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Przemysław Gorzelak, Mariusz A. Salamon,
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PALEOECOLOGY AND FUNCTIONAL MORPHOLOGY OF UNUSUAL CRINOIDS: STRETCHING THE LIMITS OF THE CRINOID BAUPLAN

Przemysław Gorzelak[1], Mariusz A. Salamon[2], and William I. Ausich[3]

[[1]Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland, pgorzelak@twarda.pan.pl; [2]Faculty of Natural Sciences, Institute of Earth Sciences, University of Silesia in Katowice, Sosnowiec, Poland, paleo.crinoids@poczta.fm; [3]School of Earth Sciences, The Ohio State University, Columbus, OH, 43210, ausich.1@osu.edu]

INTRODUCTION

The multiplated, mesodermal endoskeleton of echinoderms enabled a wide array of adult lifestyles from infaunal irregular echinoids to predaceous starfish to nektic holothurians. This is true for the Echinodermata as a whole as well as within classes, such as the Holothuroidea and Crinoidea.

All benthic organisms must adapt to the myriad of constraints imposed by the ocean floor and to water conditions above the sediment-water interface, such as the benthic boundary layer. Due to friction on the sea floor, current velocities approach zero close to the sediment-water interface. The interval of reduced current velocity near the sea floor is referred to as the benthic boundary layer (e.g., Rhodes & Boyer, 1982; Richards, 1990). The depth of the benthic boundary layer is a function of sea floor topography. In addition to changes in velocity, the amount of suspended organic particles increases toward the sediment-water interface. At positions progressively closer to the sediment-water interface (Walker & Bambach, 1974), the number of particulate organics increases and the current velocity decreases.

Crinoids presumably evolved during the late Cambrian. However, the oldest fossil crinoids are known from the Early Ordovician, and they began to diversify during the Early Ordovician in shallow-marine habitats dominated by hardgrounds (Wilson & others, 1992; Guensburg & Sprinkle, 1992). Crinoids experienced a radiation during the Middle and Late Ordovician in mixed-substrata settings during the Great Ordovician Biodiversification Event (GOBE; Webby & others, 2004). As passive, epifaunal suspension feeders, crinoids must strike a balance between the flux of water moving through their filtration fans and the concentration of organic particulates in the currents from which they fed. The stereotypical crinoid Bauplan was a set of arms that were elevated up into the water for suspension feeding by a column that was cemented onto the substratum or anchored into the sediment (Macurda & Meyer, 1974; David & others, 2006) (Fig. 1.1). Column height varied among crinoids (and other pelmatozoans), and this provided the structure for many epifaunal tiered communities characteristic of Paleozoic shallow-marine settings (Ausich, 1980; Ausich & Bottjer, 1982; Kitazawa, Oji, & Sumamura, 2007; Messing, Ausich, & Meyer, 2021). During the Paleozoic, crinoids typically occupied the highest tier levels.

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In *Unusual Forms of Fossil Crinoids*, Springer (1926a) discussed morphological departures from typical crinoids in several taxa known to him. Among others, he discussed crinoids with planispirally coiled columns, crinoids with recumbent arms, and *Gilbertsocrinus* Phillips, 1836. These and other crinoids from numerous clades abandoned the iconic crinoid Bauplan and adopted a wide variety of crinoid morphologies. Further, many of these alternative morphologies evolved iteratively in separate clades and times, implying that these unusual morphologies had a positive adaptive value. Predictably, these alternative morphologies have garnered much attention since Springer (1926a) and have been subject to divergent paleoecological interpretations (for recent comprehensive reviews see Seilacher & Hauff, 2004; Hess, 2010; Donovan, 2016).

In this contribution we discuss several of the extreme morphological departures from the prototypical crinoid Bauplan that have evolved during their +485-million-year history, and we discuss their varied functional interpretations. Categories of highly modified crinoids include, among others, those with extreme sizes, crinoids that lived at the sediment-water interface, nektonic and pelagic crinoids, crinoids with a canted crown, crinoids without arms, crinoids

