 22–34.

Baumiller TK, **Salamon MA**, **Gorzelak P**, **Mooi R**, **Messing CG**, **Gahn FJ. 2010.** Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution. *Proceedings of the National Academy of Sciences of the United States of America* **107:** 5893–5896.

Baumiller TK, **Stevenson A. 2018.** Reconstructing predation intensity on crinoids using longitudinal and cross-sectional approaches. *Swiss Journal of Palaeontology* **137:** 189–196.

Boardman RS, **Cheetham AH**, **Rowell AJ. 1987.** *Fossil invertebrates*. Cambridge: Blackwell Science.

Bobrovskaya NV, **Dolmatov IY. 2014.** Autotomy of the visceral mass in the feather star *Himerometra robustipinna* (Crinoidea, Comatulida). *Biological Bulletin* **226:** 81–91.

Boolootian RA, **Giese AC. 1959.** Clotting of echinoderm coelomic fluid. *Journal of Experimental Zoology* **140:** 207–229.

Bottjer DJ, **Jablonski D. 1988.** Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *Palaios* **3:** 540–560.

Brusca RC, **Moore W**, **Schuster SM. 2016.** *Invertebrates, 3rd edn*. Sunderland: Sinauer.

Bush AM, **Hunt G**, **Bambach RK. 2016.** Sex and the shifting biodiversity dynamics of marine animals in deep time. *Proceedings of the National Academy of Sciences USA* **113:** 201610726.

Candia Carnevali MD, **Bonasoro F. 2001.** Microscopic overview of crinoid regeneration. *Microscopy Research and Technique* **55:** 403–426.

Clark AH. 1915a. A monograph of the existing crinoids. Volume 1 - the comatulids. Part 4a - superfamily Mariametrida (except the family Colobometridae). *Bulletin (United States National Museum)* **82**.

Clark AH. 1915b. A monograph of the existing crinoids. Volume 1 - the comatulids. Part 1. *Bulletin (United States National Museum)* **82**.

Cohen BL, **Pisera A. 2017.** Crinoid phylogeny: New interpretation of the main Permo-Triassic divergence, comparisons with echinoids and brachiopods, and EvoDevo interpretations of major morphological variations. *Biological Journal of the Linnean Society* **120:** 38–53.

Dietrich HF, **Fontaine AR. 1975.** A decalcification method for ultrastructure of echinoderm tissues. *Stain Technology* **50:** 351–354.

Engle S. 2012. *Ultrastructure and development of the body cavities in* Antedon bifida *(Pennant, 1777) (Comatulida, Crinoida)*. Unpublished dissertation, Freie Universität Berlin.

Farmanfarmaian A. 1966. The respiratory physiology of echinoderms. In: Boolootian RA, ed. *Physiology of Echinodermata*. New York: Interscience Publishers, 245–265.

Finnegan S, **McClain CM**, **Kosnik MA**, **Payne JL. 2011.** Escargots through time: an energetic comparison of marine gastropod assemblages before and after the Mesozoic Marine Revolution. *Paleobiology* **37:** 252–269.

Gignac PM, **Kley NJ**, **Clarke JA**, **Colbert MW**, **Morhardt AC**, **Cerio D**, **Cost IN**, **Cox PG**, **Daza JD**, **Early CM**, **Echols MS**, **Henkelman RM**, **Herdina AN**, **Holliday CM**, **Li Z**, **Mahlow K**, **Merchant S**, **Müller J**, **Orsbon CP**, **Paluh DJ**, **Thies ML**, **Tsai HP**, **Witmer LM. 2016.** Diffusible iodine-based contrast-enhanced computed tomography (diceCT): an emerging tool for rapid, high-resolution, 3-D imaging of metazoan soft tissues. *Journal of Anatomy* **228:** 889–909.

Grimmer JC, **Holland ND. 1979.** Haemal and coelomic circulatory systems in the arms and pinnules of *Florometra serratissima* (Echinodermata: Crinoidea). *Zoomorphologie* **94:** 93–109.

Grimmer JC, **Holland ND. 1990.** The structure of a sessile, stalkless crinoid (*Holopus rangii*). *Acta Zoologica* **71:** 61–67.

Haldane JBS. 1926. On being the right size. *Harper's Magazine* **152:** 424–427.

Harvey EN. 1928. The oxygen consumption of luminous bacteria. *Journal of General Physiology* **11:** 469–475.

Heim NA, **Knope ML**, **Schaal EK**, **Wang SC**, **Payne JL. 2015.** Cope's rule in the evolution of marine animals. *Science* **347:** 867–871.

