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PART T, REVISED, VOLUME 1, CHAPTER 16
FEEDING AND ARM POSTURES IN LIVING AND FOSSIL CRINOIDS

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INTRODUCTION

Arms are the most striking aspect of living and fossil crinoids. They support the structures involved in gas exchange, reproduction, and both the capture and transfer of food particles to the mouth. Their structure and the way a crinoid arrays them for feeding—that is, its posture—are critical to a crinoid's growth and survival. Breimer (1978) and Ubaghs (1978) offer detailed reviews of the structure and diversity of living and fossil crinoid arms, respectively.

From the first observations of living crinoids in aquaria (e.g., W. B. Carpenter, 1866; Chadwick, 1907; Gislén, 1924) to *in situ* observations (e.g., Magnus, 1963, 1964, 1967; Meyer, 1973a, 1979; Fishelson, 1974; Macurda & Meyer, 1974), the positioning of the arms to form a suspension-feeding array, often called a filtration fan, has been a focus with broad implications for the ecology, paleoecology, and taphonomy of these echinoderms (Byrne & Fontaine, 1981; Messing, 1985; Fujita, Ohta, & Oji, 1987; Messing, Neumann, & Lang, 1990; Baumiller, 1997; Baumiller & Rome, 1998; Kitazawa, Oji, & Sunamura, 2007). The filtration array consists of five or more (up to ~200) arms that radiate from the central calyx and may reach ~50 cm in length (>1 m in fossil *Uintacrinus socialis* Grinnell, 1876). In the great majority of crinoids, including all extant species, each arm is lined by unbranched, shorter pinnules (length <0.5 to ~4 cm), which together give each arm a narrow feather-like appearance. Both arm and pinnule ambulacral grooves are lined on either side by minute tube feet, or podia (typically <1 mm long).

AEROSOL SUSPENSION FEEDING

The functional morphology of the crinoid filtration fan can be understood following the principles of aerosol suspension feeding (Rubenstein & Koehl, 1977). Two different physical forces—inertia and viscosity—govern flow through the filtration array, and a Reynolds number (Re) represents the ratio of these two forces. If inertia dominates, giving a high Re, flow through the array is turbulent; if viscosity dominates, giving a low Re, flow is laminar. Because each filtration array component spans a different size range (i.e., arms much larger than pinnules, which are much larger than tube feet), each has a different Re number at a given flow velocity. Consequently, for current conditions that crinoids typically encounter, the filtration array or even individual arms may experience turbulent flow, whereas at the tube feet, where particles are captured, flow is invariably laminar. (Note, however, that each component could experience a given Re value under different flow conditions.) Most critical is the behavior of flow between the pinnules and through the fine-scale array

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of primary tube feet, which occurs at low Re and is governed by viscous forces and laminar fluid motion (Vogel, 1994).

Unlike a sieve, the mechanisms of aerosol filtration depend on the adhesiveness of the filtering elements—in this case, the longer tube feet (LaBarbera, 1984). All observations indicate that crinoids feed via direct particle interception, which reflects the operation of their feeding apparatus as an adhesive fiber filter, as opposed to other mechanisms such as gravitational or diffusive deposition, inertial impaction, or simple sieving. The latter would retain all particles larger than the mesh size while allowing all those smaller to pass through (Rubenstein & Koehl, 1977). Unlike a sieve, crinoids can capture particles smaller than the spaces between tube feet (Holland, Strickler, & Leonard, 1986).

Aerosol suspension feeding theory has been widely applied to both living and fossil crinoids and explains a great deal of crinoid behavior and feeding biomechanics, including variations in posture, spacing and length of arms, pinnules and primary podia, and variations in habitat, all relative to current flow (Meyer, 1979, 1982a, 1982b; Ausich, 1980; Liddell, 1982; Kammer, 1985; Kammer & Ausich, 1987; Leonard, Strickler, & Holland, 1988; Leonard, 1989). In particular, the theory predicts that different filter arrays will function optimally under different flow regimes (Baumiller, 1997; Holterhoff, 1997).

As demonstrated conclusively by Meyer (1973a, 1979), Macurda and Meyer (1974), and others, crinoids are leeward passive suspension feeders. They do not create their own currents for feeding but rely exclusively on external currents for particle capture. However, they are active participants to the extent that they modify arm and pinnule postures to take best advantage of prevailing and changing flow velocities and patterns (Meyer, 1982a; Meyer & others, 1984; Baumiller, 1997; Messing, 1997). In addition, mobile taxa seek preferred locations. Computational and experimental fluid dynamics studies (Baumiller, LaBarbera, & Woodley, 1991; Dynowski & others, 2016) further confirm that crinoids are passive, aerosol suspension feeders (although, note alternative proposals for specialized morphologies: Jefferies, 1989; Grimmer & Holland, 1990; Heinzeller & Fetcher, 1995; Wisshak & others, 2009).

LIGAMENTS AND MUSCLES

Crinoids assume and maintain their various feeding postures through the combined action of muscles and ligaments (although muscles between skeletal ossicles associated with appendage flexibility and movement apparently arose in crinoids only during the Devonian and remained absent in several fossil clades [Ausich & Baumiller, 1993]). As in other echinoderms, crinoid ligaments include unique catch-connective or mutable collagenous (or connective) tissue (MCT) capable of rapid and reversible changes in mechanical properties (between flaccid and stiff) under neuronal control (e.g., Wilkie, 1983, 1984, 2005; Motokawa, 1984, 1985, 1988; Wilkie & Emson, 1988; see also Ribeiro & others, 2011). In the arms and pinnules, contraction of muscles on the ambulacral side of the fulcral ridge of an articular facet, coupled with the flaccid state of the large ligament on the other (abambulacral) side of the ridge, curls or collapses the arms inward toward the mouth and flexes pinnules toward the arm axis. Contrary to earlier assumptions that, when the muscles relax, elasticity of the large ligament in the stiff state extends arms and pinnules outward (e.g., Grimmer & Holland, 1987; Birenheide & Motokawa, 1994), Motokawa, Shintani, and Birenheide (2004) discovered that the abambulacral ligament in the arms is capable of both active contraction and altered stiffness. Contractility of ligament tissue had previously been recognized in cirri, which do not contain muscles (Birenheide, Yokojama, & Motokawa, 2000). Once extended, stiffened ligaments allow arms and pinnules to maintain an extended posture passively against a current for food gathering.

The crinoid column lacks muscular tissue. Bending, either in association with feeding postures (e.g., parabolic posture, see p. 11–16) or in response to strong flow conditions, and rotation in response to changing flow direction, has previously been attributed to a passive response to the resistance generated by the crown (BAUMILLER, LABARBERA, & WOODLEY, 1991). However, the discovery of ligament contractility suggests that some of this movement may be active and is in keeping with the observation that at least some living stalked crinoids can actively bend the stalk (M. VEITCH & T. K. BAUMILLER, unpublished observations of *Democrinus* PERRIER, 1883). In any case, observations so far indicate that movements derived from ligamentary contractions are much slower than those associated with muscular contractions. Also, GORZELAK, GŁUCHOWSKI, & SALAMON (2014) found that some columnals in the coiled stem of *Ammonicrinus sulcatus* KONGIEL, 1958 (Devonian flexible), exhibit stereomic microstructure resembling that in crinoid muscular arm articular facets.

TUBE FEET (OR PODIA)

In all living crinoids, the tube feet occur in triads, each consisting of a longer primary, shorter secondary, and a yet shorter tertiary tube foot (NICHOLS, 1960). The primary tube feet orient perpendicular to the flow and form the filter. Mean lengths vary with species and range from approximately 0.4 to 0.9 mm in those feather stars examined (BYRNE & FONTAINE, 1981; LAHAYE & JANGOUX, 1985; MEYER, 1979) to at least ~2.0 mm in deep-sea stalked Hyocrinidae (C. G. MESSING, unpublished observation). Spacing of primary tube feet along a pinnule also varies among species, e.g., ~4 mm^{-1} in *Antedon bifida* PENNANT, 1777 (LAHAYE & JANGOUX, 1985), 4.5–9.5 mm^{-1} in reef-dwelling feather stars (MEYER, 1979), and ~2 mm^{-1} in a small hyocrinid (C. G. MESSING, unpublished observation). In addition, a significant relationship exists between primary tube foot length and spacing, although not uniformly across all crinoids. MEYER (1979) found that, for reef-dwelling feather stars, longer tube feet are more widely spaced and characteristic of semicryptic species, whereas species that perch in the open have shorter more crowded tube feet. By contrast, Hyocrinidae that feed well above the substratum also have long, widely spaced tube feet (C. G. MESSING, unpublished observation).

FOOD CAPTURE

In those species so far examined, all three tube foot types bear papillae that enclose two types of secretory cells responsible for releasing mucus (MCKENZIE, 1992), which holds the suspended particles that strike the primary tube feet. Smaller hillocks, so far observed only in *Antedon bifida*, are restricted to the ambulacrum-facing surface of the tertiary podia and surfaces between podia and contain two other kinds of secretory cells, which also occur in the ambulacral groove (FLAMMANG & JANGOUX, 1992). These hillocks may occur in other species as well, based on their apparent function: unlike the adhesive secretions of both types of papillae cells, the hillock cells appear to represent a duo-gland system, with one cell type secreting an adhesive that contributes to the bolus of particles and the other releasing a de-adhesive that prevents particles from sticking to the groove (FLAMMANG & JANGOUX, 1992).

NICHOLS (1960), MAGNUS (1963), RUTMAN and FISHELSON (1969), and BYRNE and FONTAINE (1981) all reported mucous filaments extending from podia in the feather stars *Antedon bifida*, *Heterometra savignii* (MÜLLER, 1841), *Lamprometra klunzingeri* (HARTLAUB, 1890) (=*Dichrometra palmata* [MÜLLER, 1841]), and *Florometra serratissima* (A. H. Clark, 1907a), respectively, although it remains unclear whether this is widespread among crinoids or not. Possible functions include fishing filaments to enhance capture or an irritation response to help them discard unwanted items (M. BYRNE, personal communication). HOLLAND, STRICKLER, and

Leonard (1986) found no evidence of such strands in the feather star *Oligometra serripinna* (P. H. Carpenter, 1881). Similarly, it is not yet known whether mucus is released when a particle strikes a tube foot or if it is secreted to partially or completely cover extended tube feet in advance of particle impact (Holland, Strickler, & Leonard, 1986).

Transfer of particles to the food groove has been reported to differ with species and particle size. However, most of the following observations were made more than three decades ago in aquaria rather than *in situ* and at a time when available imaging technology made the detailed movements of such small structures as tube feet much more difficult to visualize (M. Byrne, personal communication). As examples, in *Florometra serratissima*, after contact with a suspended food particle, the longest tube foot bends rapidly toward the ambulacral groove; the shorter secondary tube foot also bends rapidly and, together with the adjacent lappet that borders the groove, they wipe or scrape the particle into the groove. When all three members of a triad have curled into the groove, they appear to wipe along each other; the shortest tube foot wipes particles and mucus from the bases of the other two and compacts them into a bolus. In addition, the tertiary tube feet intercept and propel boluses along the groove toward the arm (Byrne & Fontaine, 1981, 1983).

In *Antedon bifida*, either a primary or secondary tube foot can capture a large particle by folding over it and transferring it to the groove either by wiping it off against a rake-like tertiary tube foot or by brushing it directly against the cilia in the groove. Smaller particles may accumulate on a tube foot before being wiped off. In this species, unlike *F. serratissima*, the tertiary podia paddle rapidly against the ciliary current in the groove to comb out the cilia; this stops and rotates the food particles, and embeds more mucus in the bolus (Lahaye & Jangoux, 1985). By contrast to both of these species, Holland, Strickler, and Leonard (1986, p. 114) reported that, in *Oligometra serripinna*, the primary podia perform all "conspicuous small-scale feeding acts" unassisted by secondary podia. They also noted that capture by the intercepting tube foot of particles larger than 20–30 µm may be accompanied by gentler, slightly delayed bending of up to a dozen adjacent podia, and that captured non-nutritive particles are quickly ejected from the pinnule food grooves. Leonard, Strickler, and Holland (1988) reported that, in this species, particles were captured by coordinated bending of about 15 podia (multiple or coordinated flicks; see also Holland, Strickler, & Leonard, 1986) at all flow velocities tested (0.9–13.3 cm s^{-1}). In the unusual, five-armed, deep-sea feather star *Atopocrinus* cf. *sibogae* A. H. Clark, 1912a, Messing (2020) noted that, under near-bottom flow strong enough to force the very long primary podia into both smooth and irregular downcurrent undulations, the secondary podia (less than half the length of the primaries) on at least some pinnules extended in a straight row characteristic of direct particle interception. Such differences likely derive at least in part from differences among the species in both tube foot lengths and relative proportions of members of a triad, and flow conditions.

Under natural conditions, when subjected to slow, unidirectional, quasi-laminar flow, crinoids array their arms so that the current strikes the abambulacral side of the arms and pinnules, causing flow to wrap around them and pass through the fine-scale filter created by the closely spaced primary tube feet. Observations of fluorescent dye passing through the tube-foot filter of crinoids in a flow tank do not reveal any micro-eddying along the downcurrent side of the filter (along the food groove itself), but flow velocity slows, presumably due to viscous forces acting in the low Re number microregion of the tube feet (Meyer, 1973a). However, Colman and others (1984) found that a dye stream passing through a feather star's (*Anneissia bennetti* [Müller, 1841]) multilayered fan *in situ* disintegrates into many dye parcels spread across a much wider area than the upcurrent stream, indicating a downstream increase in turbulence, which reflected an effective diffusion coefficient an order of magnitude greater than ambient. Arms on the downcurrent side lie in the turbulent wake generated by the upcurrent arms, presumably permitting increased opportunities for food particle capture. In addition, aquarium observations of stalked *Metacrinus rotundus* P. H. Carpenter, 1885 indicate that both flow around arms and minute postural movements of arms and pinnules generate turbulence that enhances particle capture and increases when nutrients are supplied (Oji & Kitazawa, unpublished observations). Observations *in situ* of stalked crinoids (*Neocrinus decorus* [Thomson, 1864] and *Endoxocrinus parrae parrae* [Gervais, 1835]), exhibiting parabolic postures (see p. 11–16) indicate abrupt but brief slowing of dye streams on the downcurrent side (Baumiller & Messing, unpublished observations). Holland, Leonard, and Strickler (1987) noted that downcurrent-oriented ambulacra captured twice as many particles as those pointed up current in *Oligometra serripinna* during surge conditions. Thus, the advantage for the downcurrent orientation of the ambulacral groove, apparently a universal behavior among crinoids, increases particle capture and retention, as well as maintenance of the mucus-and-food-particle bolus as it moves along the open food groove.

CRINOID DIETS

Information on crinoid diets derives from analyses of gut contents and fecal material. Ingested particles are generally limited to those narrower than or equal to the width of the food groove, which places a food particle size constraint on different filtration morphologies (Meyer, 1979; Ausich, 1980), although several studies have recorded particles in gut contents larger than groove widths (Rutman & Fishelson, 1969; La Touche & West, 1980; Meyer, 1982b). Particle size spectra vary among species, with the great majority of particles commonly between ~20 and 150–200 µm in length and <100 µm in width (Meyer, 1982b; Liddell, 1982; Featherstone, Messing, & McClintock, 1998) and smaller in smaller species (e.g., <100 µm in length in *Antedon bifida*) (La Touche & West, 1980). However, Liddell (1982) recorded ~33 percent of gut content particles as 225–490 µm long in *Davidaster rubiginosus* (Pourtalès, 1869); Rutman and Fishelson (1969) recorded 26 percent of particles >200 µm in length for *Dichrometra palmata*, and Leonard (1989) fed *Antedon mediterranea* (Lamarck, 1816) coccolithophores ~11 µm across.

Identifiable dietary components vary among crinoid species based on variations in availability (seasonality, habitat, activity rhythms), density of the arm-and-pinnule filtration array and its elevation above the substratum, tube foot morphology and spacing, and ambulacral groove width (Rutman & Fishelson, 1969; Meyer 1979, 1982a 1982b; La Touche & West, 1980; Liddell, 1982; Featherstone, Messing, & McClintock 1998; Kitazawa, Oji, & Sunamura 2007), as well as on the larger scales of geography, depth, and environment. In addition, Meyer (1982b) recorded significant variability among fecal samples from different individuals of the same species collected during a single dive (see also Kitazawa, Oji, & Sunamura, 2007). Most studies have been based entirely on microscopy (e.g., Gislén, 1924, and references therein; Rutman & Fishelson, 1969; Meyer, 1982a, 1982b; La Touche & West, 1980; Featherstone, Messing, & McClintock, 1998), although Kitazawa, Oji, and Sunamura (2007) added fluorochrome-labeled oligonucleotide probes for microbial analysis and recognition of chlorophyll derivatives.

Dietary components include protists (e.g., diatoms, dinoflagellates and other unicellular algae, foraminiferans, radiolarians, tintinnid ciliates), invertebrate larvae (e.g., veligers), small crustaceans (copepods, ostracodes), ovoid fecal pellets, and detrital particles (see references in preceding paragraph), although some gut contents have included substantial non-nutritive particles (e.g., sediment grains, sponge spicules) (e.g., Gislén, 1924; Kitazawa, Oji, & Sunamura, 2007). On one hand, a combination of the latter and the capture and ingestion of non-nutritive carmine dye grains (La Touche & West, 1980) indicate that particle capture is non-selective and may not reflect digestibility. However, Holland, Strickler, and Leonard (1986) recorded substantial rejection from food grooves of non-nutritive beads following capture by tube feet in *Oligometra serripinna*, and Kitazawa & Oji (2010) found that gut contents of stalked *Metacrinus rotundus* contained a greater proportion of phytoplankton relative to non-nutritive beads than in the suspended available food, both of which point to some level of particle selectivity.

The actual energetic contributions of different dietary components remain unknown. Organisms lacking hard parts (e.g., ciliates, some microphytoplankton) may be digested or rendered unidentifiable in feces, although Holland, Strickler, and Leonard (1986) found that, in *Oligometra serripinna*, ingested particles accumulate by one hour after ingestion in the hind end of the intestine and rectum, where most digestion apparently takes place. Detritus may or may not contain significant nutritive value, e.g., from colonizing microorganisms (La Touche & West, 1980; Kitazawa, Oji, & Sunamura, 2007). Crustaceans may represent remains of living prey or low-value exuviae. West (1978) and Smith, Meyer, and Horner (1981) documented uptake of dissolved nutrients in crinoids, but their contribution to nutrition likewise remains unknown. Also, non-nutritive particles such as mineral grains and sponge spicules, as well as benthic diatom taxa (e.g., Gislén, 1924; Rutman & Fishelson, 1969; La Touche , 1978a; La Touche & West, 1980), indicate incorporation of resuspended material in diets of at least some crinoid species. Finally, Meyer (1982a) summarized suggestions that some chiefly fossil crinoids might be deposit feeders.