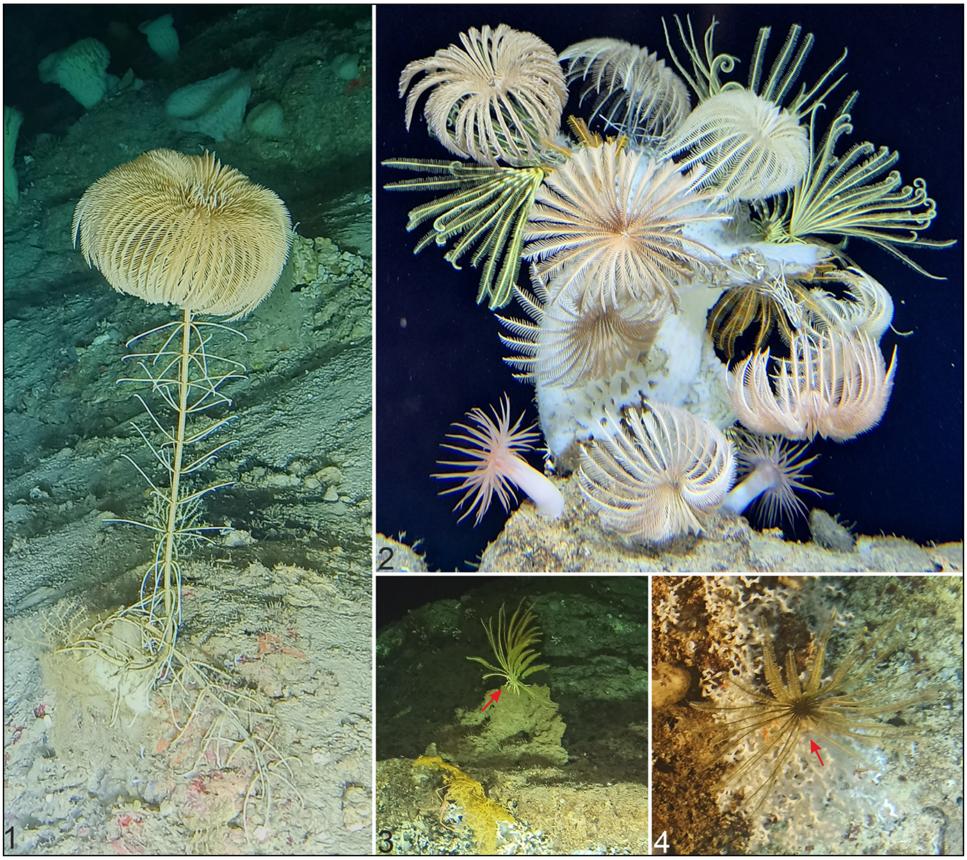

Fig. 1. Extant crinoids. 1, stalked isocrinid *Cenocrinus asterius* (Linné, 1767) 2, a large hexactinellid sponge inhabited by eight individuals of *Endoxocrinus parrae* Gervais, 1835, and two comatulid taxa (two *Neocomatella* specimens (orange, upper center) and three yellow *Crinometra* Clark, 1909) 3, 4, comatulid crinoids *Crinometra* sp. and *Neocomatella* sp. (red arrows), respectively, from the island margin of Isla de Roatán, depths: ~ 150 m (1) and ~ 360 m (2,3,4). Photos: P. Gorzelak (1–3), M.A. Salamon (4).

with the holdfast modified into a bulb, and crinoids with highly modified columnal shapes. In addition, several crinoid genera are mentioned with extreme morphologies for which paleoecological interpretations are needed.

CRINOIDS WITH EXTREME SIZES

Adult crinoids have a wide range of adult body sizes, and the average size for an adult aboral cup or calyx varied significantly during the Phanerozoic (Salamon & others, 2023). Notably, there are clearly extremes. Microcrinoids are anomalously small and are defined as adults having an aboral cup ≤ 2 mm in height (Fig. 2). The question one might ask is, "Aren't these just juvenile specimens of a 'normal'-sized crinoid?" Indeed, there are examples where this has been demonstrated (e.g., Moore & Ewers, 1942). However, the majority of known microcrinoids do not exceed 2 mm in height (Fig. 2). Most microcrinoids are from well-sampled strata. A growth sequence of many microcrinoids is known (e.g., Lane & Sevastopulo, 1981), but so-called normal-sized crinoids that could be considered adults of these microcrinoids do not exist.

Two major clades of Paleozoic microcrinoids are recognized: the disparid Allagecrinidae (Devonian to Permian) and the eucladid Codiacrinoidea (Silurian to Permian) (e.g., Arendt, 1970; Moore & Teichert, 1978; Lane & Sevastopulo, 1982). Post-Paleozoic examples include the Roveacrinida (e.g., Gale, 2023). Microcrinoid arm number varies from none to 16 or more; and, as known, their arms are atomous. In the case of Paleozoic forms, based on the presence of a columnal facet at the proximal end of the aboral cup, microcrinoids had a column, but it is presumed to have also been correspondingly small. No firm evidence for their paleoecology is established, but it can be hypothesized that they were attached to the sea floor and/or cemented to other organisms making them secondary tierers (Bottjer & Ausich, 1987). They must have either fed on very small organic particles and/or gathered nutrition by epithelium uptake (see discussion below). Paleoecology of some post-Paleozoic roveacrinids is discussed below.

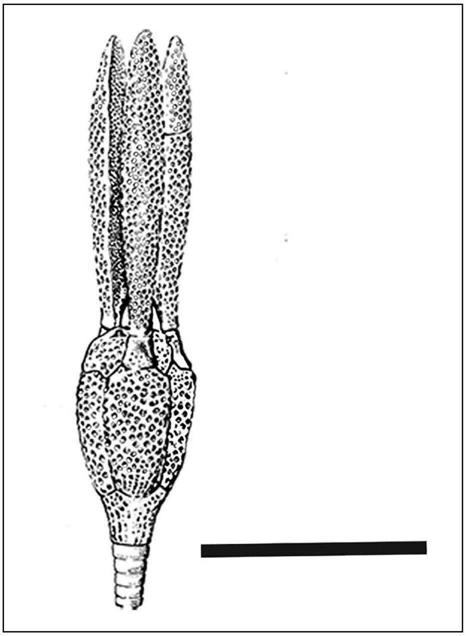

Fig. 2. The microcrinoid *Litocrinus punctatus* (Lane & Sevastopulo, 1981), Scale bar = 2.5 mm. (from Lane & Sevastopulo, 1981, text-fig. 1).