Heinzeller T, **Welsch U. 1994.** Crinoidea. In: Harrison FW, Chia FS, eds. *Microscopic Anatomy of Invertebrates, Vol. 14: Echinodermata.* Hoboken: Wiley-Liss, 9–148.

Hemery LG, **Roux M**, **Ameziane N**, **Eleaume M. 2013.** High-resolution crinoid phyletic inter-relationships derived from molecular data. *Cahiers de Biologie Marine* **54:** 511–523.

Hess H, **Messing CG. 2011.** *Treatise on invertebrate paleontology, part T, Echinodermata 2, revised, Crinoidea volume 3*. Ausich WI, ed. Lawrence: The University of Kansas Paleontological Institute.

Holland ND. 1970. The fine structure of the axial organ of the feather star *Nemaster rubiginosa* (Echinodermata: Crinoidea). *Tissue and Cell* **2:** 625–636.

Hughes GM. 1972. Morphometrics of fish gills. *Respiration Physiology* **14:** 1–25.

Hyman LH. 1955. *The invertebrates. Vol. IV. Echinodermata*. New York: McGraw-Hill.

Janevski GA. 2011. *Causes and consequences of extinction and survival in fossil marine invertebrates with a special focus on the Crinoidea (Phylum Echinodermata)*. Unpublished dissertation, University of Michigan.

Janevski GA, **Baumiller TK. 2010.** Could a stalked crinoid swim? A biomechanical model and characteristics of swimming crinoids. *Palaios* **25:** 588–596.

Kalacheva NV, **Eliseikina MG**, **Frolova LT**, **Dolmatov IY. 2017.** Regeneration of the digestive system in the crinoid *Himerometra robustipinna* occurs by transdifferentiation of neurosecretory-like cells. *PLoS One* **12:** 1–28.

Kammer TW, **Sumrall CD**, **Zamora S**, **Ausich WI**, **Deline B. 2013**. Oral region homologies in paleozoic crinoids and other plesiomorphic pentaradial echinoderms. *PLoS One* **8:** e77989.

Knoll AH, **Follows MJ. 2016.** A bottom-up perspective on ecosystem change in Mesozoic oceans. *Proceedings of the Royal Society B: Biological Sciences* **283:** 20161755.

Kondo M, **Akasaka K. 2010.** Regeneration in crinoids. *Development Growth and Differentiation* **52:** 57–68.

Krogh A. 1941. *The comparative physiology of respiratory mechanisms.* Philadelphia: University of Pennsylvania Press.

LaBarbera M. 1986. The evolution and ecology of body size. In: Raup DM, Jablonski D, eds. *Patterns and processes in the history of life: report of the Dahlem Workshop on Patterns and Processes in the History of Life, Berlin 1985, June 16–21.* Berlin: Springer-Verlag, 69–98.

LaBarbera M. 1990. Principles of design of fluid transport systems in zoology. *Science* **249:** 992–1000.

LaBarbera M, **Boyajian GE. 1991.** The function of astrorhizae in stromatoporoids: quantitative tests. *Paleobiology* **17:** 121–132.

Legendre P. 2018. *lmodel2: Model II Regression. R package version 1.7–3.* Available at: https://cran.r-project.org/web/packages/lmodel2/.

Macurda DB, **Meyer DL. 1975.** The microstructure of the crinoid endoskeleton. *The University of Kansas Paleontological Contributions* **74**.

Mandelbrot BB. 1967. How long is the coast of Britain? Statistical self-similarity and fractional dimension. *Science* **156:** 636–638.

McClain CR, **Allen AP**, **Tittensor DP**, **Rex MA. 2012.** Energetics of life on the deep seafloor. *Proceedings of the National Academy of Sciences USA* **109:** 15366–15371.

Meyer DL, **LaHaye CA**, **Holland ND**, **Arneson AC**, **Strickler JR. 1984.** Time-lapse cinematography of feather stars (Echinodermata: Crinoidea) on the Great Barrier Reef, Australia: demonstrations of posture changes, locomotion, spawning and possible predation by fish. *Marine Biology* **78:** 179–184.

Meyer DL, **Macurda DB. 1977.** Adaptive radiation of the comatulid crinoids. *Paleobiology* **3:** 74–82.

Milsom CV, **Simms MJ**, **Gale AS. 1994.** Phylogeny and palaeobiology of *Marsupites* and *Uintacrinus*. *Palaeontology* **37:** 595–607.

Moore RC, **Teichert C. 1978.** *Treatise on invertebrate paleontology, part T: Echinodermata 2.* Boulder and Lawrence: The Geological Society of America, Inc. and The University of Kansas.