Examples of the variations in gut contents among species include *Dichrometra palmata:* 50%–87% foraminiferans, radiolarians, and ciliates (Rutman & Fishelson, 1969; Meyer, 1982b); *Anneissia bennetti* and *Pontiometra andersoni* (P. H. Carpenter, 1889): 54%–57% phytoplankton (diatoms and dinoflagellates); *Capillaster multiradiatus* (Linnaeus, 1758): 32% each, phytoplankton and sediment grains (Meyer, 1982b); *Antedon bifida*: 53%–85% chiefly fecal, resuspended detritus (La Touche, 1978a; La Touche & West, 1980); *Davidaster rubiginosus*, *D. discoideus* (P. H. Carpenter, 1888), *Comactinia echinoptera* (Müller, 1841), and *Analcidometra armata* (Pourtalès, 1869): 68%–75% diatoms (Liddell, 1982); and *Neocrinus decorus* and *Endoxocrinus parrae parrae:* 59%–69% detritus (46%–59% radiolarians exclusive of detritus) (Featherstone, Messing, & McClintock, 1998).

Tiering is a strategy that subdivides resources above the substratum (Lane, 1963, 1973; Ausich, 1980; Ausich & Bottjer, 1982). Food particles pass above the substratum in horizontal currents, so organisms at different heights above the substratum partition resources (Kitazawa, Oji, & Sunamura, 2007). Further, crinoid habitats range from relatively flat, featureless substrata to complex, three-dimensional surfaces formed by reefs and other types of buildups. Crinoids have adapted various suspension-feeding strategies to exploit resources under these widely differing conditions with contrasting arm and pinnule postures, filter densities, perching habits, and column heights. First and foremost, because the arms and pinnules together constitute the great majority of a crinoid's structure, the posture in which a crinoid arrays this apparatus is a major component of its feeding ecology. However, living crinoids also display non-feeding, trauma, and regeneration postures; and fossils with well-preserved arms display characteristic preservational postures, all of which are discussed in the sections to follow.

RHEOPHILIC AND REHOPHOBIC POSTURES VERSUS FLOW REGIME

Breimer (1969) and other authors (see Fell, 1966) distinguished two primary crinoid behaviors: rheophilic (current seeking) and rheophobic (current avoiding). Ausich (1977) argued that this dichotomy is at best misleading, because crinoids rely exclusively on external currents to bring food to their filtration arrays. A true rheophobic behavior, in which a crinoid is always in slack water, would dictate that feeding could only depend on a detrital rain of food particles, ciliary currents, and/or epidermal uptake of dissolved nutrients. Whereas this is theoretically possible, it is not clear if such a habit could provide sufficient nutrition for both growth and reproduction. Effectively, slack water would also severely reduce respiratory gas exchange by a crinoid.

Ausich (1977) used the terms high-energy and low-energy rheophilic, and Meyer (1979, 1982a) described crinoids as adapted to a generally more exposed habitat with uni- or bidirectional currents versus a weaker, more turbulent habitat with multidirectional currents that occur within the infrastructure of a reef. In both instances, because ambient currents bring food to the crinoid, rheophobic is a misnomer. Accordingly, filtration postures are best envisioned within the context of the current regime and the crinoid's means of anchoring to or elevating above the substratum. We suggest that current regime, i.e., high- versus low-velocity, and uni-, bi-, or multidirectional, be used as environmental parameters that influence a crinoid's filtration posture.

ARM POSTURES

Initial studies of crinoid behavior were made in aquaria with feather stars. In this slack-water setting, crinoids were idle, and their arms typically radiated outward more-or-less horizontally with the mouth and ambulacra oriented upward. This posture led to the interpretation that crinoids arranged their arms in a collecting-bowl posture in order to feed on a detrital rain of food (Nichols, 1960). As discussed on p. 26–27, this is a non-feeding, slack-water posture. *In situ* observations allowed a radically different interpretation of crinoid ecology. Pérès (1958, 1959) first documented living, deep-sea stalked crinoids *in situ*, and Magnus (1963, 1964, 1967) and Rutman and Fishelson (1969) were the first to use scuba diving to document the ecology of living feather stars. Meyer (1973a, 1973b, 1979, 1982a), Macurda and Meyer (1974), and others extended these initial studies to develop our current understanding of crinoid ecology (La Touche, 1978a, 1978b; Conan, Roux, & Sibuet, 1981; Roux, 1985a; Bradbury & others, 1987; Leonard, Strickler, & Holland, 1988; Messing & others, 1988, 2006; Messing, Neumann, & Lang, 1990; Vail, 1990; Messing & Llewellyn 1991; Baumiller, 1992, 2008; Roux, 1994; Baumiller & Ausich, 1996; Roux & Pawson, 1999; Messing, 2004; Baumiller & Messing, 2007; Kitazawa, Oji, & Sunamura, 2007; Baumiller, Mooi, & Messing, 2008; Bowden & others, 2011; Eléaume & others, 2011; Baumiller & Gahn, 2013; Syverson & others, 2015; Baumiller & Stevenson, 2018). These studies revealed that living crinoids assume arm postures dependent chiefly on morphology and current regime. Generally, each study independently described and distinguished filtration posture shapes, but no single encompassing classification of crinoid postures has been attempted. Here, we recognize four major categories of arm postures in living and fossil crinoids: 1) feeding, 2) non-feeding, 3) regeneration, and 4) preservational postures. Within each category, other than regeneration posture, specific postural types are described. With living crinoid arm postures understood, fossil crinoid postures can be interpreted with realistic models, as opposed to problematic reconstructions (see discussion by Donovan, 2011).

It is also worth noting that, although arm division patterns differ widely among crinoids, they commonly do not parallel feeding posture. As examples, the feather star *Pontiometra andersoni* has many arms divided near their bases, whereas the arms of stalked *Phrynocrinus* sp. branch nearly to arm tips, yet both assume a parabolic posture. Similarly, the feather star *Basilometra boschmai* A. H. Clark, 1936, with an arm branching pattern similar to that of *P. andersoni*, assumes a disk posture similar to that of deep-sea hyocrinids with five undivided arms. Oji and Okamoto (1994) proposed that an optimal pattern for reducing damage from predation would have divisions restricted to near the arm bases (a pattern characteristic of shallow-water feather stars). In contrast, in an optimal pattern for harvesting, a filtration array would have divisions extend to nearly half of each arm length with an arm density as constant as possible throughout the filtration array (characteristic of deep-water stalked crinoids).

FEEDING POSTURES

Arm postures described below represent various morphologies documented in living crinoids in their natural habitats, with a few extrapolated to similar fossil taxa and others suggested for distinctive fossil taxa. For each of these distinctive postures, we include terms previously used for each. A crinoid may exhibit more than one of these postures, either when it alters the arrangement and orientation of its arms with changing ambient flow conditions, or, as in many species, it increases arm number with growth (Meyer & others, 1984). Note that, although the widely used term filtration fan refers to all arrangements of a crinoid's arms and pinnules for feeding, we here restrict the use of the term fan to describe the posture in which arms assume a truly fan-shaped array and avoid overlapping terms such as parabolic fan or radial fan.

As noted above, crinoids are leeward suspension feeders—when capturing food, a pinnule's ambulacrum faces down current regardless of posture. In situations in which some grooves would face into the current either because of overall posture, morphology, or current direction, pinnules will swivel to maintain a downcurrent orientation of individual ambulacra (Meyer, 1982a). Baumiller and Meyer (2000) reported that pinnules on amputated arms could swivel passively when subjected to oscillating flow, suggesting that the swiveling is generated by the extended tube feet behaving like weathervanes in the moving fluid, perhaps supported by activity of MCT in the articulations between pinnulars. It is this MCT that permits all crinoids to maintain arm and pinnule arrays that resist the pressure of ambient flow (Birenheide & Motokawa 1996, 1998; Birenheide, Yokojama, & Motokawa, 2000; Motokawa, Osamu, & Birenheide, 2004; Baumiller, Mooi, & Messing, 2008).

Fan Posture

In this posture, assumed by feather stars that attach to the substratum, the arms project upward and to the sides to form a fanlike array spanning an arc of < 90 to ~200°. In a fan posture, pinnules of each arm are aligned in a roughly feather-like array, the fan orients normal to the current, and ambulacra face down current (Fig. 1.1). Arms on the downcurrent side of the calyx swivel near their bases so that their ambulacra also face down current (e.g., Magnus, 1967; Meyer, 1973a, 1982a) (Fig. 1.2). Although the pinnules and primary tube feet also array basically normal to current flow with ambulacra facing down current, both typically curve so that their tips face more or less into the current (e.g., Magnus, 1963, fig. 8; Byrne & Fontaine, 1981, fig. 2a, 5; Baumiller, 2008, fig. 7). Feather stars subjected to a basically laminar flow commonly assume a fan posture. In cases when the current reverses, e.g., tidally, arms swivel near their bases so that the ambulacra face down current (Meyer, 1979, 1982a). When the current reverses rapidly, e.g., at depths shallower than wave base, ambulacra will face both into and away from the flow (Messing, 1997).

The precise shape of the fan varies with the substratum to which the crinoid anchors, current velocity and pattern (i.e ., uni- versus

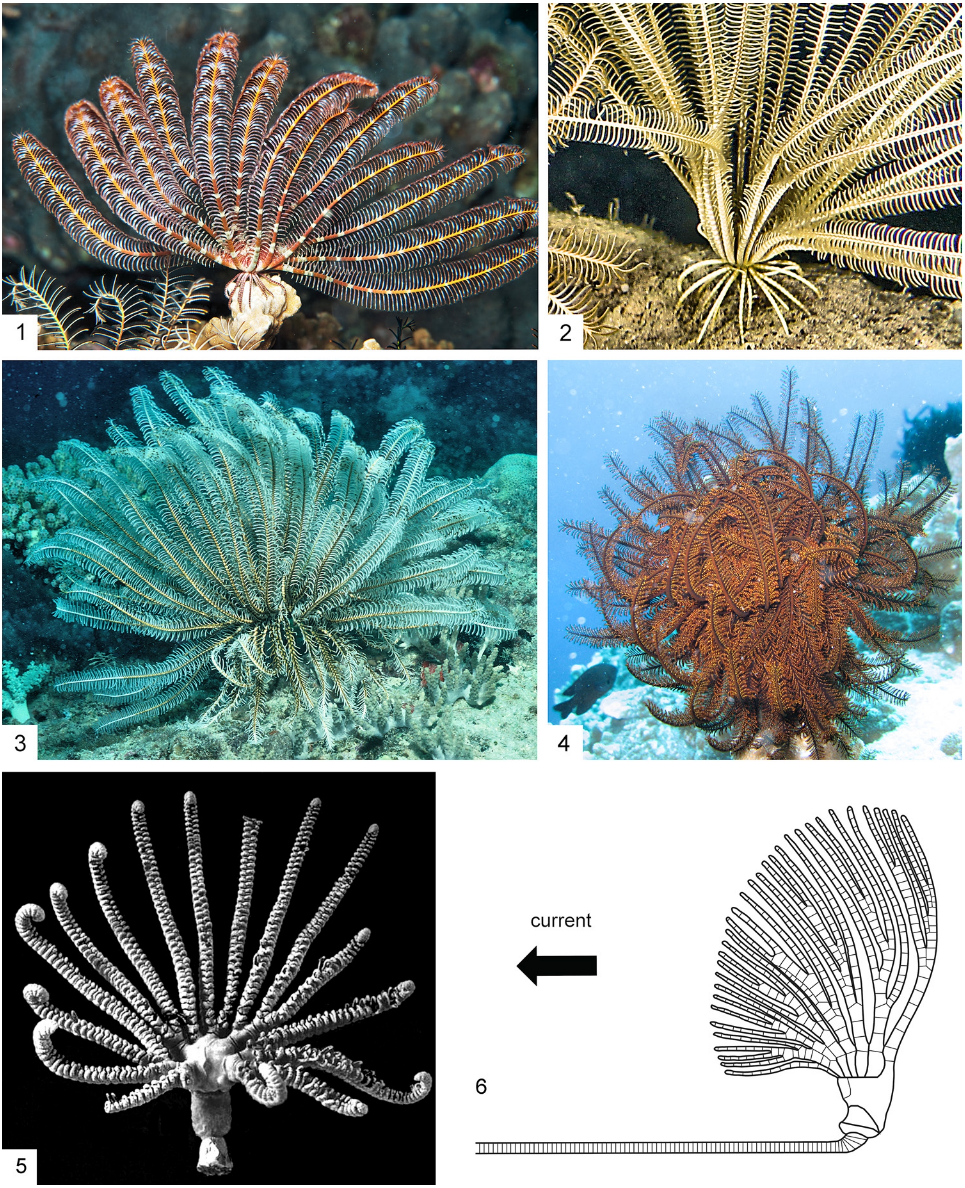

Fig. 1. Fan postures. *1,* single-layered fan, *Heterometra* A. H. Clark, 1909b (Himerometridae), direction of current into image; Liuqiu Island, Taiwan (photo, Jung Hsua/Shutterstock). *2,* Two-layered fan, *Crinometra brevipinna* (Pourtalès, 1868) (Charitometridae), direction of current toward viewer showing swiveling of arms (at center) on downcurrent side to orient ambulacra down current; note abrupt re-orientation of pinnules immediately distal to swiveling of arm; off Half Moon Bay, West End, Isla Roatán, Honduras, depth 305 m (new; photo, C. G. Messing & T. K. Baumiller, taken 2013). *3,* Multilayered fan, *Clarkcomanthus alternans* (P. H. Carpenter, 1881) (Comatulidae), upcurrent view (current flow into image); note concave posture of arms and pinnules; lower arms anchor and raise the calyx above the substratum; adults of this species lack cirri; Lizard Island, Great Barrier Reef, Australia, depth 14 m (new; photo, D. L. Meyer, taken 1976). *4,* Multilayered fan with dense downcurrent tangle of arms, *Clarkcomanthus alternans*, downcurrent view (current flow toward viewer); note arms forming fan posture at rear; north end of Kri Island, Raja Ampat, Indonesia, (new; photo, C. G. Messing, taken 2013). *5,* Fan/canted posture attributed to *Neogymnocrinus richeri* (Bourseau, Amézaine-Comindardi, & Roux, 1987) (Sclerocrinidae); specimen collected off New Caledonia (photo, N. Améziane, in Bourseau & others, 1991, pl. 8,*1a*). *6,* Fan posture attributed to Calceocrinidae (Paleozoic disparid), *arrow* indicates current direction from right (new; W. I. Ausich).

bidirectional), and number of arms. Feather stars with relatively few arms (fewer than ~20) array them in a monoplanar fan. Those with more arms array them into two or more planes to form a biplanar or multilayered fan, respectively, with arms on the leeward side of the calyx swiveled (Fig. 1.2). Those with large numbers of arms (~80 or more) form thick, bushy fans with arms forming a crowded irregular baffle (MESSING, 1994) (Fig. 1.3). Depending on flow conditions, the fan may widen into a multilayered funnel or bowl, a variation on the conical posture, and grade into a slack-water, non-feeding posture, both described in sections to follow. Upcurrent arms may form a multilayered fan or parabolic array with downcurrent arms forming a dense tangle or meridional array (MEYER & MACURDA, 1980; STEVENS, 1989) (Fig. 1.4). With a weakening current, multilayered fans become irregularly bushy with no orientation normal to flow, which also grade into slack-water postures (see also *Alternative and Unusual Postures,* p. 21–26).

In most many-armed, reef-dwelling Comatulidae (formerly Comasteridae) that assume a multilayered fan posture, successive pinnules are offset—by ~30° under high-velocity current conditions and up to 90° under quieter, deeper, or sheltered conditions—which intergrades with the multidirectional posture described on p. 19–20. Exceptions include *Nemaster grandis* A. H. CLARK, 1909a and *Anneissia bennetti,* in which pinnules maintain a typical feather-like array (MEYER, 1973a; MEYER & MACURDA, 1980). Semicryptic feather stars, which hide the calyx in a hole, crevice, sponge, or under a ledge, and extend arms for feeding, may assume this fan posture (e.g., *Alloeocomatella* MESSING, 1995, *Comactinia* A. H. CLARK, 1909a, *Tropiometra carinata* (LAMARCK, 1816) (MEYER, 1973a, fig. 5–3; MESSING, 1985, fig. 1), although it intergrades with the independent arm fan posture described on p. 18. In addition to arms forming the fan, Comatulidae with many arms (often more than 100) and with cirri reduced or absent (e.g., some species of *Clarkcomanthus* ROWE & others, 1986, *Comaster* AGASSIZ, 1836, and *Phanogenia* LOVÉN, 1866) splay many arms radially outward both to anchor and to raise the calyx above the substratum MEYER & MACURDA, 1980, fig. 4a, 6b) (Fig. 1.3–1.4).

Among stalked crinoids, the extant sclerocrinid *Neogymnocrinus richeri* (BOURSEAU, AMÉZIANE-COMINARDI, & ROUX, 1987) (Cyrtocrinida) has a strongly asymmetrical calyx with arms of four rays radiating outward in a single fanlike plane, and arms of one ray strongly reduced (BOURSEAU, AMÉZIANE-COMINARDI, & ROUX, 1987) (Fig. 1.5). (Note that a crinoid ray consists of the radial ossicle—part of the calyx—and the ossicles that arise from it; almost all crinoids, living and fossil, have five rays. An arm, which may be branched or unbranched, refers to the series of ossicles that arise from a radial ossicle.) This species displays a fan posture in life with mouth and ambulacra oriented down current. However, because the asymmetrical calyx tilts permanently sideways with the reduced arms closest to the substrate, the posture might best be considered a combination of the fan and canted posture, described on p. 21. Similarly, asymmetrical confamilials, such as *Hemicrinus* D' ORBIGNY, 1850 in 1850–1852, *Strambergocrinus* ŽÍTT, 1979 (Upper Jurassic to Lower Cretaceous), and other cyrtocrinids likely assumed similar postures (HESS, 2011).