The largest crinoids are the pseudoplanktonic crinoids. As discussed below, these Mesozoic crinoids had large crowns and, in some cases, extremely high columns.

LIFE AT THE SEDIMENT-WATER INTERFACE

Crinoids evolved as suspension-feeding organisms in which the column elevated the arms above the sediment-water interface into higher levels within the benthic boundary layer that had higher current velocities, which was advantageous for a passive suspension feeder. However, rather than being positioned in tiers above the ocean floor, many clades evolved morphologies adapted to life at the sediment-water interface. Examples include crinoids whose crowns were cemented directly to the substratum, crinoids that were unattached, free-living benthos (including living feather stars; Fig. 1.2–1.4), calceocrinids, and species of *Hoplocrinus* Grewingk, 1867.

Crowns cemented directly to the substratum

Among stemless crinoids, there are forms that are directly cementing to hard substrates. The most striking examples are members of cyrtocrinid families: Hemibrachiocrinidae Arendt [including *Brachiomonocrinus* Arendt, 1974, known from the Lower Cretaceous (e.g., Arendt, 1968; Hess & Messing, 2011, Benyoucef & others, 2022); Eudesicrinidae, with *Eudesicrinus* de Loriol, 1882, in 1882–1889 known from the Lower Jurassic–Upper Jurassic (Tithonian); e.g., Hess, Salamon, & Gorzelak, 2011)]; Cotyledermatidae (with *Cotylederma*, Quenstedt, 1852, known from the Lower Jurassic (e.g., Hess & Messing, 2011; Salamon, 2019); and Holopodidae (with *Holopus* d'Orbigny, 1837 and *Cyathidium* Steenstrup, 1847), which are both known from the fossil record and modern oceans. Among the latter family, *Holopus* (Fig. 3) is known from as early as the Early Cretaceous (see Arendt, 1968) and has been recorded from a number of paleoenviroments (including shallow sea) across Europe; today, *Holopus* is only present at great depths (typically below 200 m) in the Caribbean Sea and in New Caledonia (Hess & Messing, 2011). *Cyathidium* is known from as early as the Late Jurassic and was also recorded from various paleoenvironmental settings (including inner shelf and reefs), but it is currently confined to deeper environments with weak or negligible flow conditions in the Caribbean Sea, the Azores, and the Comoros (Hess & Messing, 2011).

Holopus and *Cyathidium* are morphologically similar. They have a cup-shaped

Fig. 3. Different arm postures in adult *Holopus* d'ORBIGNY, 1837; off Half Moon Bay, West End, Isla de Roatán, Honduras, 350 m depth: almost completely closed (upper left), almost fully open (upper center), and partially closed with distal arm tips curled (upper right), red asterisk indicates a dead individual. Photo by P. Gorzelak.

theca directly cementing to the substrate. It is comprised of fused radials and short arms (sometimes asymmetric), which can be rolled spirally, protecting the oral side of the cup (Grimmer & Holland, 1990; Donovan, 1992). Both taxa typically occur attached to vertical boulders, overhanging walls, and cave ceilings (e.g., Macurda & Meyer, 1974) (Fig. 3). It was speculated that these crinoids can be raptorial feeders; i.e., they are capable of contracting their arms to capture larger prey items (Grimmer & Holland, 1990). However, several submersible observations revealed that the arm closure is due to external stimuli (e.g., water movements generated by the approaching submersible); thus, arm closure may have a defensive function (Syverson & others, 2015). The arms of *Holopus* are arranged in a funnel facing down current or are cone-shaped and opened outward or sideways (Macurda & Meyer, 1974; Donovan & Pawson, 2008; Syverson & others, 2015), and its theca can be asymmetric, which might be affected by prevailing unidirectional flow conditions (Žitt, 1983).

Crinoids as unattached, free-living benthos

Through the Phanerozoic many different crinoid clades shed their column during ontogeny and as adults were free-living benthos on the sea floor or epizoic on other organisms (Fig. 1.2). These crinoids were primarily in the lowest suspension-feeding tier that had a high density of particulate organics but low current velocities. Paleozoic examples, among others, include the Ordovician *Trecrinus* Semenov & others, 2021, and some species of *Hoplocrinus*; Devonian eucladid *Edriocrinus* Hall, 1858; the Mississippian to Permian Agassizocrinidae; the Mississippian Staphylocrinidae; and the Permian *Timorocidaris* Wanner, 1920. During the post-Paleozoic, examples among the Articulata include some members of Roveacrinida (Middle Triassic–Late Cretaceous?), and the largest group of stemless crinoids—the feather stars of the order Comatulida (Jurassic? to Holocene) that are present throughout the oceans today. Examples of this morphology are described in several sections below.

Agassizocrinus Owen & Shumard, 1852 and *Paragassizocrinus* Moore & Plummer, 1940

Agassizocrinus and *Paragassizocrinus* are late Mississippian and Pennsylvanian examples, respectively. Juveniles of these genera had a narrow column that was truncated proximally through ontogeny and overgrown by the large, robust, fused infrabasal circlet called the infrabasal cone. The shape of the infrabasal cone varied from high conical to low bowl. Isolated infrabasal cones of *Agassizocrinus* are quite common in many upper Mississippian marine strata in the United States (Ettensohn, 1975, 1980, 1981, 1984). These crinoids have been interpreted to have inserted their infrabasal cone into the substratum with longer arms erect for feeding and shorter arms spread along the substratum for stability (Ettensohn, 1975, 1980) (Fig. 4). The lifestyle of these crinoids may have been similar to *Uintacrinus* Grinnell, 1876 and *Marsupites* Mantell *in* Miller, 1821, discussed below, and to the living crinoid *Comatula rotalaria* Lamark, 1816 (see Messing, Ausich, & Meyer, 2021).