Mozzi D, **Dolmatov IY**, **Bonasoro F**, **Candia Carnevali MD. 2006.** Visceral regeneration in the crinoid *Antedon mediterranea*: basic mechanisms, tissues and cells involved in gut regrowth. *Central European Journal of Biology* **1:** 609–635.

Oji T. 1996. Is predation intensity reduced with increasing depth? Evidence from the West Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic Marine Revolution. *Paleobiology* **22:** 339–351.

Rasmussen HW. 1961. A monograph on the Cretaceous Crinoidea. *Biologiske Skrifter udgivet af Det Kongelige Danske Videnskabernes Selskab* **19:** 1–83.

Rouse GW, **Jermiin LS**, **Wilson NG**, **Eeckhaut I**, **Lanterbecq D**, **Oji T**, **Young CM**, **Browning T**, **Cisternas P**, **Helgen LE**, **Stuckey M**, **Messing CG. 2013.** Fixed, free, and fixed: the fickle phylogeny of extant Crinoidea (Echinodermata) and their Permian–Triassic origin. *Molecular Phylogenetics and Evolution* **66:** 161–181.

Roux M, **Pawson DL. 1999.** Two new Pacific Ocean species of hyocrinid crinoids (Echinodermata), with comments on presumed giant–dwarf gradients related to seamounts and abyssal plains. *Pacific Science* **53:** 289–298.

Ruppert EE, **Barnes RD**, **Fox RS. 2004.** *Invertebrate zoology: a functional evolutionary approach.* Belmont: Thompson Brooks/Cole.

Saulsbury J, **Zamora S. 2019.** Detailed nervous and circulatory anatomy in a Cretaceous crinoid: preservation, paleobiology, and evolutionary implications. *Palaeontology* (in press).

Schick JM. 1983. Respiratory gas exchange in echinoderms. In: Jangoux M, Lawrence JM, eds. *Echinoderm studies.* Rotterdam: A.A. Balkema, 67–109.

Schmidt-Rhaesa A. 2007. *The evolution of organ systems.* Oxford: Oxford University Press.

Seibel BA, **Drazen JC. 2007.** The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. *Philosophical Transactions of the Royal Society B: Biological Sciences* **362:** 2061–2078.

Slattery M. 2010. Bioactive compounds from echinoderms: ecological and evolutionary perspectives. In: Harris LG, Boetger SA, Walker CW, Lesser MP, eds. *Echinoderms: Durham - Proceedings of the 12th International Echinoderm Conference*. London: Taylor & Francis Group, 591–600.

Steneck RS. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* **9:** 44–61.

Taylor KH. 2015. *A phylogenetic revision of superfamily Himerometroidea (Echinodermata: Crinoidea).* Unpublished dissertation, Nova Southeastern University.

Vermeij GJ. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* **3:** 245–258.

Weibel ER, **Taylor CR**, **Hoppeler H. 1991.** The concept of symmorphosis: a testable hypothesis of structure–function relationship. *Proceedings of the National Academy of Sciences USA* **88:** 10357–10361.

Whittle RJ, **Hunter AW**, **Cantrill DJ**, **McNamara KJ. 2018.** Globally discordant Isocrinida (Crinoidea) migration confirms asynchronous Marine Mesozoic Revolution. *Communications Biology* **1:** 46.

Zamora S, **Aurell M**, **Veitch M**, **Saulsbury J**, **López-horgue MA**, **Ferratges FA**, **Arz JA**, **Baumiller TK. 2018.** Environmental distribution of post-Palaeozoic crinoids from the Iberian and south-Pyrenean basins, NE Spain. *Acta Palaeontologica Polonica* **63:** 779–794.

Ziegler A. 2012. Broad application of non-invasive imaging techniques to echinoids and other echinoderm taxa. *Zoosymposia* **7:** 53–70.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Pearson correlation between calyx volume and file size of 3D models of coelomic anatomy. When the data are subset to include only moderate to large-sized crinoids (calyx volume > 20 mm^3), no positive correlation is observed.
Table S2. Specimens shown in main text Figure 2.
Table S3. Morphometric data.
Fig. S1. Size (kB) of coelomic anatomy 3-D models, plotted against calyx volume for the same specimens. This is visualized to test whether larger featherstars have higher-quality 3-D models of coelomic anatomy, which might spuriously generate the appearance of positive allometry in the quantitative analysis. No significant positive relationship between calyx volume and file size of coelomic morphology is observed among crinoids above a 20-mm^3 size cutoff (grey vertical line) (Table S1). Positive allometry is still observed when the data are subset in this way. Blue data points are stalked crinoids; orange data points are featherstars.
Theoretical Exercises. More detailed quantitative exploration of crinoid circulatory physiology.
3D models. Shapefiles used in quantitative morphometrical analysis plotted in Fig. 4.