The Calceocrinidae (Ordovician to Permian disparids) lived with the column recumbent along the seafloor (MOORE, 1962; BROWER, 1966; AUSICH, 1986). These crinoids positioned three or four arms vertically. Although they were stalked and their filtration array exhibited some curvature (Fig. 1.6), these crinoids should be regarded as having displayed a fan posture.

The basic form of this posture, with arms arrayed in a single plane, was first described and figured by MAGNUS (1963, fig. 6.9; 1964, fig. 4.6; 1967, fig. 8.9) and referred to as a filtration fan. Other terms have included planar semicircular fan (MACURDA & MEYER, 1983); slightly arched fan (PERÉS & PICARD, 1955); fan perpendicular to currents (Perés, 1959); flat filtration fan (Magnus, 1967); vertical filtration fan (Magnus, 1963; Breimer, 1969; Meyer, 1973a, fig. 5,*3*); vertical plane (Macurda & Meyer, 1974); arcuate fan (Meyer & Macurda, 1980; Meyer, 1979, 1982a; Messing, 1995, 1997); and biplanar fan (Kirkendale & Messing, 2003). The multilayered version was previously referred to as a vertical filtration fan (Meyer, 1973a, fig. 3,*2*) and multilayer filtration fan (Meyer & Macurda, 1980, fig. 4c). All are variations of the fan posture.

Disk Posture

Many feather stars that cling to narrow or finely branched perches (e.g., wire corals, sea fans, and some sponges) spread their arms like wheel spokes in a disk posture normal to unidirectional laminar flow, with ambulacra and the oral surface oriented down current (Meyer, 1973b, fig. 8; Macurda & Meyer, 1974, 1983; Fishelson, 1974, fig. 5) (Fig. 2.1, 2.4) and with pinnules often concave up current (Fig. 2.5). The arms are usually slightly concave up current as well, so this posture grades into the parabolic posture described below (Messing, 1994, 1997). The posture also exists among living stalked crinoids and has been attributed to some fossil forms, most commonly among species with five or ten arms (Fig. 2.2). A distinction between a conical and disk posture for a fossil crinoid may be difficult to determine. In *Pisocrinus* (Fig. 2.3), although the plane of the radial facet faced roughly distally, the range of movement at this articulation may have permitted the arms to approach a disk posture. However, this was even more probable in crinoids with the plane of the radial articular facets more-or-less parallel to the oral-aboral axis of the crinoid (e.g., *Alloprosallocrinus* Casseday & Lyon, 1862 or *Steganocrinus* Meek & Worthen, 1866).

Among variations, the colobometrid feather star, *Basilometra boschmai*, maintains a similar posture, but with its numerous (as many as 80) arms overlapping to form a dense, multilayered disk. Messing (1994, 1997) noted that some feather stars that cling to elevated perches (e.g., *Capillaster multiradiatus* [Linnaeus, 1758] and *Cenometra bella* [Hartlaub, 1890]) commonly interrupt this posture with several irregularly arrayed or curled arms, and that nocturnally active mariametrid feather stars sometimes spread their arms in this posture across coral perches and not oriented normal to flow. The latter has also been observed in a variety of deep-sea feather stars (e.g., Pentametrocrinidae, Antedonidae, Atelecrinidae) on both sediment and irregular rocky substrata (Tokeshi, 2002, fig. 3; van den Beld & others, 2017, fig. 2H) (Fig. 2.6). Here, it is unclear if the posture is restricted to slack-water conditions, because some close-up imagery shows primary tube feet fully extended and coplanar with pinnules and arms. The disk posture in these deep-sea species also intergrades with others, e.g., with the proximal arms alone forming a cone, with the arm tips raised to form a shallow bowl, or with a few upcurrent arms partly raised to form a partial fan posture (Fig. 2.7, also see Fig. 6.1). It also may appear as a transition between the parabolic and conical postures (described in the following two sections) as current velocity increases.

Meyer (1973b) first described this posture as a circular, planar filtration fan. It has also been called a radial fan (Meyer & Macurda, 1980; Meyer, 1979, 1982a), which has also been used for other postures as described herein. However, as the arms of all crinoids radiate from the central calyx, and radial is a general term for much of echinoderm morphology (and counterpart to interradial), we recommend not using the term radial to describe any crinoid posture.

Parabolic Posture

Most extant stalked crinoids subject to laminar near-bottom flow array their arms in an iconic parabolic posture, with the calyx tilted so that the oral surface faces down current and with arms radiating outward as in the disk posture but flexed back into the

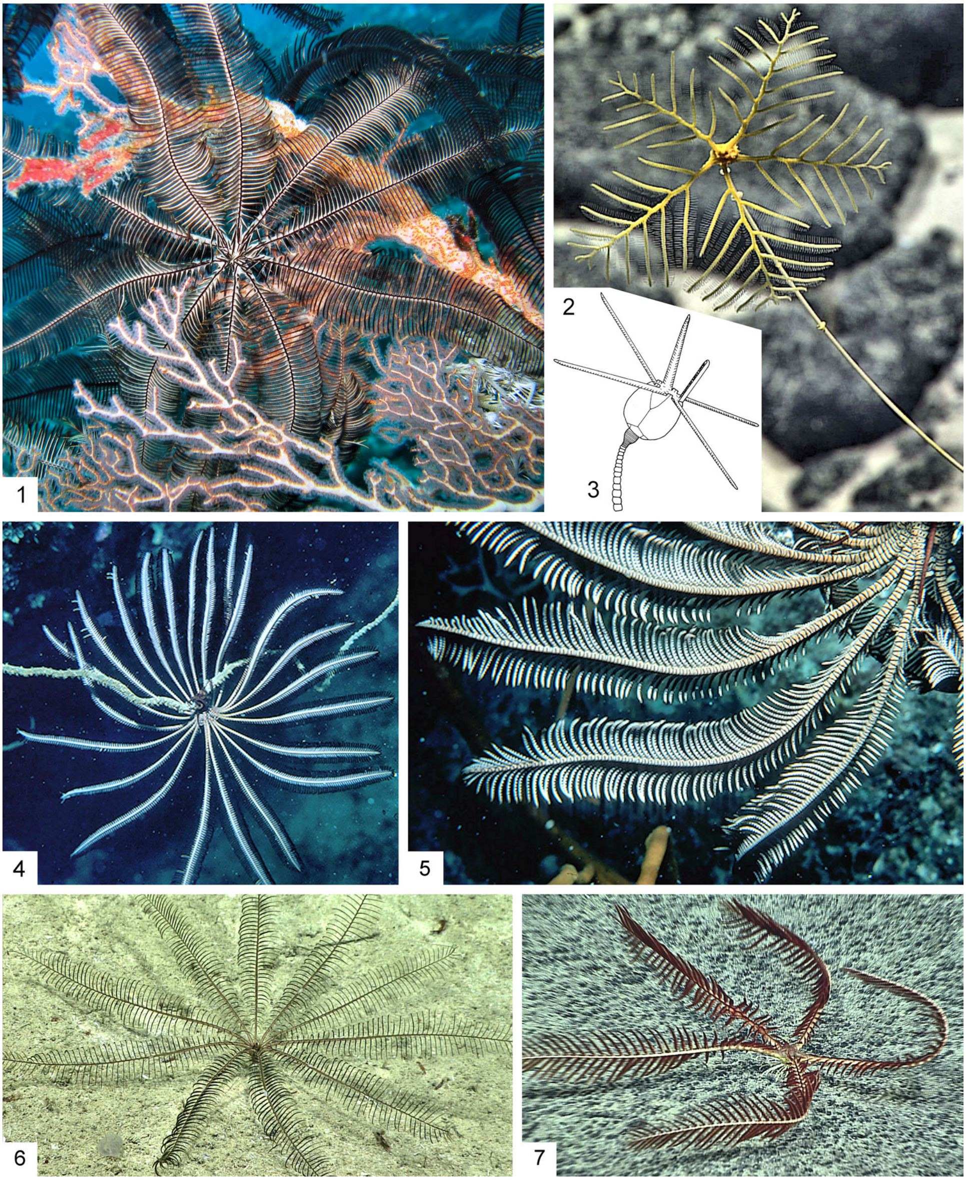

Fig. 2. Disk postures. *1, Colobometra perspinosa* (P. H. Carpenter, 1881) (Colobometridae), current direction toward viewer; north end of Kri Island, Raja Ampat, Indonesia (new; photo, C. G. Messing, taken 2013). *2,* Unidentified Hyocrinidae; R/V 'Okeanos Explorer' cruise EX1606, Alba Guyot between Wake Atoll and Guam, Pacific Remote Islands Marine National Monument (PRIMNM), depth 2,114 m (photo, National Oceanic and Atmospheric Administration [NOAA], taken 2016). *3, Pisocrinus* Koninck, 1858, diagrammatic illustration (Ausich, 1977, fig. 7b). *4–5, Cenometra bella* (Hartlaub, 1890) (Colobometridae), arm length ~14 cm; Lizard Island, Great Barrier Reef (new; photo, D. L. Meyer). *4,* Direction of current into image. *5,* Close-up showing pinnules concave upcurrent. *6,* ?*Paratelecrinus* Messing, 2013 (Atelecrinidae); R/V 'Okeanos Explorer' cruise EX1811, south of Isla Mona, Caribbean Sea, 1,138 m (photo, NOAA, taken 2018). *7, Pentametrocrinus* A. H. Clark, 1908a (Pentametrocrinidae), with two arms raised in a partial fan posture; R/V 'Okeanos Explorer' cruise EX1605 L3, near Molokai Fracture Zone, east of Hawaiian Islands, depth 1,609 m (photo, NOAA, taken 2016).

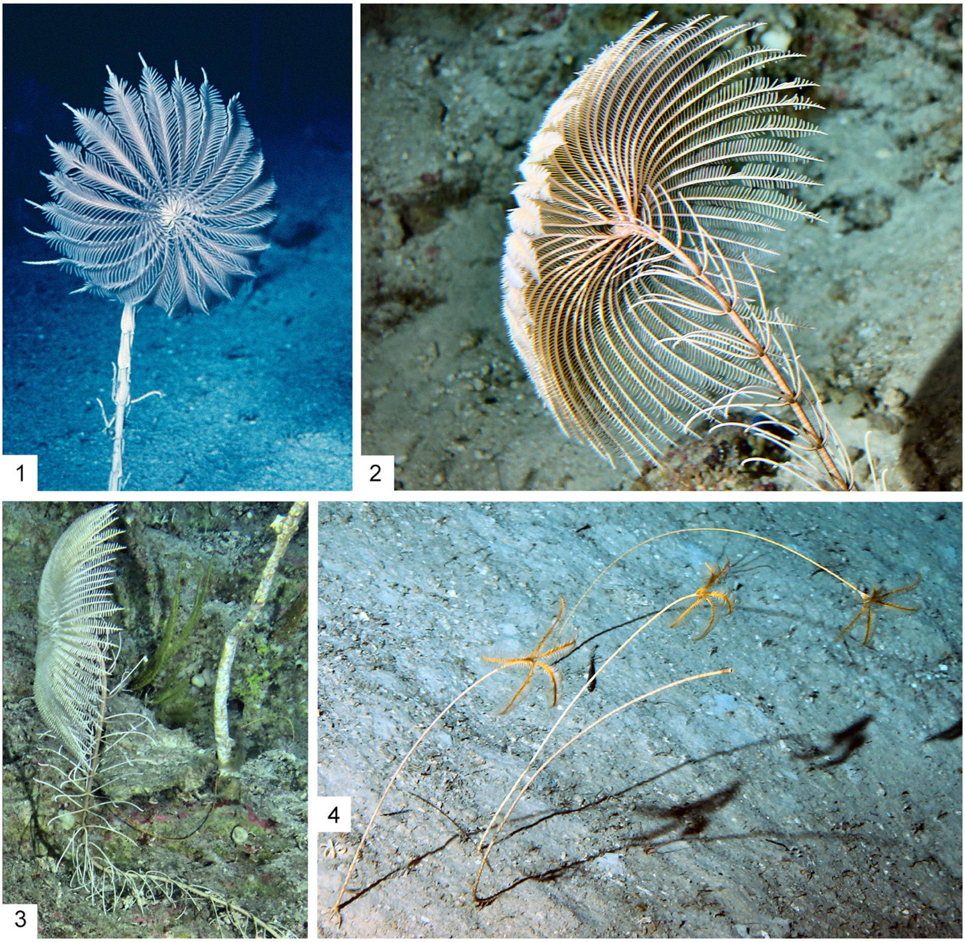

Fig. 3. Parabolic postures. *1, Neocrinus decorus* (Thomson, 1864) (Isocrinidae); south of West End, Grand Bahama Island, depth ~420 m (new; photo, C. G. Messing/National Science Foundation (NSF), taken 1993). *2–3, Cenocrinus asterius* (Linnaeus, 1767) (Isselicrinidae); off Half Moon Bay, West End, Isla Roatán, Honduras, depth ~150 m (new; photo, C. G. Messing & T. K. Baumiller, taken 2012). *4, Democrinus* Perrier, 1883 (Rhizocrinidae); off Half Moon Bay, West End, Isla Roatán, Honduras, depth ~220 m (photo, C. G. Messing & T. K. Baumiller, taken 2014, in Byrne & O'Hara, eds., 2017, p. 222). Direction of current is toward viewer in *1,* from right in *2* and *3,* and from left in *4.*

current so that the crown roughly resembles an umbrella held sideways with a concave center where the brachitaxes radiate from the calyx (Fig. 3.1–3.3) (Macurda & Meyer, 1974, fig. 1; Messing, 1985; Conan, Roux, & Sibuet, 1981, fig. 3–6). As with the preceding postures, ambulacra face down current.

When current direction shifts, several arms on the now upstream side of the crown straighten, and the entire crown rotates around its central axis like a wheel. As it does, successive series of arms straighten and then return to their curved parabolic posture, with ambulacra facing down current throughout. To accomplish this rotation, the proximal stalk columnals roll over each other with the outer edges of their symplectial articular facets behaving essentially as gears (Baumiller, LaBarbera, & Woodley, 1991). Baumiller (2008) also discussed mechanisms by which an isocrinid could raise its crown from a prone position, e.g., after crawling (MESSING & OTHERS, 1988; BAUMILLER, MOOI, & MESSING, 2001) to resume a parabolic posture for feeding, although the recent discovery of contractility of MCT ligaments (see p. 2) represents the likeliest means by which this takes place. WARNER (1977) demonstrated experimentally that this parabolic shape was more efficient in particle capture than a planar fan (disk posture).

This posture is characteristic of most extant stalked crinoids ranging from five-armed Rhizocrinidae, Phrynocrinidae, and Hyocrinidae (BOWDEN & others, 2011; TUNNICLIFFE & others, 2015) (Fig. 3.4, Fig. 4.1), through ten-armed Bathycrinidae (ROUSE & others, 2013, fig. 1c) and Septocrinidae (MIRONOV & PAWSON, 2010, fig. 7) (Fig. 4.2), to many-armed Phrynocrinidae (TUNNICLIFFE & others, 2015) (Fig. 4.3), and almost all Isocrinida that have been observed *in situ*, i.e., Isselicrinidae, Isocrinidae, and Proisocrinidae (MACURDA & MEYER, 1983; ROUX, 1985a, 1994; MESSING, NEUMANN, & LANG, 1990; MESSING & others, 2007; TUNNICLIFFE & others, 2015) (Fig. 4.4). Some feather stars, notably large Zygometridae, Colobometridae (*Pontiometra andersoni, Cenometra bella*) and some Thalassometridae, assume this posture while clinging to a variety of perches, including corals, sponges, rocks, algae, shells, and tunicates (STEVENS & CONNOLLY, 2003; MESSING & others, 2006). Those that exhibit this posture while clinging to narrow perches (e.g., wire corals or stalked crinoid columns), effectively function as stalked crinoids (MEYER & MACURDA, 1977; MEYER, 1979, fig. 1d; MESSING, 1985, 2004) (Fig. 2.4–2.5, Fig. 4.5). Similarly, the exceptionally long cirri of *P. andersoni* and some *Zygometra* A. H. CLARK, 1907b elevate their calyces enough above the substratum to permit the crown to tilt into a parabolic fan (MEYER & MACURDA, 1977, fig. 3; MEYER & MACURDA, 1980, fig. 5h; MEYER, 1979, fig. 4c) (Fig. 4.6).

Variations in this posture relative to taxon and flow velocity include the extent to which the arms flex into the current, e.g., from almost disklike to deeply bowl-shaped, and in the arrangement of pinnules. In many-armed Isocrinida, the relatively stiff and straight pinnules vary in length and angle of projection to fill the gaps between the arms (except distally where pinnule size diminishes) (Fig. 3.1). Viewed in cross section, the pinnules on opposite sides of an arm form a V that opens facing down current; the V is narrow nearer the more crowded arm bases to reduce overlap between pinnules of adjacent arms, and widens to span the gap as the distance between adjacent arms increases distally. In most other crinoids, the pinnules are more flexible. In species with fewer arms (e.g., Rhizocrinidae, Bathycrinidae, Hyocrinidae and some Phrynocrinidae), pinnules increase in length along much of the arm to span the increasing distance between adjacent arms, but they leave a gap distally (Fig. 4.1,4; Fig. 5.1). They may extend straight and laterally from the arm, at an angle as in Isocrinida, or in a curve. In many-armed feather stars, the pinnules of adjacent arms may or may not span the gaps, but they tend to curve (concave up current) as in the fan posture (see Fig. 2.5). In large-crowned forms, especially Isocrinida, as flow velocity increases across the height of the crown, arms farthest from the substratum often flex more gently—even approaching a disk posture—than the more strongly flexed lower arms (Fig. 5.2). As current velocity increases and flexing arms into the current becomes more difficult, the arms spread more widely, passing through a disk posture to a collapsed, eventually non-feeding, conical posture (see p. 29–30). As current velocity weakens, stalked crinoids typically assume the wilted flower posture described on p. 29. Feather stars may assume a variety of slack-water postures.