Hybocrinidae

The Hybocrinidae is an Ordovician family with morphologically unusual crinoids that include variations in thecal symmetry, position of ambulacra (only on the arms, on the arms and on the surface of aboral cup plates, and only on the surface of aboral plates) (for the latter, see the discussion of *Tripatocrinus* Sprinkle, 1973 and *Cornucrinus* Regnèll, 1948 below in the section on "Crinoids without arms").

Another unusual character among some hybocrinids is the lack of a column in adults. As discussed in Männil (1959) and Rozhnov (1985a, b) (e.g., *Hybocrinus usvensis* Rozhnov, 1985b) had a typical crown with arms and *Hybocrinus* a medium cone/bowl-shaped aboral cup, but the column was absent in adults. Presumably, the life position of these species was similar to that of *Agassizocrinus* and *Paragassizocrinus* that had the aboral cup inserted into the substratum and were low-tier suspension feeders.

Even more striking is *Trecrinus* (Fig. 5). *Trecrinus* lacks a column as an adult and has an aboral cup comprised of five basal plates, five radial plates, and a radianal plate. However, only three of the radial plates have arms, and these arms extend straight outward. The result is a crinoid with three stout arms that laid directly on the substratum. If on an unconsolidated substratum, *Trecrinus* would have employed the "snowshoe" strategy to keep from sinking into the sediment. It fed from water directly above the sediment-water interface (Semenov & others, 2021).

Feather stars

Feather stars are used herein to refer as a general term for the Comatulida (Articulata) that lack a column as an adult. The term "feather stars" is used because, with genomic phylogenetic study, Rouse & others (2012) demonstrated that columns re-evolved through paedomorphsis at least twice within the Comatulida.

Various lifestyles have evolved among feather stars (Messing, Ausich, & Meyer, 2021). The basal-most plate of the feather star aboral cup is the centrodorsal to which grasping cirri are attached. Some feather stars attach directly to the sea floor and project their arms upward to form a filtration fan (Fig. 1.3, 1.4). The fan posture can be disk-shaped, parabolic, or conical (Messing, Ausich, & Meyer, 2021). Some feather stars

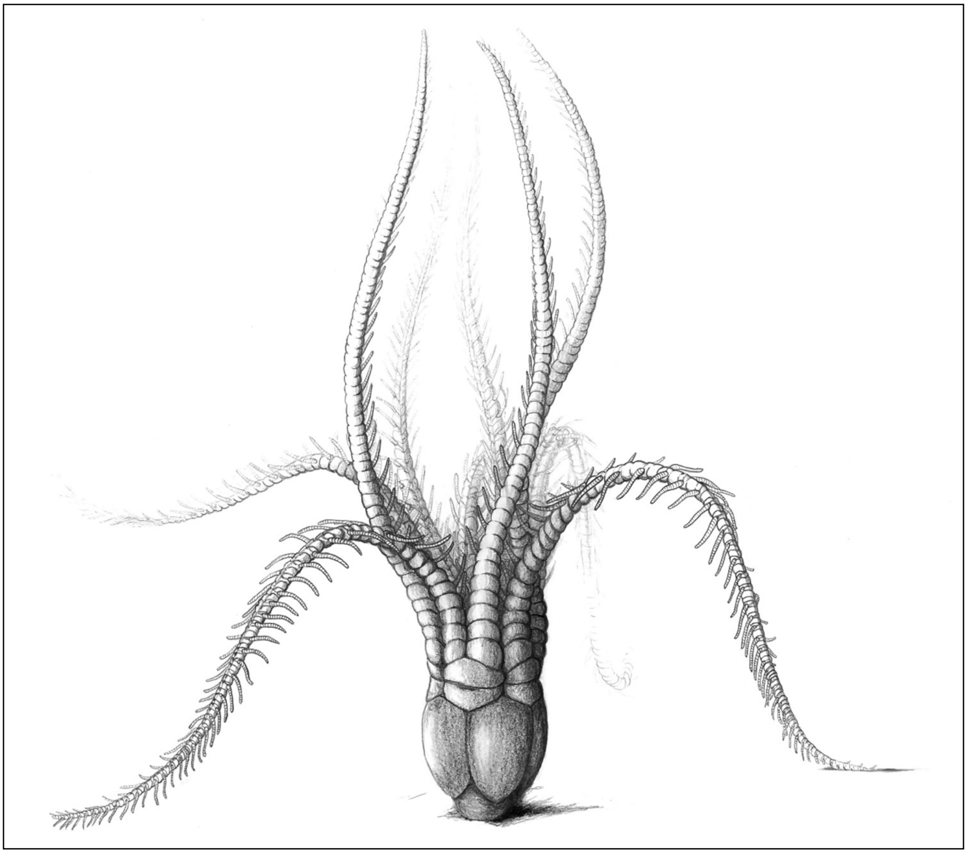

Fig. 4. Life reconstruction of *Agassizocrinus papillatus* Worthen, 1882. Reconstruction: Magdalena Łukowiak (based on Ettensohn, 1975, text-fig. 8). Width of the calyx ~1.0 cm.

attach to reefs. Many of these may form a filtration fan while perched on a high point to take advantage of current flow, whereas others are semicryptic and tucked within the reef infrastructure. The currents in and around shallow-water reefs have a wide range of turbulence with multiple current directions. Feather stars adapt to a unidirectional flow regime by extending one or more arms upward or by forming a filtration fan. Alternatively, crinoids in more cryptic reefal niches assume a multidirectional posture (Messing, Ausich, & Meyer, 2021). Some feather stars are secondary tiers that attach to other organisms well above the substratum into a higher suspension-feeding tier (Fig. 1.2).