A parabolic posture can also be inferred for many post-Paleozoic fossil crinoids and many fossil articuliformes with arm articulations and connective tissues similar to those of living crinoids (AUSICH & BAUMILLER, 1993). Many Paleozoic crinoids have been

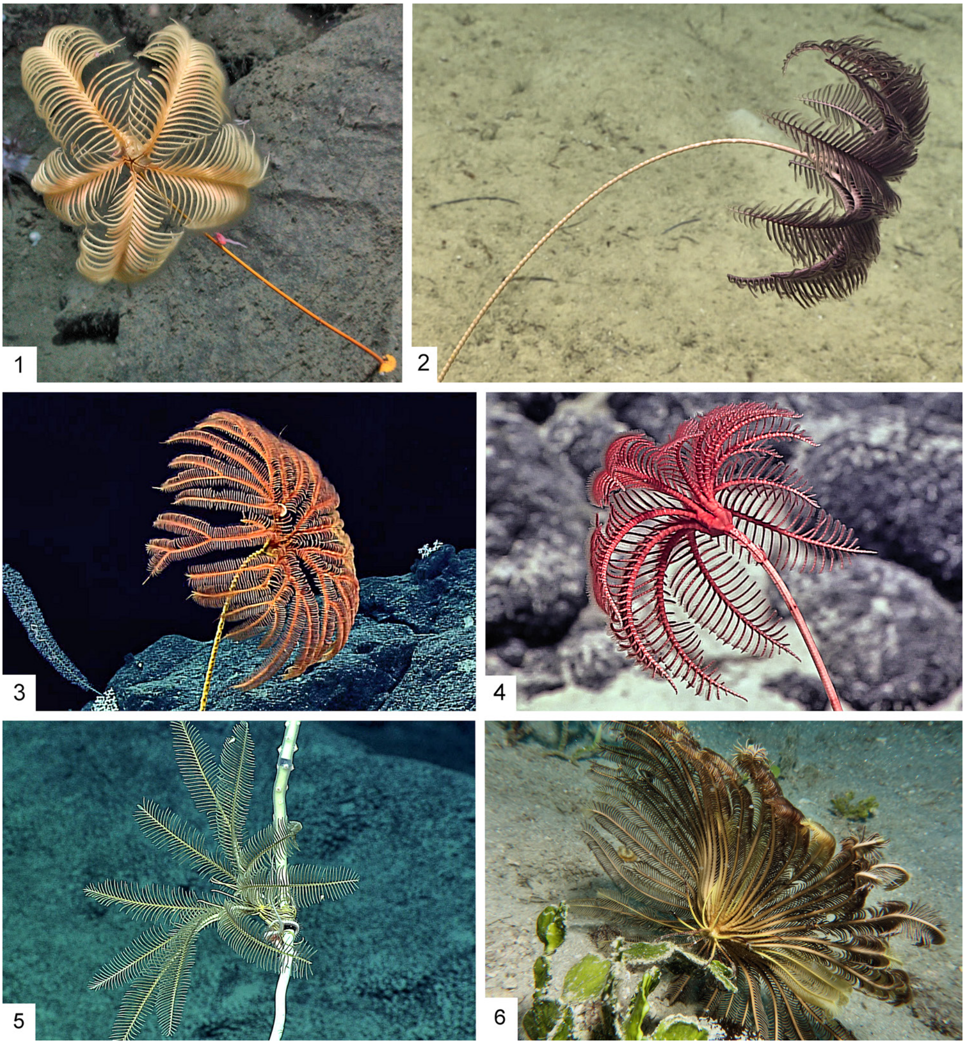

Fig. 4. Parabolic postures. *1, Parahyocrinus claguei* Roux in Roux & Messing, 2017 (Hyocrinidae); North Monterey Canyon, California, depth 2,500–2,893 m (photo, © 2002, Monterey Bay Aquarium Research Institute, previously published in Roux & Messing, 2017). *2, Rouxicrinus vestitus* Mironov & Pawson, 2010 (Septocrinidae); R/V 'Okeanos Explorer' cruise EX1811, La Parguera Ridges, south of Puerto Rico, depth ~960 m (photo, NOAA, taken 2018). *3, Phrynocrinus* A. H. Clark, 1907c (Phrynocrinidae); R/V 'Okeanos Explorer' cruise EX1605 L1, north of Guam, depth 1,166 m (photo, NOAA, taken 2016). *4, Proisocrinus ruberrimus* A. H. Clark, 1910 (Proisocrinidae); R/V 'Okeanos Explorer' cruise EX1606, "Batfish" Seamount, ~189 miles south of Wake Island, Pacific Remote Islands Marine National Monument (PRIMNM), depth ~1,280 m (photo, NOAA, taken 2016). *5, ?Thalassometra* A. H. Clark, 1907b (Thalassometridae), on isidid bamboo octocoral; "Revolver" Seamount, southeast of Wake Island, PRIMNM, depth 1,181 m, (photo, NOAA, taken 2016). *6, Zygometra microdiscus* (Bell, 1884) (Zygometridae), clinging to green alga *Halimeda* Lamouroux, 1812; on sediment between reefs; Lizard Island, Great Barrier Reef, Queensland, Australia (photo, L. Vail, in Byrne & O'Hara, eds., 2017, p. 203). Direction of current is toward viewer in *1;* from left in *2* and *3;* from right front in *4;* from right in *5;* and from left front in *6.*

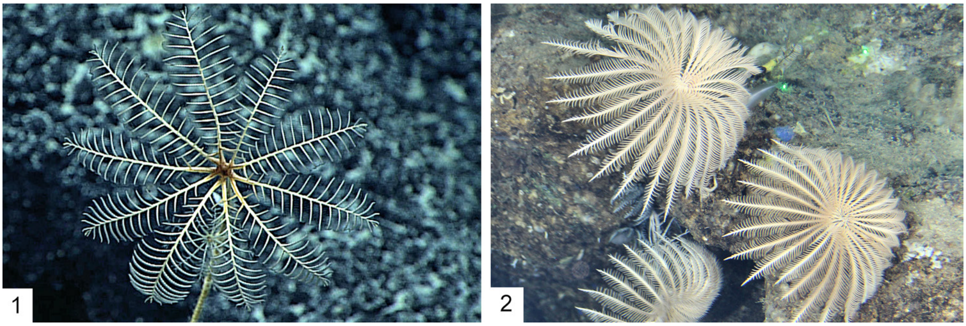

FIG. 5. Parabolic postures. *1, Naumachocrinus* A. H. CLARK, 1912c (Bathycrinidae); R/V 'Okeanos Explorer' cruise EX1504 L4, southeast of Johnston Atoll, Pacific Remote Islands Marine National Monument, depth 2,083 m (photo, NOAA, taken 2015). *2, Endoxocrinus parrae carolinae* (A. H. CLARK, 1934) (Isselicrinidae); off Half Moon Bay, West End, Isla Roatán, Honduras, depth 372 m (new: photo, T. K. Baumiller & C. G. Messing, taken 2014). Direction of current is toward viewer in both images.

reconstructed in the parabolic posture (e.g., HAUGH, 1979), but detailed analyses of arm facets (e.g., LANE & BURKE, 1976), particularly in clades in which brachials lack muscular articulations (AUSICH & BAUMILLER, 1993), are required to demonstrate that their arms had sufficient potential for the flexure necessary for a parabolic posture. Much further research is needed on this topic.

This posture has also been referred to as a parabolic filtration fan (MACURDA & MEYER, 1974, 1983; BAUMILLER, LABARBERA, & WOODLEY, 1991) and parabolic fan (MEYER & MACURDA, 1980; MESSING & others, 2007).

Conical Posture (feeding)

This posture ranges from arms arranged in a narrow adoral cone or funnel to spread nearly into a disk. Unlike the previous three postures, both stalked crinoids and feather stars may assume a similar, apparently non-feeding version of this conical posture either under slack water or when the current is too strong to maintain a disk or parabolic posture (see p. 29–31). Similar feeding postures described as funnels or bowls and derived from planar or multilayered fan or parabolic postures (MESSING, 1994) should probably be placed here. However, flow velocities and patterns under which postures change from a feeding to a slack-water posture or collapse under strong flow undoubtedly vary among taxa. For example, with near-bottom flow from the right rear, the large feather star in the foreground (Fig. 6.1) has almost all of its ten arms similarly curved upward to form an almost symmetrical bowl with pinnules arrayed in a multidirectional posture (see p. 19–20), whereas the two smaller feather stars have fewer of their ten arms oriented in a slanted monoplanar posture. As another example, although bathycrinids, rhizocrinids, and phrynocrinids usually assume a parabolic posture for feeding, the individual in Figure 6.2 exhibits a conical posture with curved pinnules and tube feet arrayed for feeding despite the bent stalk and trailing distal arm filaments, reflecting an elevated flow velocity (see also ROUX, 2004, fig. 5).

Figure 6.3 includes more than 30 *Florometra* cf. *serratissima*, each in a conical posture, on a spherical farreid glass sponge, all arrayed apparently to take advantage of the sponge's radiating exhalant current. Some reef-dwelling as well as deep-sea feather stars, including members of Comatulidae, Mariametridae, Himerometridae, and Thalassometridae, assume conical, funnel- or bowl-shaped postures, either single- or multilayered, shallow or deep, depending on species and flow conditions. Semicryptic Comatulidae normally assume

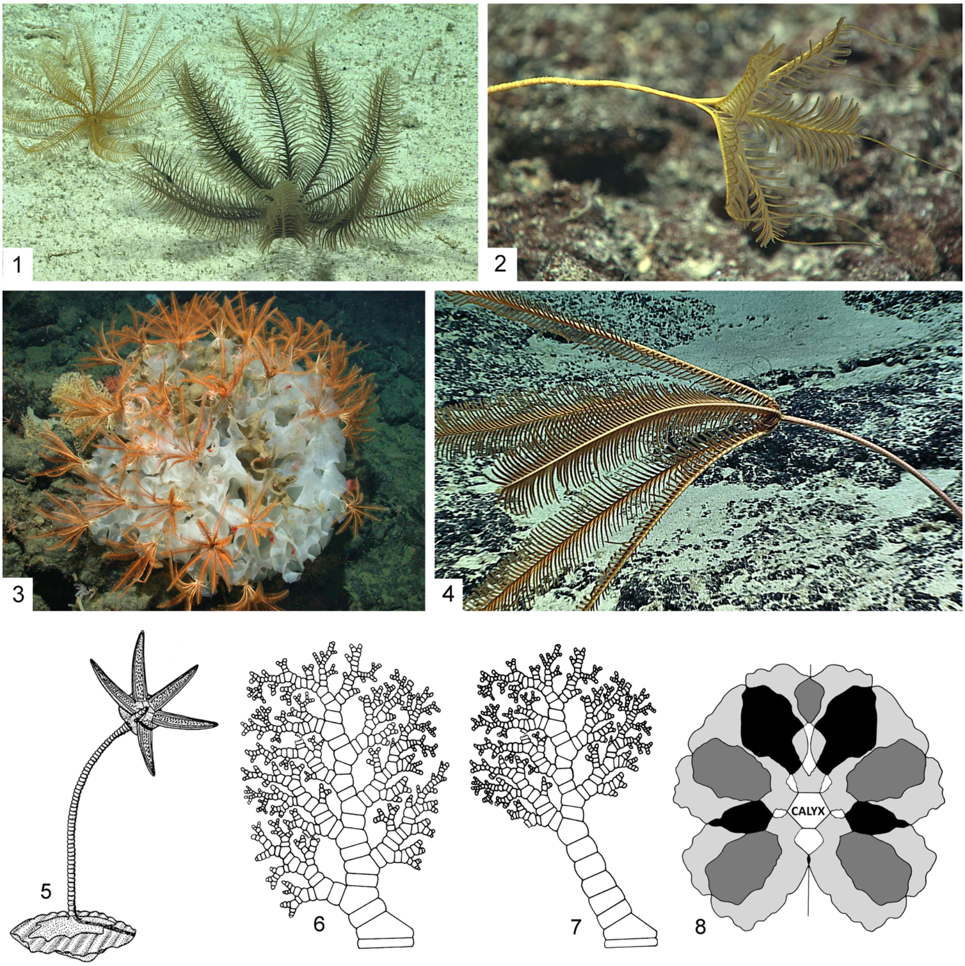

Fig. 6. Conical/bowl posture (feeding). *1,* Unidentified deep-sea feather stars in bowl posture, current direction from right rear; large individual (right foreground) has arms raised in a bowl posture and pinnules in multidirectional posture, an array characteristic of family Comatulidae; members of this family known from this region and depth include *Comatulides decameros* (A. H. Clark, 1908b) and *Comissia* A. H. Clark, 1909a; two smaller individuals (left and rear, probably Antedonidae) in partial monoplanar fan postures; R/V 'Okeanos Explorer' cruise EX1705, off Jarvis Island, Pacific Remote Islands Marine National Monument, depth ~680 m (photo, NOAA, taken 2017). *2–8,* Conical postures (feeding). *2, Porphyrocrinus* Gislén, 1925 (Phrynocrinidae), direction of current from left; R/V 'Okeanos Explorer' cruise EX1702, Ta'u Unit of National Marine Sanctuary of American Samoa, depth 420 m (photo, NOAA, taken 2017). *3, Florometra* cf. *F. serratissima* (A. H. Clark, 1907a) (Antedonidae) on a farreid sponge (Hexactinellida); R/V *Western Flyer*, northwestern flank of Pioneer Seamount, off California, depth 1,606.5 m (photo, © Monterey Bay Aquarium Research Institute, taken 2002). *4, Guillecrinus* Roux, 1985b (Guillecrinidae), direction of current from right; R/V 'Okeanos Explorer' cruise EX1703, Carondelet Reef southwest ridge, Phoenix Islands Protected Area, depth 1,701 m (photo, NOAA, taken 2017). *5, Parapisocrinus* Mu, 1954 (Rozhnov, 2007 fig. 3c). *6–8, Barycrinus stellatus* (Hall, 1858), Mississippian cyathoformes; 6–7, reconstructions of arm branching; *6,* arm branching in one-half of a ray in B-, C-, D-, and E-ray arms; *7,* arm branching in one-half of the A-ray arm; *8,* diagram of crown with all arms in place, *light gray* areas indicate rays with no overlap, *dark gray* areas indicate overlap within a ray, *black* areas indicate overlap of two adjacent rays, and *white* areas indicate openings through the arm array (*6–8,* adapted from Ausich, 1983, fig. 1a, 1b, and 4, respectively).

a multidirectional posture but take on a funnel or bowl posture when perched in the open, keeping their pinnules in the multidirectional posture described on p. 19–20. (Messing, 1985, 1994, 1997; Stevenson & others, 2017, fig. 4).

Some other stalked crinoids also appear to maintain this conical posture for feeding. *Guillecrinus neocaledonicus* Bourseau & others, 1991, which has five extremely long arms, typically assumes a conical posture with arms straight or gently curved outward and the stalk ranging from almost erect to bent strongly down current (Tunnicliffe & others, 2015, fig. 2C–D) (Fig. 6.4). Although the conical array and bent stalk suggest a strong-flow collapse response, close-up imagery shows pinnules and primary tube feet curved into the current as in many fan and parabolic postures, and the arm closest to the substrate (subject to the weakest flow) may curl up current as in the parabolic posture (Tunnicliffe & others, 2015).

This posture can be inferred for many fossil crinoids, such as the five-armed Silurian *Parapisocrinus* Mu, 1954 (Rozhnov, 2007) (Fig. 6.5), based on the morphology of facets on the radial and brachial plates, which imply that the arms lacked the ability to either form a planar fan or to recurve their distal arms into a parabolic shape. Ausich (1983) inferred a multilayered conical posture for *Barycrinus* Meek & Worthen, 1868 (Mississippian cyathoformes), based on the lack of accommodation space for all of the arm branches to be arrayed in a disk posture (Fig. 6.6–6.8).

Macurda and Meyer (1974) treated the arms of the cyrtocrinid *Holopus* d'Orbigny, 1837, as forming a funnel-like arrangement rather than a filtration fan. Grimmer and Holland (1990) recorded a similar posture but noted that the oral surfaces faced down current and suggested that asymmetries among rays might be generated with growth under the influence of prevailing unidirectional flow, as suggested by Žitt (1983). Subsequent observations found that the funnel or cone opened outward, sideways, and downward relative to the typically vertical or overhanging substrata on which *Holopus* species grow (Donovan & Pawson, 2008; Syverson & others, 2015). Although asymmetrical individuals might better be treated under the canted posture (see p. 21), *Holopus* may also be symmetrical, and adjacent individuals may orient in different directions, likely a result of growing on differently oriented areas of rugged substrata (Fig. 7.1). They are typically found under weak or negligible flow conditions, and Grimmer and Holland (1990) posed the possibility that they might be carnivorous on small crustaceans. The extremely short arms of the cyrtocrinid *Cyathidium* Steenstrup, 1847, also appear to open outward in a truncated cone (Fig. 7.2), and some fossil cyrtocrinids may have also utilized a conical posture (Fig. 7.3–7.4). Dynowski and others (2016) modeled the feeding posture of Triassic *Encrinus liliiformis* Lamarck, 1801 as a variation on the conical posture: the stalk bent down current with a teardrop-shaped crown—a narrow funnel with arm tips somewhat incurved—that generated a backward recirculation of particle-laden water into the funnel (Fig. 7.5).

Other terms for this posture have included conical, radial filtration fan (Messing, 1985), and conical or quasiconical fan (Macurda & Meyer, 1983) for semicryptic feather stars with arms radiating outward from a crevice, and conical fan for Silurian *Pisocrinus* (see Ausich, 1977).