Perhaps the most radical departure from the crinoid Bauplan are crinoids that can swim. Widely considered an antipredation adaptation (e.g., Meyer & Macurda, 1977), if disturbed, some feather stars can detach from the substratum and, with coordinated arm and pinnule motion, can gain positive buoyancy and swim away from potential danger.

Uintacrinids

The stratigraphically important Late Cretaceous uintacrinoids (Uintacrinoidea *sensu* Zittel, 1879) are among the most peculiar of all feather stars. These stalkless crinoids had a large, globular and non-cirriferous theca with long arms comprised of low brachials with muscular and syzygial articulations (Rasmussen, 1961). Two uintacrinoid genera are known. *Marsupites* is characterized by a theca consisting of 16 plates that are almost equal in size and shape (i.e., one centrale, five infrabasals, five basals, and five radials). *Uintacrinus*, in turn, had longer arms and had a theca comprised of many small plates (one centrale, up to five infrabasals, five basals, five radials, ten primibrachials, and a variable number of fixed interradial and pinnular plates, and secundibrachials). Structurally, the theca of both genera reveals similarities to carbon fullerene and fulleroid molecules, respectively (Hoyal & Hunter, 2020).

Owing to their highly bizarre anatomy, the mode of life of uintacrinoids has been a matter of long debate. Initially, a pelagic or pseudopelagic mode of life for these crinoids was favored. For instance, the presence of an enlarged globular theca without holdfast with long flexible arms led Bather (1896), Kirk (1911), Abel (1927), Hyman (1955), and Breimer & Lane (1978) to conclude that these crinoids were able to swim actively (with the oral side either directed downward or upward) in the water column, and they were considered to have positive buoyancy

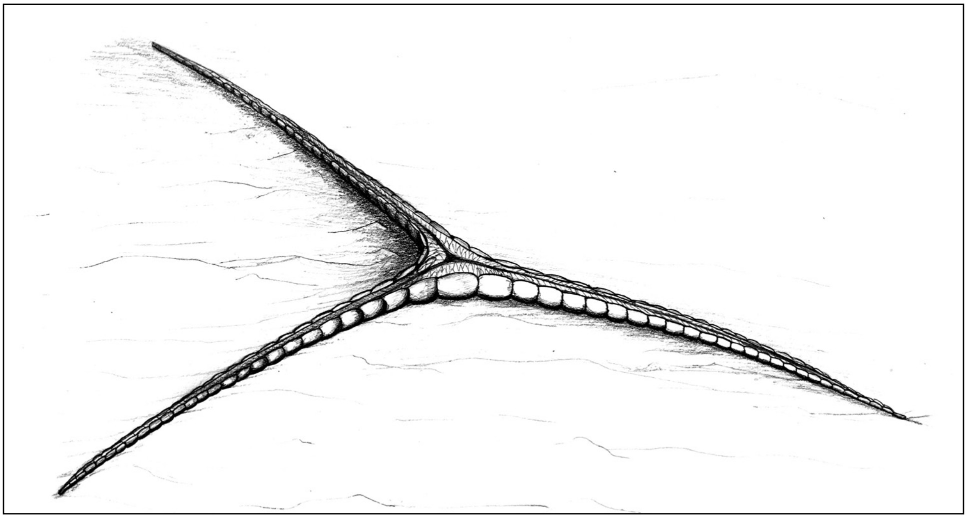

Fig. 5. Life reconstruction of *Trecrinus schmidti* Semenov & others, 2021. Reconstruction: Magdalena Łukowiak (based on Semenov & others, 2021, fig. 2). Length of the arm ~5.0 cm.

thanks to the supposedly entrapped gas or oil within the theca. A pseudopelagic lifestyle was also proposed, for example by Springer (1901), who speculated that these crinoids were living attached to floating objects. More recently, Seilacher & Hauff (2004) suggested, based on morphologic (i.e., the presence of a balloon-like cup comprised of thin plates with no central ballast and with reduced branching of arms) and taphonomic (supposedly no specimens with splayed arms preserved) grounds, that these crinoids might have been hemipelagic dredgers (passive deposit feeders) with a theca drifting just above the bottom and dragging heavier long arms on the sediment to collect food detritus. In contrast, a benthic mode of life for uintacrinoids was advocated by Jaekel (1918), Dacqué (1921); Struve (1957); Milsom, Simms, & Gale (1994); Meyer & Maples (1995); Meyer, Milsom, & Webber (1999); Meyer & Milsom (2001); Webber, Meyer, & Milsom (2008); and Gorzelak & others (2017). Arguments used to support the benthic hypothesis include: (1) functional morphology (poorly developed muscular arm articulations and incorporation of proximal brachials into the thecae, both of which restrict arm mobility (arguing against a nektonic lifestyle), and the presence of robust and heavily calcified skeletal plates rather than thin plates, which would negatively impact buoyancy) and (2) taphonomy (preferential preservation of theca lying on their side and no associated driftwood). Most of the latter authors postulated an oral-up posture, except Struve (1957), who suggested that uintacrinoids could have lived in a similar way as asteroids, with the oral side facing downward. There were also different opinions on whether these crinoids were rheophobic semi-infaunal (Milsom, Simms, & Gale, 1994) or rheophilic epibenthic (Hess, 1999c). Most recently, however, epizoans (serpulids and bryozoans) encrusting thecal plates of *Marsupites* were reported (Salamon & Gorzelak, 2017). The fact that these epizoans are attached to the convex side (latera) of plates only, and in some cases of partially articulated theca, is suggestive of *syn vivo* infestation, which strongly favors the rheophilic epibenthic mode of life of uintacrinoids. Furthermore, infaunal fossils are not expected to be preserved on the bedding planes with cups lying on their side. Notably, Messing & others (2004) stressed that some modern non-cirriferous comatulids (e.g., *Comatula rotalaria* Lamark, 1816) with similar brachial morphology as uintacrinids may hold some of their long arms for feeding in a vertical position and a few other arms flexed slightly downward and touch the bottom for stability. Additionally, the arm length/theca height ratio of uintacrinoids is comparable to those observed in some modern crinoids.

Notably, data on skeletal microstructure (Gorzelak & others, 2017) indicated that the thecal plates of uintacrinoids have no stereom adaptations for preventing putative gas leaks and/or ingress of water (such as imperforate stereom layers) in the case of epidermal perforation. Instead, their thecal and arm plates are massive and comprised of medium to coarse, clearly structural galleried stereom and fine, deeply penetrating galleried stereom characteristic for the through-going ligaments binding adjacent plates. These stereom types are disrupted by growth bands comprised of perforate layers, which are known to increase plate strengthening and resistance to abrasion. It is noteworthy that similar stereom banding occurs in many shallow-water epifaunal regular echinoids and is not observed in modern infaunal irregular echinoids (Smith, 1980). The stereom organization in uintacrinoids is similar to that observed in modern benthic crinoids, but it differs markedly from microstructural design displayed by pelagic and pseudoplanktonic crinoids. Most importantly, as noted below, minute pelagic roveacrinids are characterized by “spongy” microarchitecture of thecal and brachial plates to reduce their weight, whereas pseudopelagic traumatocrinids or seirocrinids had lightweight construction to reduce the load of the driftwood by having pore systems of intercolumnal fossulae and longitudinal tubuli or possessing a distally tapered column with lensoid intercolumnar spaces, respectively. Thus, based on the current state of knowledge, it seems that uintacrinids were epibenthic (Fig. 6). Their enlarged globular cup, finely ornamented with ridges and domed microstructure increased the bearing surface and appeared to have been an adaptation (the so-called iceberg strategy) to live on soupy, muddy bottoms. A wide geographic distribution of these crinoids within a short stratigraphic range can be explained by a prolonged planktotrophic larval stage allowing dispersal over great distances.

Calceocrinids - column recumbent along the sediment-water interface

The origination and initial radiation of the Calceocrinidae occurred during the Great Ordovician Biodiversification Event (GOBE) (Webby & others, 2004) and was a striking departure from the prototypical crinoid Bauplan. Calceocrinoids had a column that laid recumbent along the sea floor (Fig. 7). The basal and radial circlets were connected across a moveable articular ridge. The crown was poorly or perfectly bilaterally symmetrical with crown symmetry along the E-BC plane.

Despite the unorthodox Bauplan, this morphology was the basis for the longest-ranging, well-defined crinoid family: Late Ordovician to Permian (Cisuralian). Predictably, the paleoecology of a clade with such a radical departure from crinoid morphology has engendered much discussion (e.g., Ringueburg, 1889; Jaekel, 1918; Springer, 1926b; Moore, 1962; Brower, 1966, 1977, 1985, 1990; Kesling & Siegler, 1969; Breimer & Webster, 1975; Brett, 1981; and Ausich, 1986, 2022). Ausich (2022) reexamined the

Fig. 6. Life reconstruction of *Marsupites*. Reconstruction: Magdalena Łukowiak (based on Gorzelak & others, 2017, fig. 5). Width of the calyx ~3.0 cm.

various paleoecological hypotheses proposed for the Calceocrinidae and studied the preserved stereom of *Halysiocrinus tunicatus* (Hall, 1860).