Independent Arm Fan Posture

Irregular, three-dimensional substrata, whether shallow reefs or deep rocky bottoms, interrupt laminar near-bottom currents and generate locally multidirectional and sometimes turbulent flow conditions, for which fan, disk, and parabolic postures are unsuitable. Many feather stars that occur in such habitats are semicryptic. They hide the calyx in a hole or crevice, under a ledge, or within a sponge, and extend the arms for feeding (Meyer, 1973a, 1973b, 1979, 1982a; Meyer & Macurda, 1980). Such

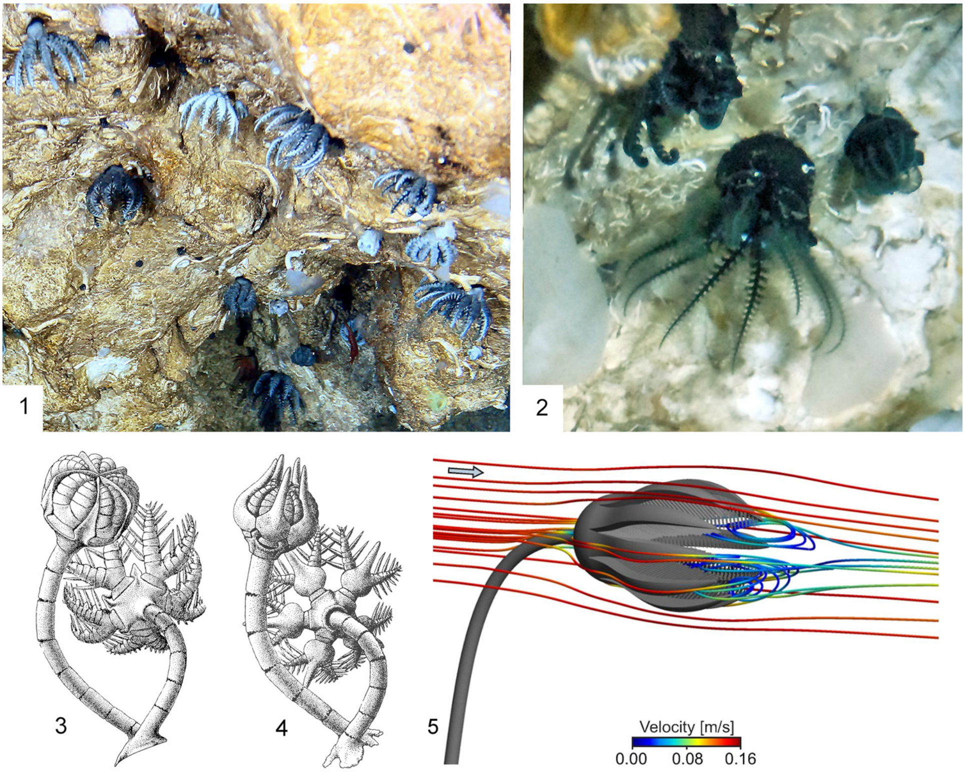

Fig. 7. Conical postures (feeding). *1*, *Holopus* cf. *mikihe* Donovan & Pawson, 2008 (Holopodidae); off Half Moon Bay, West End, Isla Roatán, Honduras; note small juvenile (partly visible at top center) and large pale dead calyx (right center), depth ~442 m (new: photo, C. G. Messing & T. K. Baumiller, taken 2013). *2*, *Cyathidium foresti* Cherbonnier & Guille, 1972 (Holopodidae); submersible 'LULA', southern Faial Channel, Azores Archipelago, depth ~500 m (Wisshak & others, 2009, fig. 2D, original photo provided by Wisshak and cropped). *3–4*, Fossil cyrtocrinids; *3, Lonchocrinus pskaboirensis* Arendt, 1974 (Eugeniacrinitidae), (Pisera & Dzik, 1979, fig. 8a, © Swiss Geological Society); *4*, *Psalidocrinus armatus* (Zittel, 1870) (Psalidocrinidae) (Pisera & Dzik, 1979, fig. 9a, © Swiss Geological Society). *5*, Triassic *Encrinus liliiformis* Lamarck, 1801 (Encrinidae), schematic diagram illustrating modeled flow around the crown showing backward recirculation of particle-laden water into the funnel (*blue*) (Dynowski & others, 2016, fig. 10A).

crinoids exhibit one of two postures. In the first, the independent arm fan posture, each arm arrays its pinnules and tube feet in a single feather-like plane perpendicular to local flow, with ambulacra oriented down current (Fig. 8.1). However, the arms do not form an organized fan but radiate more or less independently from the typically hidden calyx (e.g., Meyer, 1973a, fig. 5,*3*; Summers, Messing, & Rouse, 2017, fig. 1A).

Multidirectional Posture

In the second posture, again a response by semicryptic feather stars to weak non-laminar or turbulent near-bottom flow, arms extend in various directions, and each successive pinnule orients at ~90^0 from its neighbor, which produces a four-pinnule repeated pattern along the arm (Meyer, 1979, fig. 1b, 1e) (Fig. 8.2). Viewed along an arm, the pinnules line up in two planes that cross the arm and appear as a + or x in cross section, with four successive pinnules pointing in four directions sometimes referred to as a tetrad (Fig. 8.3). This alternating pinnule orientation creates wider spacing between successive pinnules relative to those in a monoplanar, feather-like

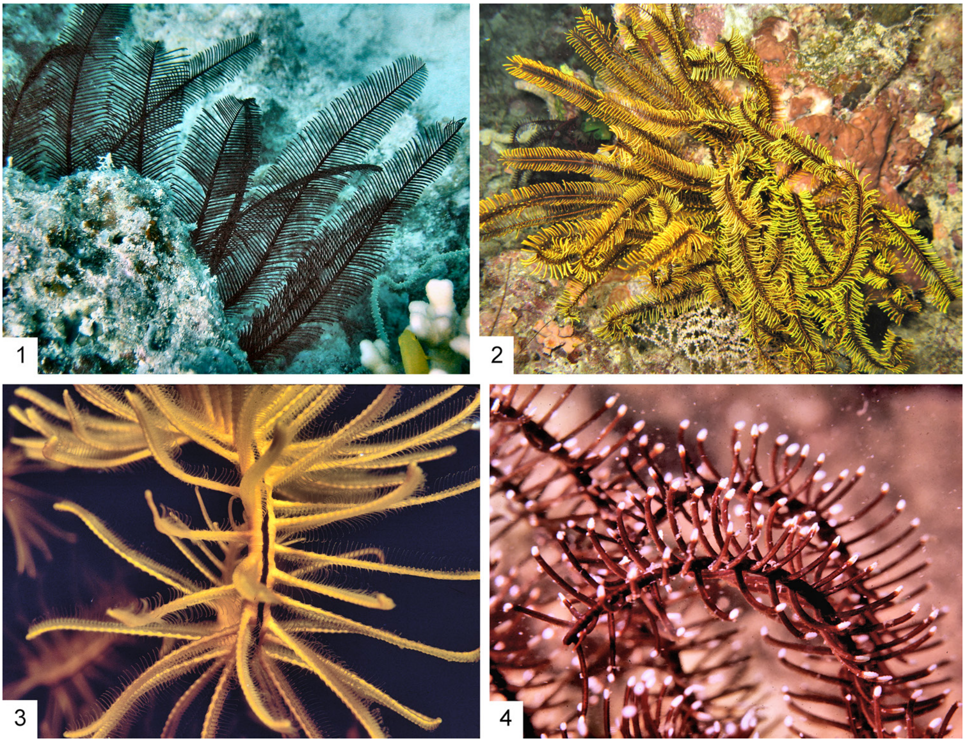

FIG. 8. *1,* Independent arm fan, *Tropiometra afra* (HARTLAUB, 1890) (Tropiometridae); Lizard Island, Great Barrier Reef, Queensland, Australia (photo, G. W. Rouse, taken 2001). *2,* Multidirectional posture, *Phanogenia gracilis* (HARTLAUB, 1890) (Comatulidae); Kri Island, Raja Ampat, Indonesia, depth <6 m (photo, C. G. Messing, taken 2013). *3–4,* Multidirectional posture, positioning of pinnules; *3, Davidaster rubiginosus* (POURTALÈS, 1869) (Comatulidae), showing alternating orientation of successive pinnules on each side of arm and minute tube feet; San Salvador, Bahamas, (new; photo, D. L. Meyer, taken 1979); *4, Nemaster grandis* A. H. CLARK, 1909a (Comatulidae), showing alternating orientation of pinnules on each side of arm under conditions of reduced, multidirectional flow; Santa Marta, Colombia, depth 20 m (photo, W. K. Sacco, taken 1969, in Meyer, 1973a, fig. 4.*4,* p. 109). Fig. *1* and *2* published in Byrne & O'Hara, eds., 2017, p. 209 and 201, respectively.

arrangement, and the tube feet are both more widely spaced and longer (MEYER, 1979). Tube feet thus arrayed can feed from any current that finds its way into a reef's infrastructure or other irregular substratum from any unpredictable direction, thereby increasing feeding capacity (MEYER 1973a, fig. 6; 1973b, fig. 3, 6; MEYER & MACURDA, 1980, fig. 4h). Unlike independent arm fans described above, this posture so far appears restricted to members of family Comatulidae, with the exception of the semicryptic antedonid *Ctenantedon kinziei* MEYER, 1972. Some species, such as *Nemaster grandis*, that normally exhibit a monoplanar pinnule array, may assume a multidirectional posture under reduced flow conditions (Fig. 8.4).

This has previously been termed radial posture (MEYER, 1973a) and conical or quasi-conical fan (MACURDA & MEYER, 1983). The former has been used for multiple fan types (as noted above).

Common Fans

Functionally analogous to the multi-layered fan posture, multiple arm baffling can be achieved by the overlapping crowns of more than one individual that typically display either fan or parabolic postures. These common fans (MAGNUS, 1964, fig.

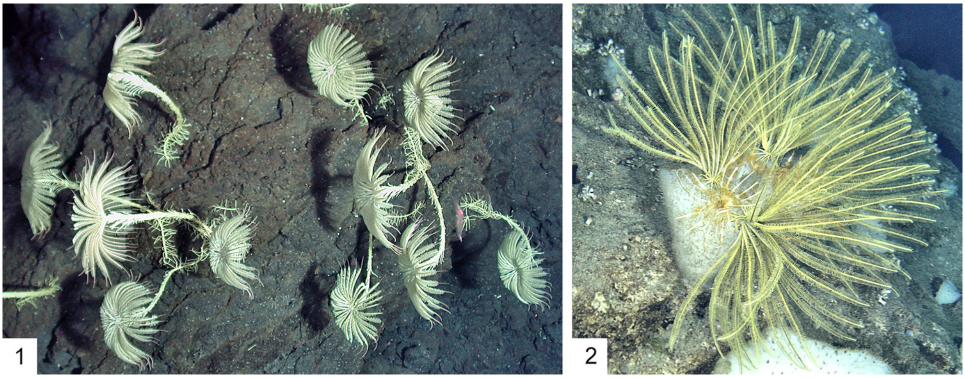

FIG. 9. Common fans. *1*, Metacrininae (Isselicrinidae); R/V 'Melville' cruise MGLN02MV, Ruby volcano, north of Saipan Island, northern Mariana Islands, depth 273 m (photo, NOAA/W. Embley, taken 2006). *2*, *Crinometra brevipinna* (POURTALÈS, 1868) (Charitometridae); off Half Moon Bay, West End, Isla Roatán, Honduras, depth 340 m (new; photo, C. G. Messing & T. K. Baumiller, taken 2014).

8; MEYER, 1973a, fig. 3,*4,* 1982a) occur in locally dense populations of both stalked crinoids (CONAN, ROUX, & SIBUET, 1981, fig. 3; MESSING & others, 1988, fig. 2A; MESSING, NEUMANN, & LANG, 1990, fig. 5; and BAUMILLER, 1997) (Fig. 9.1) and feather stars (Fig. 9.2).

Canted Postures

In a parabolic or conical feeding posture, an erect column bends below the crown, so that the oral surface orients either upward at an angle or, with sufficient current velocity, perpendicular to the substratum (e.g., Fig. 3.2–3.3, Fig. 6.2,4). In some living and fossil crinoids that exhibit an asymmetrical calyx, this tilting of the crown is obligate, and this is termed a canted posture. As noted above, examples include cyrtocrinids such as extant and fossil Sclerocrinidae and *Holopus* (e.g., DONOVAN & PAWSON, 2008; HESS, 2011) (Fig. 7.1, Fig. 10.1–10.3). A canted posture also evolved in some Permian flexible crinoids, including *Calycocrinus* WANNER, 1916, in which canting is the result of crown asymmetry (Fig. 10.5). In *Nevadacrinus* LANE & WEBSTER, 1966 (Fig. 10.4) and *Trampidocrinus* LANE & WEBSTER, 1966, the generating columnal between the proxistele and mesistele is wedge-shaped, resulting in an obligate bend in the column, presumably to facilitate a canted posture. AUSICH (1988) referred to the asymmetrical canted posture of *Calycocrinus* as a fist design.

Alternative and Unusual Postures

The following are treated as alternative and unusual postures: either distinctive arrays observed in living crinoids or because unusual and limiting morphologies in some fossil forms suggest different postures. Although most feeding postures of extant crinoids may intergrade depending on morphology and flow conditions, three feather star postures do not fit easily into any of those described, although they are clearly related. Some reef-dwelling Comatulidae with usually more than ~40 but fewer than ~80 arms form more-or-less completely irregular bushy masses with no fanlike broadening across the current even under flow conditions strong enough for feeding, e.g., *Comaster audax* ROWE & others, 1986, *Phanogenia gracilis* (HARTLAUB, 1890), and *P. multibrachiatus* (P. H. CARPENTER, 1888) (MESSING, 1994). STEVENS (1989) recognized a multidirectional ball posture, observed in many-armed *Clarkcomanthus alternans* (P. H. CARPENTER, 1881) feeding in a strong current, in which the arms arched over the disk in a meridional arrangement or formed a tangled mass, with tips overlapping and

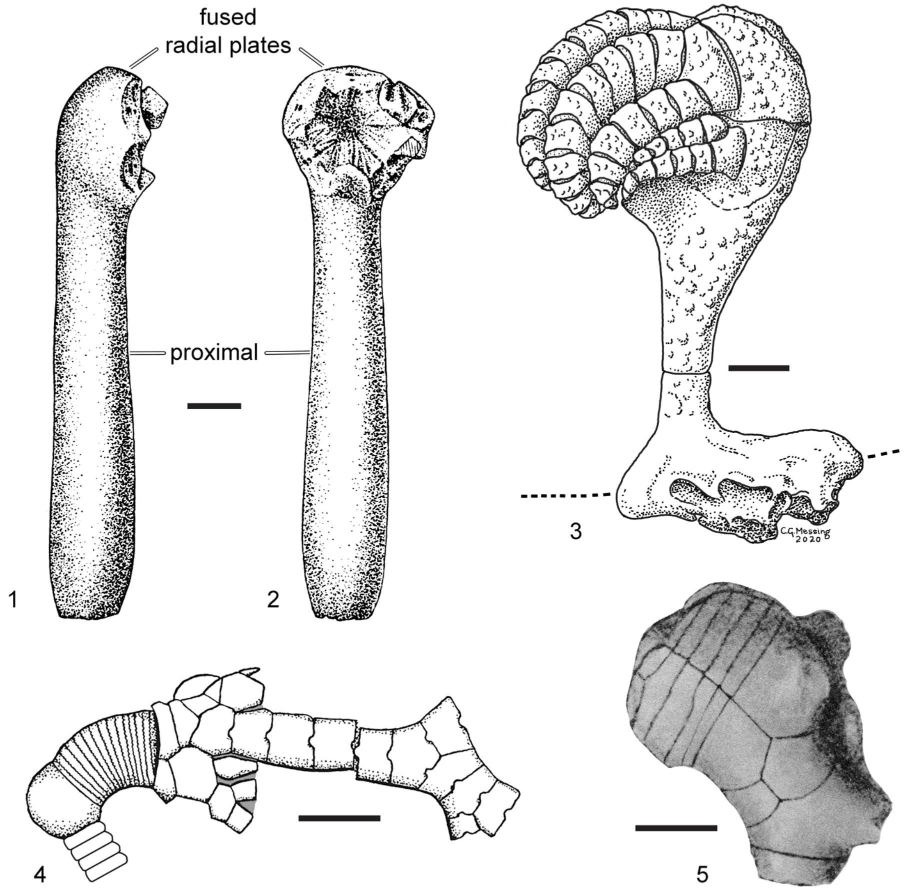

FIG. 10. Obligate, canted posture. *1–2,* lateral (*1*) and oral (*2*) view of *Torynocrinus canon* SEELEY, 1866 (Sclerocrinidae), scale bar 5.0 mm (Rasmussen, 1961, pl. 33,*7a–b*). *3, Hemicrinus astierianus* D'ORBIGNY, 1850 in 1850–1852 (Sclerocrinidae), lateral view of crown in trauma posture; Museum für Naturkunde der Humbolt-Universität zu Berlin cat. no. B14793, scale bar 2.5 mm (new; C. G. Messing; redrawn from Jaekel, 1918). *4, Nevadacrinus geniculatus* LANE & WEBSTER, 1966 (Taxocrinidae), wedge-shaped columnal, producing an obligate canted posture for the crown, scale bar 5.0 mm (adapted from Lane & Webster, 1966, fig. 4). *5, Calycocrinus curvatus curvatus* WANNER, 1916 (Calycocrinidae), DE-interray lateral view illustrating asymmetry (especially in interradial circlet), scale bar 5.0 mm (Wanner, 1916, pl. 60,*10c*).

curled inward. This should be distinguished from the slack-water meridional posture described below.

Comatula rotalaria, LAMARCK, 1816, which lacks cirri and, uniquely among crinoids, has ~10 longer interior arms and ~10 shorter exterior arms, exhibits a unique variation on the multilayered posture: five to eight of its long interior arms bend into U- or V-shapes to elevate the calyx, as in confamilials with reduced or no cirri; the remainder flex slightly but do not touch the sediment substratum, and the ~10 exterior arms orient upward as a multilayered central tuft (MESSING & others, 2006, fig. 2c) (Fig. 11.1).

This posture offers a potential model for arm posture and substrate adaptation in Late Cretaceous *Uintacrinus socialis*—arms bent proximally to elevate the calyx and the majority of the length erect to form a fan or independent arm fan posture (MESSING & others, 2004) (Fig. 11.2). This species has been variously treated as pelagic, pleustonic, hemipelagic, and benthic (see MILSOM,

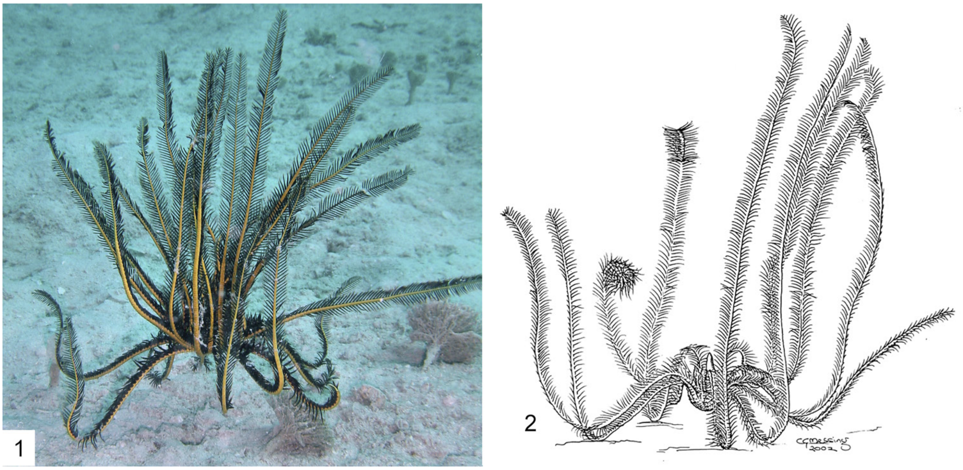

FIG. 11. Alternative postures. *1, Comatula rotalaria* LAMARCK, 1816 (Comatulidae), on sediment and rubble bottom between reefs; Lizard Island, Great Barrier Reef, Queensland, Australia, depth ~15 m (photo, G. W. ROUSE, 2001, in Byrne & O'Hara, eds., 2017, p. 201). *2, Uintacrinus socialis* GRINNELL, 1876, proposed posture. (new; C. G. MESSING).