The competing hypotheses for the calceocrinid life style include: 1, the drooper model with an erect column and the crown hanging downward (Ringueburg, 1889); 2, the runner model with the column recumbent along the sediment-water interface, and the crown opening up into the lower suspension-feeding tier (Jaekel, 1918; Springer, 1926b; Ramsbottom, 1952; Moore, 1962; Brower, 1966, 1977, 1990; Brett, 1981; Ausich, 1986); 3, free swimming pelagic crinoids (Schmidt, 1934); 4, the weather vane model (Kesling & Sigler, 1969); and 5, the kite model (Breimer & Webster, 1975). Ausich (2022) agreed with most previous authors that calceocrinoids lived with their column recumbent along the sediment-water interface. In a resting posture, the arms would have been closed over the proximal column, and when feeding, their arms were raised into the lowest epifaunal tier with currents striking the aboral side of the arms. This runner life position is based on several studies that identified features of the column and holdfast that indicate an obligate runner posture (Brower, 1977; Ausich, 1984; Eckert, 1984; Eckert & Brett, 1985; Donovan, 2016). Further, ligaments were the only connecting tissue between moveable articulations in the Calceocrinidae (Ausich, 2022), so all aboral cup opening and closing would have been relatively slow, compared to movement controlled by muscles.

As noted previously, the Calceocrinidae are the longest-ranging crinoid family, and calceocrinids were an integral part of shallow-water suspension-feeding paleocommunities from the Late Ordovician through the Middle Devonian (Ausich, 2022). Ausich (1986) speculated that the Devonian radiation of fenestrate bryozoans may have altered the nature of the lower tiers making it less favorable to passive suspension feedings. Despite the post-Givetian decline in calceocrinid generic biodiversity, one calceocrinid (*Halysiocrinus* Ulrich, 1886) was commonly abundant in many Viséan suspension-feeding communities. Calceocrinids persisted into the early Permian.

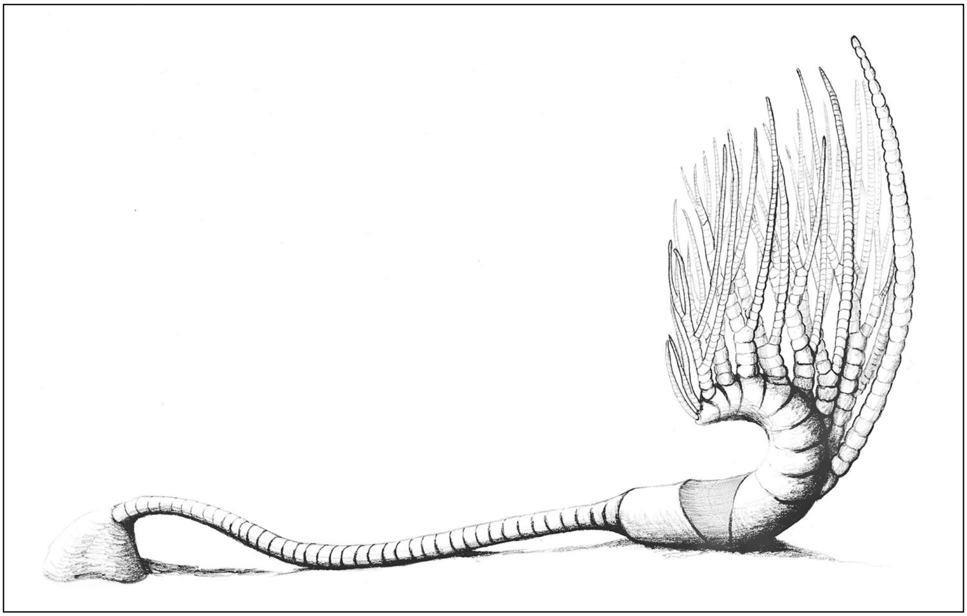

Fig. 7. Life reconstruction of a calceocrinid. Reconstruction: Magdalena Łukowiak (based on Ausich & others, 1999, fig. 29). Width of the calyx ~1.0 cm.

NEKTONIC AND PELAGIC CRINOIDS

Roveacrinids

Roveacrinids (Roveacrinida) (Middle Triassic to Upper Cretaceous?) are highly miniaturized, stalkless post-Paleozoic crinoids. The largest roveacrinids have an aboral cup height up to ~4 mm, but the aboral cup of most roveacrinids is < 2 mm (Hess & Messing, 2011). They are characterized by an aboral cup comprised of thin radial plates, which overgrew small basals, thereby forming the characteristic double cavity – an upper (oral) cavity above the basals and a lower one below the basals (Rasmussen, 1978). Their delicate cups and arms with sloping cryptosynarthries are both typically sculptured by spines, ridges, "wings", and flanges. Given that their small size and characteristic morphologic features increased surface and/or frictional drag to reduce the sinking rate and skeletal weight, these crinoids have been commonly interpreted as pelagic forms (Hess, 2010). This interpretation is consistent with their widespread distribution and occurrence in both euxinic and high-energy facies (e.g., Gale, 2016). According to some authors, the lower aboral cavity in the theca might have stored gas or oil and, thus, functioned as a hydrostatic organ (e.g., Schneider, 1989, 1995; Jagt, 1999, 2005). However, this hypothesis is highly conjectural; as rightly noted by Hess (2015), this might even turn the cup over so that the arms might have been hanging down toward the bottom.