SIMMS, & GALE, 1994; WEBBER, MEYER, & MILSOM, 2008; GORZELAK & others, 2017). The proposed posture would spread the arm bases as in extant feather stars, including those with similar interbrachial plates, and eliminate the acute, abrupt bend in the ambulacrum at the base of the arms present in some *Uintacrinus* fossils. Assuming this is an accurate reconstruction and based on the high density of uintacrinids preserved on a single bedding surfaces, it is probable that *Uintacrinus* individuals formed a common fan, as discussed on p. 20–21.

Whereas living crinoids actively position their arms to adjust to the flow conditions of their habitat, which in many cases offer insights into the postures of extinct forms, the morphologies of many extinct Paleozoic crinoids suggest that some had more obligate filtration postures dictated by skeletal structure—apart from the canted fans described on p. 21. For instance, arm mobility in most Paleozoic crinoids was limited by radial plate and arm facets lacking articular ridges and presumably lacking muscular tissue on articulations along each ray (AUSICH & BAUMILLER, 1993) (although ligament contractility may have at least partly overcome the absence of muscles). In addition to these potential restrictions on arm movement, the morphologies of several extinct crinoids significantly deviate from modern analogs, so that alternative arm posture interpretations are required. Nevertheless, it is still reasonable to assume that these crinoids should be interpreted within the framework of aerosol suspension feeding, downcurrent orientation of ambulacra, and a likely range of near-bottom flow velocities. Although it remains uncertain how much of a fossil crinoid's feeding posture can be reconstructed from a preservational posture, the absence of muscles in many Paleozoic taxa suggests that they could not alter their posture rapidly, which increases the likelihood of retaining a life posture postmortem, at least in response to rapid burial (e.g., obrution; see *Preservational Postures,* p. 32).

Presumably, obligatory arm postures existed in crinoids with arm trunks, such as in *Eucladocrinus millebrachiatus* WACHSMUTH & SPRINGER, 1878 (Mississippian camerate) (Fig. 12.4), which had biserial feeding appendages attached to reasonably stout, multiplated arm trunks. Crinoids with arm trunks are interpreted to have formed a disk (or perhaps slightly conical) arm posture when alive.

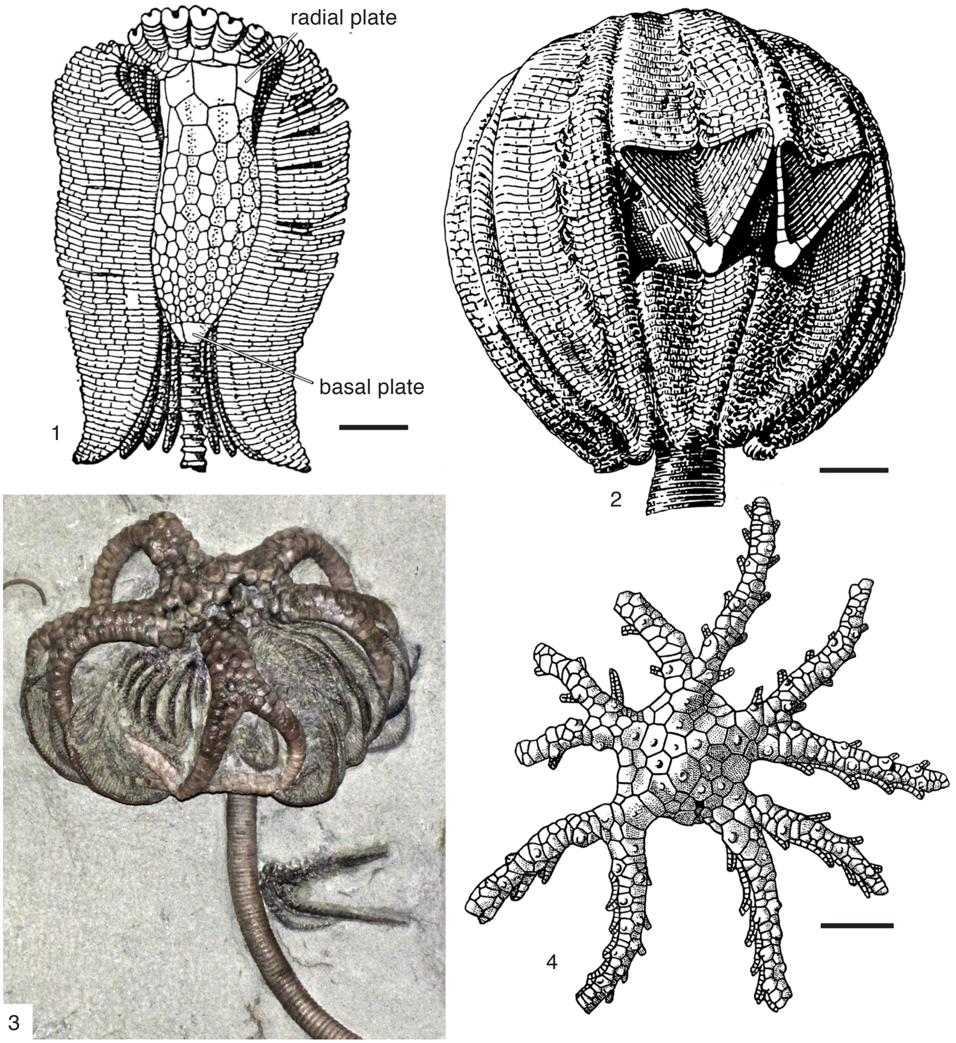

Fig. 12. Alternative postures: recumbent, obligate, and unusual. *1, Amphoracrocrinus amphora* (Wachsmuth & Springer, 1897), Mississippian, scale bar 5.0 mm (Bather, 1900, fig. 73). *2, Barrandeocrinus sceptrum* Angelin, 1878, scale bar 5.0 mm (Moore, 1952, fig. 18–23,*1*). *3, Gilbertsocrinus dispansus* (Wachsmuth & Springer, 1897) showing slender pinnulate arms beneath and between the thick inverted Y-shaped crown appendages, no scale available (photo, J. St. John). *4, Eucladocrinus millebrachiatus* Wachsmuth & Springer, 1881 in 1880–1886, bearing arm trunks; biserial arms attached to arm trunks mostly broken away, scale bar 5.0 mm (Wachsmuth & Springer, 1897, pl. 73,*3*).

Some crinoids presumably had obligate recumbent arms recurved downward along the sides of the calyx and upper stalk, reminiscent of the non-feeding reversed meridional posture described on p. 31–32, which must have exposed the ambulacral side of the arms to currents. Most crinoids with this arm posture were camerates with pinnulate arms, e.g., *Acanthocrinus* Roemer, 1850 (Devonian), *Amphoracrocrinus* Moore & Strimple, 1969 (Mississippian) (Fig. 12.1), *Artaocrinus pendens* (Springer, 1926a) (Mississippian), and *Dichocrinus* Münster, 1839 (Mississippian–Permian). In a specialized variation, the arms of the Silurian camerate *Barrandeocrinus* Angelin, 1878 were recumbent along

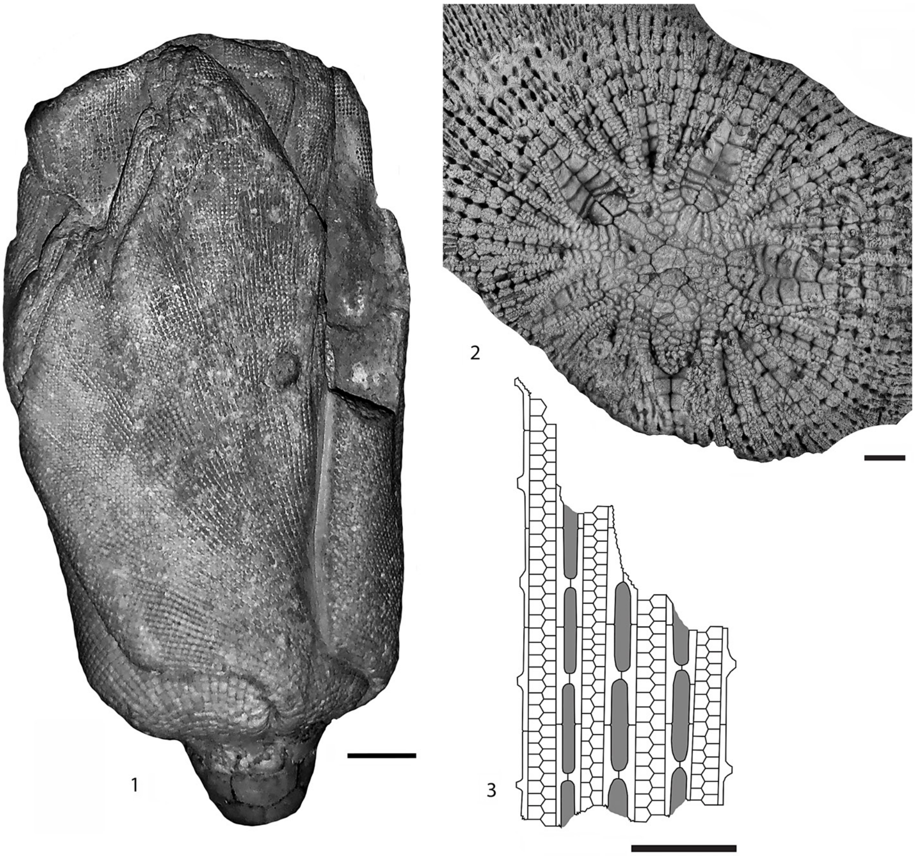

FIG.13. Alternative postures: laterally merged arms with a mesh texture. *1, Crotalocrinites pulcher* HISINGER, 1840 in 1837–1841, United States National Museum cat. no. 2291, crown with arms folded into a trauma posture, scale bar 1 cm (new; photo, W. I. Ausich). *2–3, Crotalocrinites rugosus* (MILLER, 1821). *2,* Oral view of tegmen and proximal arms, Paleontological Museum, Uppsala University cat. no. 26505, scale bar 5.0 mm (new; photo, W. I. Ausich). *3,* Enlargement of the oral side of arms, with laterally fused brachials and ambulacral cover plates in place, scale bar 2.5 mm (new; W. I. Ausich, based on Ubaghs, 1953, fig. 83b).

the column, and the pinnules were bent into a V halfway along their lengths, so that the tips of opposing pinnules just touched and formed a palisade along the arms, covering the ambulacra and forming an elongate heart-shaped chamber along each arm (Fig. 12.2). It is not known if this was a feeding, non-feeding, or trauma posture.

The unusual camerate *Gilbertsocrinus* PHILLIPS, 1836 had thick, branching tegmen appendages that extended beyond the typical periphery of the tegmen and thread-like arms that dangled beneath them (Fig. 12.3), which combined to form a unique filtration array. *Gilbertsocrinus* also had an extremely flexible column (LANE, 1963; 1973; RIDDLE, WULFF, & AUSICH, 1988; HOLLIS & AUSICH, 2008).

The eucladids *Crotalocrinites* AUSTIN & AUSTIN, 1843 (Silurian) (Fig. 13.1) and *Pernerocrinus* BOUŠKA, 1946 (Devonian) had arms laterally fused into continuous sheets, with and without perforations, respectively. Their crowns are commonly preserved with the arms rolled inward over the oral surface. Only a high-velocity current could have generated a flux of water through such dense filtration arrays. Perhaps these crinoids fed primarily via currents that eddied around the solid or finely perforate arms (perhaps

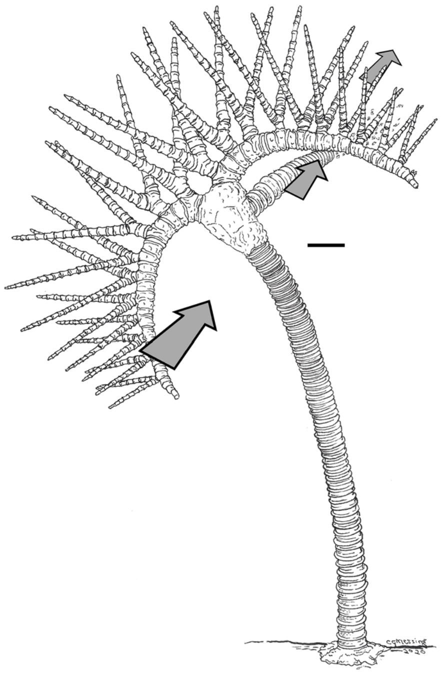

FIG. 14. Alternative, obligate posture. *Scoliocrinus ubaghsi* Haude, 2007 reconstruction in anterior view showing the two arm-bearing radials A and E, with ambulacra and large posterior-lateral anal tube oriented down current; direction of flow (*arrows*) is into image, scale bar 1 cm (new; C. G. Messing, based on Haude, 2007, fig 1,5).

like fenestrate bryozoans), but details are not known.

The Devonian eucladid *Scoliocrinus* Jaekel, 1895 had branched feeding appendages attached to two or four arm trunks. Haude (2007) reconstructed its posture as having the arm trunks arched outward and downward (as in the preservational posture) with branching appendages arrayed in an erect monoplanar fan on each trunk as an adaptation to unidirectional or tidal flow (Fig. 14).

In the Petalocrinidae (Ordovician–Devonian eucladid), each arm consisted of two brachial plates: a small, tetragonal first primibrachial and a second large and triangular (*Petalocrinus* Weller & Davidson, 1896 and *Sinopetalocrinus* Mu & Lin, 1987) (Fig. 15.1–15.5) or cylindrical (*Spirocrinus* Mu & Wu, 1974) brachial (Mao & others, 2017; Ausich, Mao, & Li, 2019) (Fig. 15.6–15.8). Ambulacra branched multiple times on the aboral side of the second brachial (*Petalocrinus* and *Sinopetalocrinus*) or spiraled around the cylindrical second brachial (*Spirocrinus*). *Petalocrinus* and *Sinopetalocrinus* presumably fed with either a fan or conical posture (Fig. 15.9). The few known *Petalocrinus* specimens with articulated arms are preserved in a starburst posture (Mao & others, 2017, fig. 2) (see p. 36–37). Similarly, *Spirocrinus* had either a fan or conical posture (Fig. 15.10).

Barrandeocrinus, *Crotalocrinites*, and the petalocrinids are commonly associated with reefs. Mao and others (2017) suggested that the three-dimensional spiraling of the ambulacra around the second brachial in *Spirocrinus* may have been an adaptation for multidirectional currents on Silurian reefs. It is also possible that the unusual arm morphologies of *Barrandeocrinus*, *Crotalocrinites*, and other petalocrinids were adaptations to reef and reef-associated habitats.

NON-FEEDING POSTURES

Crinoids assume a variety of non-feeding postures when little to no particle capture occurs via the normal feeding method. Slack-water postures are assumed by crinoids when water movement is negligible or not detectable. They assume a trauma posture when attacked by a predator, when regenerating, or when the current is too strong to feed. In some cases, a crinoid may assume a similar posture in response to slack water or strong flow. Of course, a crinoid could presumably capture a particle that fell onto or otherwise impacted a tube foot while in any of these postures, and epidermal uptake of dissolved nutrients would remain possible as well.

Collecting-bowl Posture

As noted above, living crinoids were initially observed in aquaria, where a crinoid was lying on the substratum with its distal arms raised in a collecting-bowl posture (W. B. Carpenter, 1866; Chadwick, 1907;

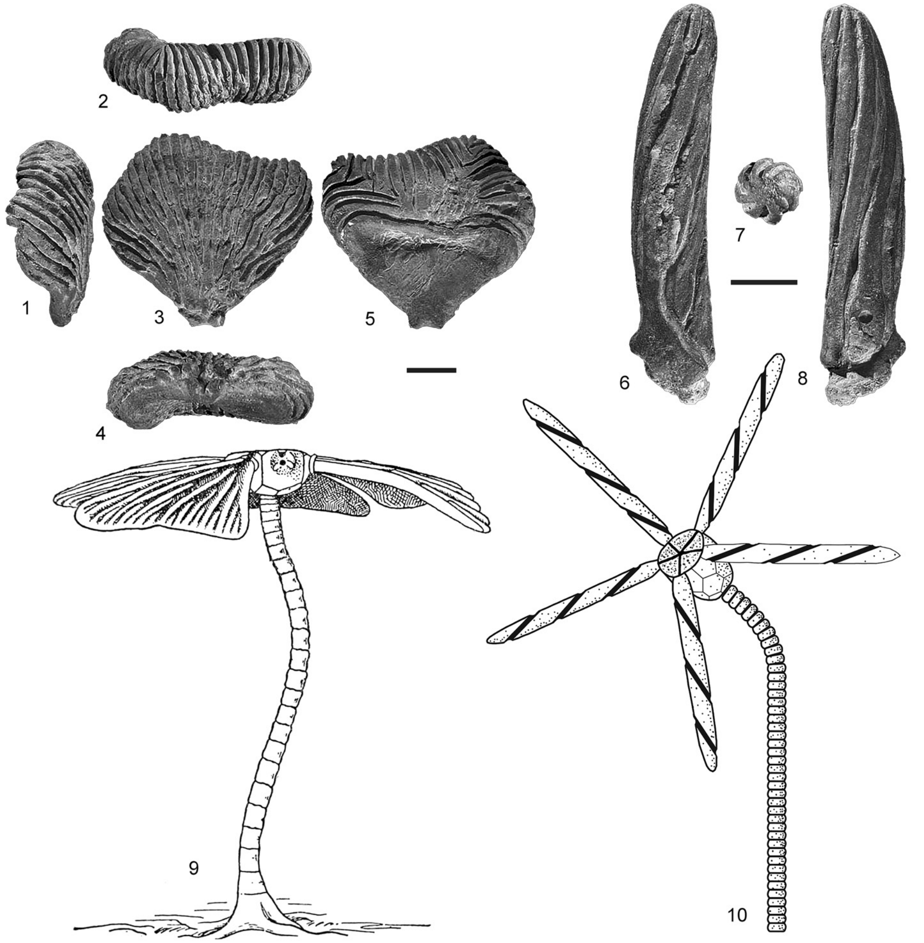

FIG.15. Alternative obligate postures. Petalocrinidae with subtriangular and cylindrical arms. *1–5, Sinopetalocrinus involutus* Mu & Lin, 1987, second brachial plate in various views, Nanjing Institute of Geology and Paleontology (NIGP) cat. no. 163729; lateral (*1*), distal (*2*) oral (*3*), proximal (*4*), and aboral (*5*) views, scale bar 5.0 mm (Mao & others, 2017, 4,*5a–e*). *6–8, Spirocrinus dextrosus* (Mao & others, 2017), NIGP cat. no. 163743; left-lateral (*6*), distal (*7*) and right-lateral (*8*) views, scale bar 5.0 mm (Mao & others, 2017, fig. 8,*5a–c*). *9–10,* Diagrammatic reconstructions of complete specimens; *9, Petalocrinus mirabilis* (Weller & Davidson, 1896) (Bather, 1900, fig. 91); *10, Spirocrinus* Mu & Wu, 1974 (new; W. I. Ausich).

Gislén, 1924). This posture has rarely been encountered in *in situ* observations of shallow-water crinoids. In one unusual occurrence, Meyer (unpublished observations) observed unidentified feather stars with arms splayed radially on a cohesive mud substratum within shallow crater-like depressions in depths of 1–2 m in Bowling Green Bay, Queensland, Australia. As noted above, deep-sea Pentametrocrinidae, Antedonidae, and Atelecrinidae may assume a shallow bowl posture (see Fig. 2.6), although, because some close-up imagery shows primary tube feet fully extended and coplanar with pinnules and arms, it is not clear when this array becomes a slack-water posture. In particular, five-armed *Pentametrocrinus* A. H. Clark, 1908a, have been observed to form both a shallow collecting bowl (Tokeshi, 2002) and to spread their arms out along the substrate, so they look like ophiuroids (Van den Beld & others, 2017).

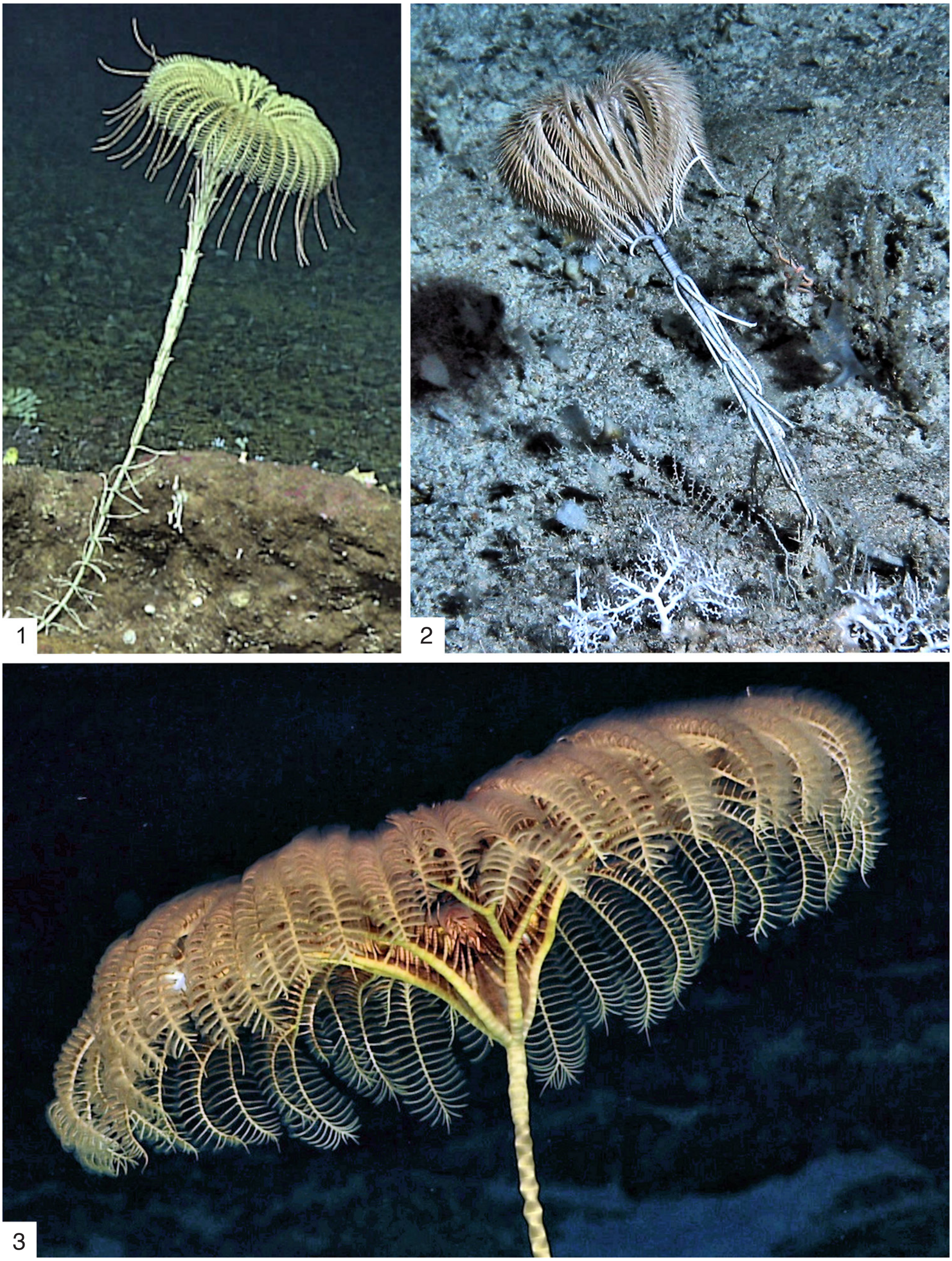

FIG. 16. Wilted flower posture. *1,* Metacrininae (Isselicrinidae, either *Metacrinus* P. H. CARPENTER, 1884 or *Saracrinus* A. H. CLARK, 1923); R/V 'Okeanos Explorer' cruise EX1605 L1, North Esmeralda Bank, west of Saipan, northern Marianas Islands, depth 447 m (photo, NOAA, 2016) (note, in all Metacrininae, the pinnules along the distal portion of the arms are strongly reduced). 2*, Endoxocrinus parrae prionodes* (H. L. CLARK, 1941) (Isselicrinidae); "Johnson Sea-Link II" 3685, northeastern Strait of Florida, north-northwest of West End, Grand Bahama Island, Bahamas, depth 598–621 m (photo, Bioluminescence 2009 Expedition, NOAA Office of Ocean Exploration and Research [OER], taken 2009). *3, Phrynocrinus* A. H. CLARK, 1907c (Phrynocrinidae); R/V 'Okeanos Explorer' cruise EX1705, Kahalewai Seamount, Pacific Remote Islands Marine National Monument, depth 1,677 m (photo, NOAA, taken 2017).

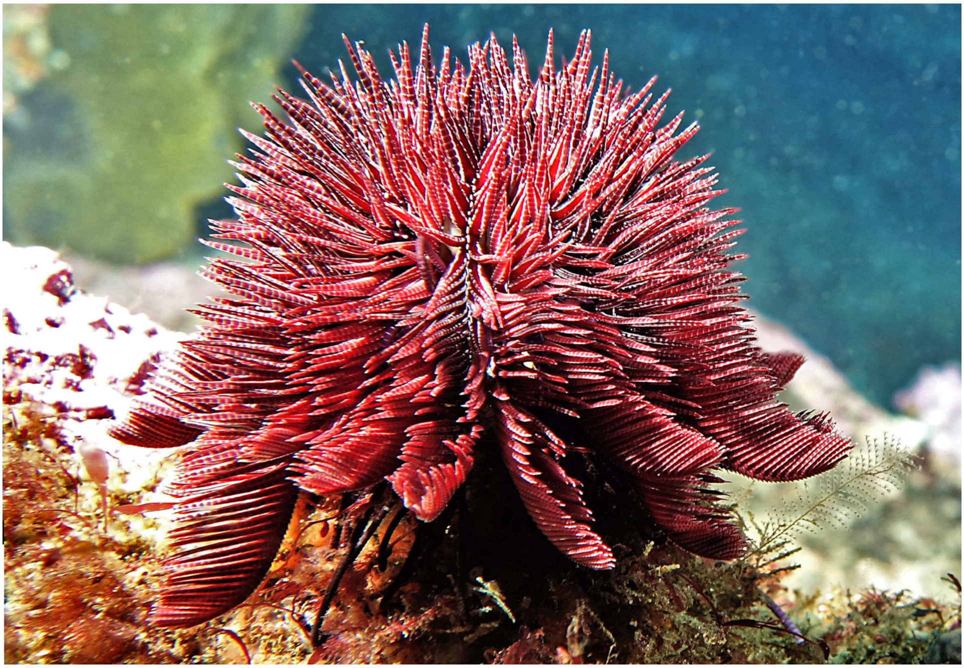

FIG. 17. Wilted flower posture. *Ptilometra australis* WILTON, 1843; Shark Point, Clovelly, New South Wales, Australia (photo, J. Turnbull, 2007).

Wilted Flower Posture

In slack-water conditions, the stalk of a stalked crinoid usually stands more or less erect, with one or more of its arms drooping downward in a wilted flower posture (MACURDA & MEYER, 1974, fig. 1e; BAUMILLER, LABARBERA, & WOODLEY, 1991; YOUNG & EMSON, 1995) (Fig. 16). Although the animal looks rather pathetic, if not dead in some cases, with increased current velocity, a crinoid in this posture will raise its arms and, in a sustained current, will eventually form a parabolic posture. However, note that tube feet may remain extended in this posture, perhaps for respiration, but also suggesting that feeding may still take place (Fig. 16.3). This posture also occurs in some feather stars, which MESSING (1997) referred to as a reversed meridional posture: under slack conditions, the asterometrid *Pterometra venusta* A. H. CLARK, 1912b, the ptilometrid *Ptilometra australis* WILTON, 1843 (and perhaps other members of those genera), and the colobometrid *Pontiometra andersoni* curve their arms aborally with pinnules and ambulacra facing outward (MEYER & MACURDA, 1980, fig. 3c; STEVENS, 1989) (Fig. 17). Although traditional understanding of Paleozoic crinoids that lacked muscular articulations suggests that those taxa could not have assumed this position, the discovery of contractility in MCT may require rethinking of such limits. Detailed studies of crinoid articulations are required to answer this question.

Conical Posture (non-feeding)

Both stalked crinoids and feather stars may assume a conical posture under slack water (LA TOUCHE, 1978b; BYRNE & FONTAINE, 1981) or when the current is too strong to maintain a disk or parabolic posture. However, it may also represent a transition between a feeding posture and either a slack-water or trauma posture. A series of time-lapse images (Fig. 18) illustrates how an assemblage of *Neocrinus decorus* and *Endoxocrinus parrae parrae* respond to increasing near-bottom

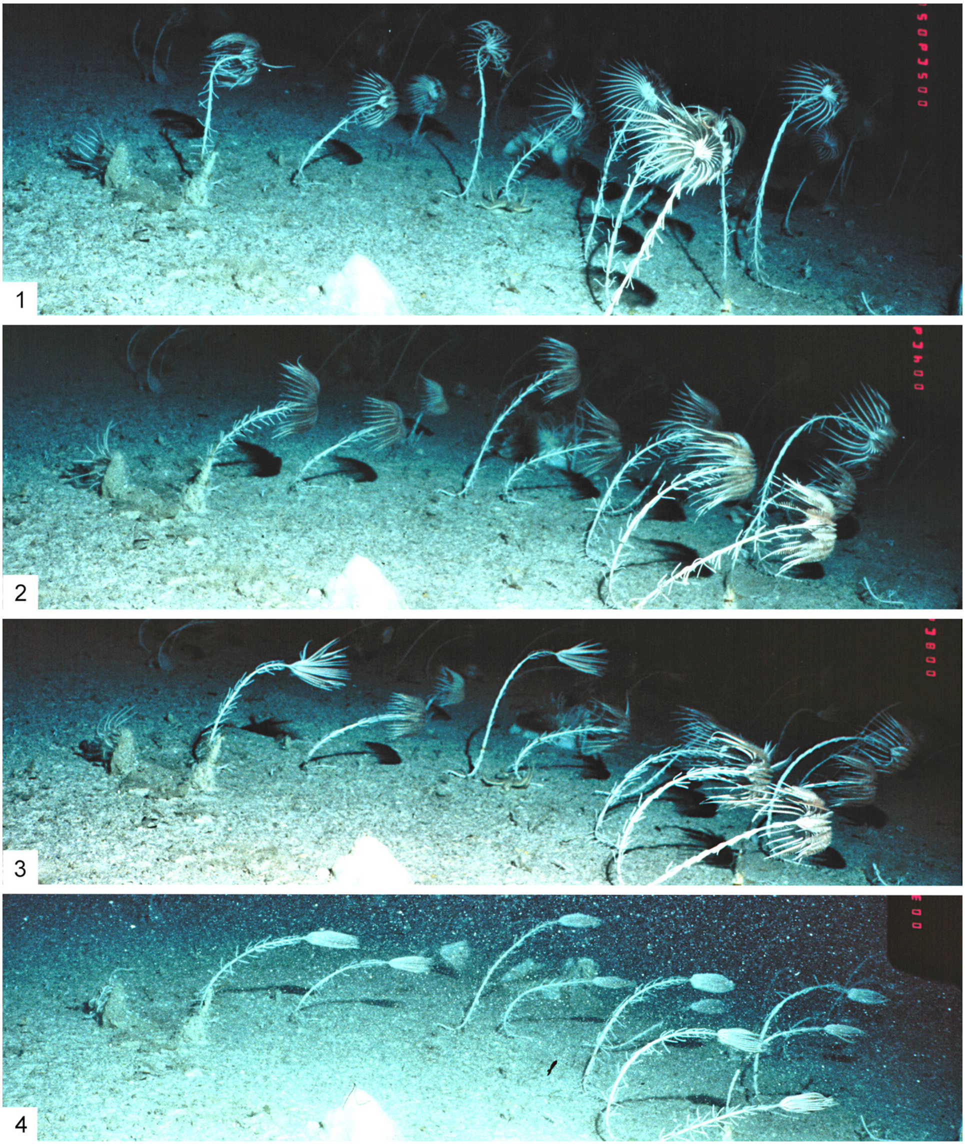

FIG. 18. Time-lapse images of a group of *Neocrinus decorus* (THOMSON, 1864) (Isocrinidae) and one *Endoxocrinus parrae parrae* (GERVAIS, 1835), short stalk, center rear (Isselicrinidae), on a carbonate ridge. Images show changes from parabolic (*1–2*) through non-feeding conical posture in the two tallest *N. decorus* (*3*), to fully collapsed to a trauma posture (*4*) with increasing near-bottom current from left, except for the *E. parrae parrae,* which remains exposed to weaker flow closer to the substrate. Flow velocities estimated 1–2 m above bottom: *1,* ~5 cm sec^{-1}; *2,* ~15 cm sec^{-1}; *3,* ~25–30 cm sec^{-1}; *4,* ~50 cm sec^{-1}; northeastern Strait of Florida, west of Grand Bahama Island, ~420 m (photos, C. G. Messing/NSF, taken 1993).

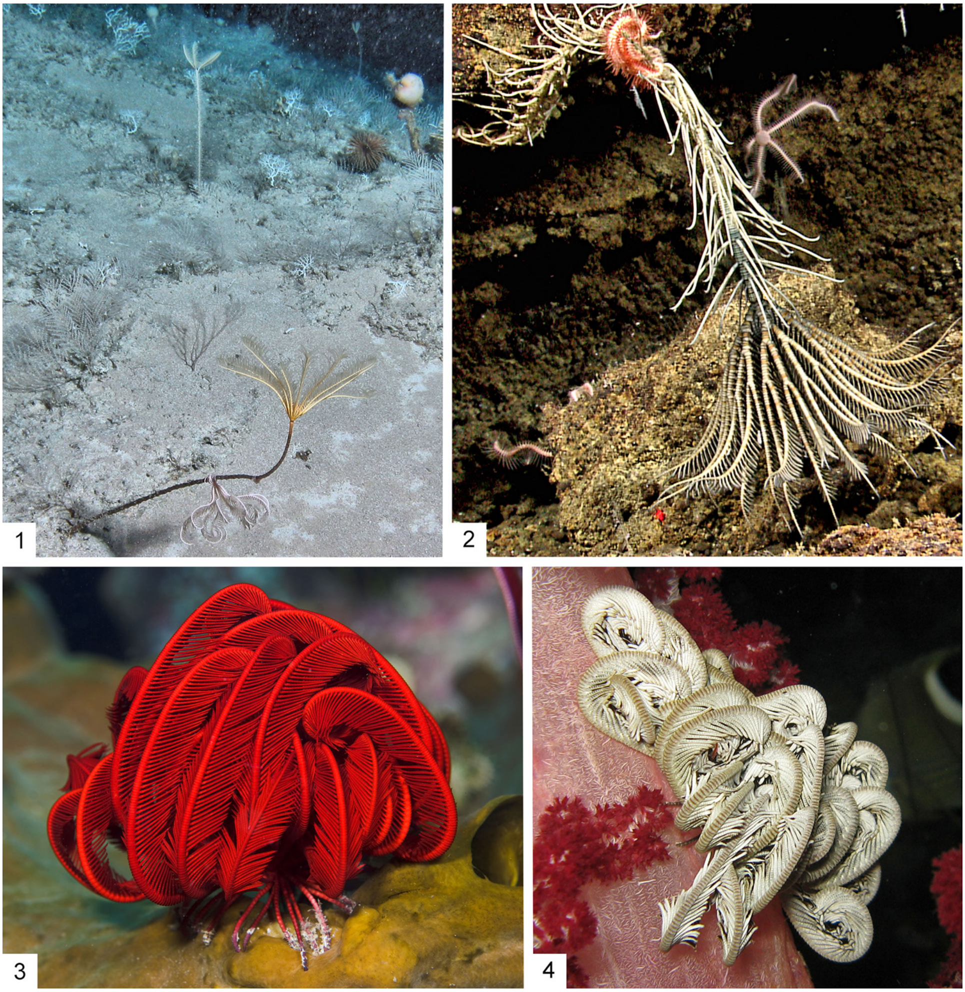

Fig. 19. *1–2,* Conical posture (non-feeding). *1,* Stalked crinoids with upright conical posture in slack water, *Democrinus* Perrier, 1883 (Rhizocrinidae) (top), *Porphyrocrinus daniellalevyae* Messing, 2016 (Phrynocrinidae) (bottom), with feather star, *Trichometra cubensis* (Pourtalès, 1869) (Antedonidae), clinging to its stalk in conical non-feeding posture with inrolled arm tips; *Johnson Sea-Link II* 3685, northeastern Strait of Florida, north-northwest of West End, Grand Bahama Island, Bahamas, 598–621 m (photo, Bioluminescence 2009 Expedition, NOAA/OER, taken 2009, previously published in Messing, 2016). *2,* Metacrininae (*Metacrinus* P. H. Carpenter, 1884 or *Saracrinus* A. H. Clark, 1923) in drooping slack-water conical posture on cliff face; R/V 'Barun Jaya IV,' INDEX-SATAL cruise 2010, Gelembung II site, South Sangihe Arc, Sangihe Talaud Region, Indonesia, 1,175 m (photo, NOAA, taken 2010). *3–4,* Meridional postures; *3, Himerometra robustipinna* (P. H. Carpenter, 1881) (Himerometridae); Pulisan, Sulawesi, Indonesia (photo, L. Pitkin). *4*, *Capillaster multiradiatus* (Linnaeus, 1758) (Comatulidae); Kri Island, Raja Ampat, Indonesia, (new; photo, C. G. Messing, taken 2013).

flow velocity, passing from parabolic through conical to a shaving-brush trauma posture (see p. 36).

Under slack-water conditions, some stalked crinoids hold the arms in an upright cone instead of the wilted flower (Fig. 19.1), while others droop (Fig. 19.2), the latter likely associated with local topography. In many feather stars, the cone orients in any direction and the arm tips commonly curl inward, approaching the meridional posture (see p. 32) (Fig. 19.1). It is important to

Fig. 20. Camouflage posture. *Oligometra carpenteri* (Bell, 1884) (Colobometridae) on *Halimeda* green algae; Lizard Island, Great Barrier Reef, Australia (photo, G. W. Rouse, taken 2001, Byrne & O'Hara, eds., 2017, p. 205).

note, however, that it may be impossible to determine if a crinoid assuming a conical posture is actually feeding or not, particularly if tube feet cannot be observed. Too few observations exist to generalize whether particles are being captured or not.

Meridional Posture

In a meridional posture, a crinoid arches its arms over the tegmen, creating an overall subspherical shape with ambulacra oriented inward (Meyer, 1973a, fig. 4,*4;* Meyer & Macurda, 1980, fig. 4f; Meyer, 1982a; Zmarzly, 1984) (Fig. 19.3–19.4). As an alternative to a collecting-bowl posture, many multi-armed feather stars assume this posture under slack flow conditions, although Stevens (1989) reported a similar posture in *Clarkcomanthus alternans* actively feeding under strong flow. This posture offers some protection for the visceral mass, which would be fully exposed in a collecting-bowl posture.

This was considered an inactivity posture in Magnus (1963; 1964, fig. 6), a radial posture in Meyer (1973a, fig. 5,*2*) and a multilayered hemispherical posture in Macurda and Meyer (1983).

Camouflage Posture

Although the feather star, *Oligometra carpenteri* (Bell, 1884), which clings to octocorals and branching *Halimeda* Lamouroux, 1812, green algae, may assume a disk posture, it is most commonly observed in a unique posture: pinnules appressed against arms, pairs of its ten arms pressed together, and as many as four of five arm pairs lying along or parallel to the branches of its perch. This is an apparent camouflage posture (Vail, 1990; Messing & others, 2006) (Fig. 20).

REGENERATION POSTURE

Two feather stars are photographed (in Fig. 21.1) attached to a wire coral. The one on the right exhibits a typical parabolic feeding posture, but the other hangs downward with the arms closed about the oral-aboral axis in a regeneration posture similar to the non-feeding conical posture described earlier (p. 29), but with pinnules particularly closely pressed against the arms. It is regenerating its visceral mass (and some arms) following a nonlethal predation encounter, presumably with a fish. The corresponding posture for a stalked crinoid is not known, although both stalked crinoids and feather stars can maintain feeding postures while regenerating at least some arms (Fig. 21.2–21.3). For instance, note that one *Democrinus* in Fig. 3.4 (p. 13) has lost all five arms yet maintains the same stalk posture as its intact neighbors.

PRESERVATIONAL POSTURES

Preservational postures are those exhibited by crinoids preserved as fossils in the rock record. Because crinoids consist of a modular, multi-plated mesodermal skeleton, in which ossicles are typically bound together during life by soft tissues, a dead crinoid decays very rapidly (Meyer, 1971). Thus, most complete or nearly complete crinoid fossils were most likely buried during catastrophic events (Taylor & Brett, 1996; Donovan, 1991; Ausich, 2001, 2016). Crinoids have a typical reaction to catastrophic disturbance that leads in most cases to two characteristic preservational patterns when crowns remain intact. Baumiller, Mooi, and Messing (2008) discussed both the conditions and morphologies that contribute to one or the other.

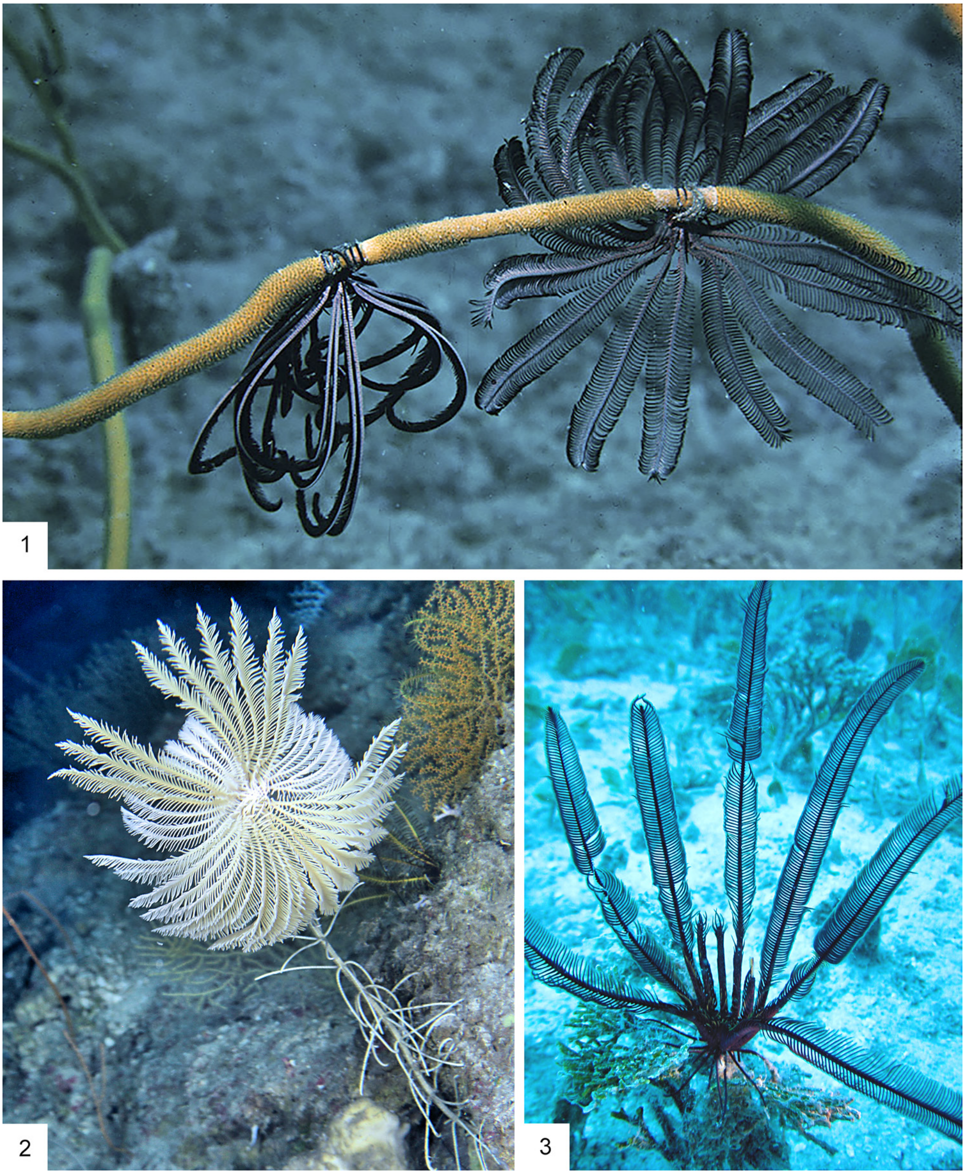

Fig. 21. Regeneration posture. *1, Cenometra bella* (Hartlaub, 1890) (Colobometridae), two individuals attached to octocoral *Junceella* Valenciennes, 1855; drooped individual (left) eviscerated or regenerating visceral mass, individual at right in normal feeding parabolic posture, arm length ~10 cm; Lizard Island, Great Barrier Reef, Australia (new; photo, D. L. Meyer, taken 1975). *2–3,* Crinoids maintaining feeding postures while regenerating arms; *2, Cenocrinus asterius* (Linnaeus, 1767) (Isselicrinidae); Isla Roatán, Honduras, depth ~150 m (new; photo, T. K. Baumiller & C. G. Messing, taken 2014); *3, Amphimetra tessellata* (Müller, 1841) (Himerometridae); Lizard Island, Great Barrier Reef, Australia, depth ~15 m (photo, G.W. Rouse, taken 2001).

Fig. 22. Trauma posture. *1, Sarametra triserialis* (A. H. Clark, 1908c) (Zenometridae); Rapano Ridge, Musicians Seamounts, north of the Hawaiian Islands, depth 1,930 m (photo, NOAA, taken 2017). *2,* Shaving-brush posture in Mississippian crinoids; Hampton Formation at LeGrand, Iowa, USA, scale bar 10.0 mm (new; W. I. Ausich).

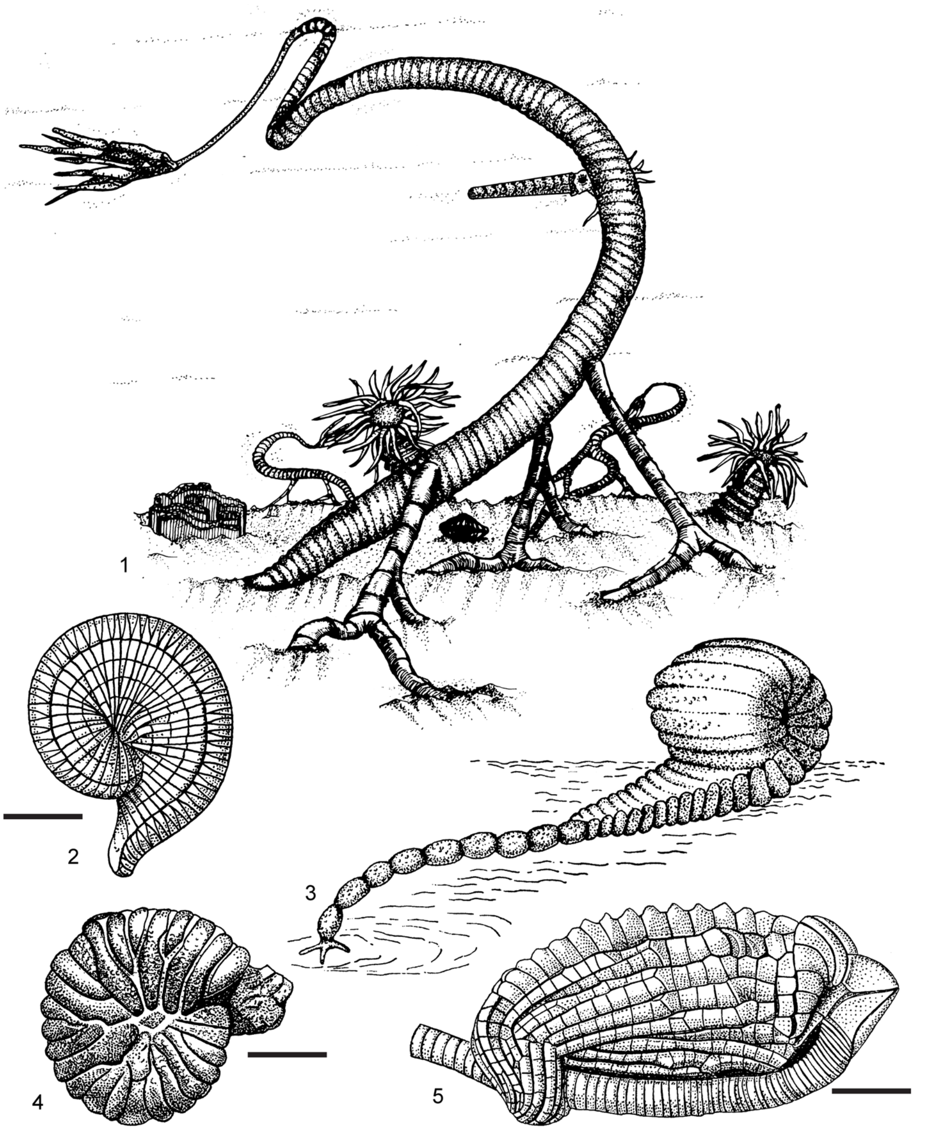

Fig. 23. Trauma postures (diagrammatic) in Paleozoic crinoids with unusual morphology, *1,* Feeding posture interpretation of *Crinobrachiatus brachiatus* (Hall, 1852) (Donovan & Sevastopulo, 1989, fig. 3). *2,* Trauma posture of *Myelodactylus ammonis* (Bather, 1893) (Springer, 1926a, pl. 2,*1*). *3–4,* Trauma posture of *Ammonicrinus; 3, A. sulcatus* Kongiel, 1958 (Piotrowski, 1977, fig. 2); *4, A. wanneri* Springer, 1926a (Krause, 1927, pl. 8,*3*). *5,* Trauma posture of *Halysiocrinus tunicatus* (Hall, 1860) (Springer, 1926b, pl. 30,*19*). Scale bars in *2, 4,* and *5,* 10.0 mm.

Trauma Posture

If a crinoid is subjected to current velocities considerably higher than those in which feeding can occur, its arms close along the oral-aboral axis into a trauma posture, which is either an elongated subcylindrical or subspherical shape, depending on the morphology of the radial and brachial articular facets and arms (Fig. 18.4, Fig. 22.1). The closure of the arms likely results from a combination of the pressure of the current, softening of the MCT that held the arms and

FIG. 24. Preservational postures. *Glyptocrinus decadactylus* (HALL, 1847) from a large bedding surface with specimens displaying both shaving-brush trauma posture and starburst posture, Geier Center, Cincinnati Museum Center catalog no. 50668, scale bar 20.0 mm (new; photo by M. Milam).

pinnules in the feeding posture, and contraction of the adambulacral interbrachial muscles, if present (which also contribute to the meridional posture described on p. 32). When current velocity diminishes (assuming the specimen is still attached to the substratum), the crinoid can resume its normal feeding posture.

If a crinoid in the trauma posture is subject to sustained or further increased current disturbance, whether or not the holdfast or cirri are dislodged or the column breaks, it may be buried in this posture. BAUMILLER and others (2008) called this a shaving-brush posture (Fig. 22.2). If a buried crinoid is not disturbed by subsequent re-exhumation or other sediment disturbance, this trauma posture remains intact and is a characteristic posture for well-preserved fossil crinoids. Tempestites are regarded as a common mode of rapid burial required for preservation of complete crowns (TAYLOR & BRETT, 1996; DONOVAN, 1991; AUSICH, 2001, 2016), and this form of burial would commonly preserve a crown in a trauma posture. Rapid burial of two *Metacrinus rotundus* specimens under muddy volcanic ash in an aquarium produced a closed, straight-armed posture similar to the shaving brush. However, when two other specimens were subjected to slow, intermittent burial, their arms curved strongly aborally, and some autotomized at proximal cryptosyzygial articulations. Detached arms also curved aborally (OJI, MATSUMOTO, & BURNS, 2015, and unpublished observations).

The myelodactylids (Ordovician disparids) have one of the more unusual morphologies among crinoids. Their columnals are elliptical with a fulcral ridge along the long axis of the articular facet, which allows for planispiral coiling of the column parallel to the oral-aboral axis of the crown (Fig. 23.1). When completely coiled, the crown is tucked within a compact coil, and rhizoids along the stalk may further conceal the crown (Fig. 23.2). A variety of feeding postures has been suggested for myelodactylids (e.g., DONOVAN & FRANZÉN-BENGTSON, 1988; DONOVAN & SEVASTOPULO, 1989; SEILACHER & MACCLINTOCK, 2005; DONOVAN, 2006, 2016), but details of their ecology remain uncertain. However, it is probable that the trauma posture for these crinoids involves the crown enclosed within the tightly coiled column and rhizoids. Interestingly, similar crinoid morphologies evolved two more times among Paleozoic crinoids, i.e., Ammonicrinidae (Devonian flexibles) (Figs. 23.3–23.4) and Camptocrinidae (Mississippian–Permian camerates). As in myelodactylids, the trauma coil in ammonicrinids is tight, whereas the coiling in camptocrinids does not fully enclose the crown.

Similarly, calceocrinids (Ordovician–Permian disparids) (see Fig. 1.6), which have a unique morphology and feeding posture, are commonly preserved in a trauma posture (Fig. 23.5). Because calceocrinids lived with the column along the substratum, individuals in this posture could have easily folded their arms along the column and then be readily buried. Consequently, preservation of arms in calceocrinids is relatively more common than in sympatric disparids (AUSICH, 1986).

Starburst Posture

In response to a high-velocity current of sufficient magnitude and rapid enough onset, a crinoid may be dislodged, forced onto the substratum oral surface downward, and buried in a starburst posture before its arms could close into a trauma posture. In this posture, which is less common than the trauma posture, the arms are splayed out into a more-or-less planar fan that conformed to the substratum onto which they were thrust prior to burial. BAUMILLER, MOOI, and MESSING (2008) recognized both starburst-up and starburst-down postures, which depended on the direction of the powerful burial current. MILAM and others (2017) reported an extensive bedding surface with many specimens of *Glyptocrinus decadactylus* HALL, 1847 (Ordovician monobathrid), splayed out into a starburst posture (Fig. 24). The most common crinoid in Silurian inter-reef facies of the midcontinental United States is *Macrostylocrinus styo* LANE & AUSICH, 1995, which is also typically preserved in a starburst posture (LANE & AUSICH, 1995).

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