Whether roveacrinids were nektonic or floating passively has long been a matter of debate. Furthermore, a benthic mode of life (during at least part of their lives) for some roveacrinid species was proposed (e.g., Hess, 2002). For instance, some roveacrinid species with or without much arm reduction (Applinocrininae; Gale, 2016) and those with rigid plates without any flanges, hollow microstructure, or evidence of skeletal lightening were suggested to have been benthic (Milsom, 1994, 1999). Furthermore, it has been suggested that Jurassic saccocomids, the most iconic representatives of the group, were mud-stickers, in that their stiff lateral "wings" served as a protection against sinking into loose sediment (the so-called snowshoe strategy) (Milsom, 1994; Manni, Nicosia, & Tagliaozzo, 1997). Indeed, the hypothesis that the "wings" of these crinoids played a role as parachutes to facilitate floating and prevent sinking (Jaekel, 1892; Hess, 1999b, 2002; Seilacher & Hauff, 2004) is problematic given their non-horizontal position (Fig. 8). Furthermore, these structures added some weight, thus negatively affecting the buoyancy. However, as noted by Brodacki (2006), these "wings" may have simply increased the crinoid surface and/or drag friction and, together with sculptured morphology and highly flexible muscular arms, are indicative of a pelagic mode of life (Fig. 8). Interestingly, Seilacher & Hauff (2004) suggested that these crinoids were able to actively feed in the water column by adopting a so-called snap-swimming lifestyle (successive coiling

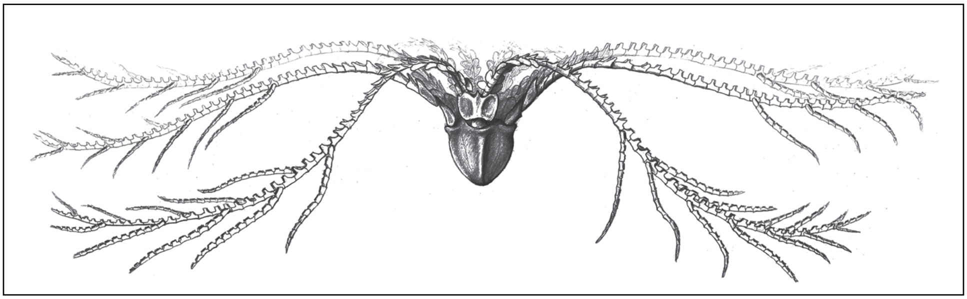

Fig. 8. Life reconstruction of a roveacrinid. Reconstruction: Magdalena Łukowiak (based on Brodacki, 2006, fig. 1). Width of the calyx ~2.0 mm.

and outstretching the arms provided by the antagonistic role of muscles joining oral processes and aboral ligaments). However, this hypothesis was challenged by Hess & Etter (2011) who argued that food collection during the downward arm movement is improbable because: (1) food particles would have not reached the food grooves but rather streamed past the oral processes, and (2) there is no evidence for extending muscles into the paired oral processes of brachials. Hess & Etter (2011), in turn, advocated a "pulsating funnel" model in which the food was collected by active upward movement of the arms enabled by contraction of muscles proximally, leading to inward and upward flexure of the arms. However, this model is also not without problems. First, modern crinoids are leeward suspension feeders with oral-downstream posture; this orientation prevents direct impingement of the current on the amubulacral grooves and enables food particle manipulation by tube feet (Meyer, 1982). Direct impaction of a food particle on to a tube foot is another type of particle capture (Rubenstein & Koehl, 1977; Baumiller, 1997). Thus, saccocomids would represent a highly unusual case of crinoids actively feeding on particles directly captured on the oral side of the arms. Second, it should be highlighted that, in common to some modern crinoids having knobby processes on interior faces of brachials or comb-like structures in pinnules, tube feet in sacccocomids might have been simply extended between the armlets, enabling more food collection. Third, it is noteworthy that some Cretaceous roveacrinids have brachials with muscle fossae extending to the processes that arise from the articular facet (Jagt, 2005, fig. 3c). Thus, it seems theoretically probable that food might have been collected actively during the downward stroke of ligament recoil. Nevertheless, the energetic cost of such an active feeding mode would be probably too high. Assuming the roveacrinoids were only slightly negatively buoyant, active swimming at times upwards, and then feeding downstream during passive sinking, remains a possibility. A passive drifting and entirely planktonic mode of life should be rejected because crinoid food capture essentially depends on movement of particles through the arms. The mode of life of many roveacrinid species remains a mystery.

PSEUDOPLANKTONIC CRINOIDS

At different times during geological history, some crinoid taxa have convergently adapted to a pseudoplanktonic mode of life. Iconic examples are *Traumatocrinus* Wöhrmann, 1889 and *Seirocrinus* Gislén, 1924, which are commonly preserved attached to driftwood preserved in anoxic sediments (Simms, 1986). These Mesozoic crinoids evolved distinct morphologic features that are considered to have been critical to the so-called tow-net filtration function (Seilacher & Hauff, 2004). For instance, they developed extremely long columns, approaching ~11 m in *Traumatocrinus* (Hagdorn, 2016) and ~20 m in *Seirocrinus* (Simms, 1986), which enabled their crowns to be dragged through the water due to the vertical velocity gradient between the surface and deeper water layers. In addition, the stalk of both taxa has some features to maintain the buoyancy and reduce the load of the driftwood. In particular, traumatocrinids developed special pore systems of intercolumnal fossulae and longitudinal tubuli, whereas seirocrinids formed distally tapered columns with lensoid intercolumnar spaces (Hagdorn, 2016; Gorzelak et al., 2025). Furthermore, columns of *Traumatocrinus* are commonly bent proximally, which enabled them to keep their filtration fan in a vertical position. Proximal flexure of the column in seirocrinids was not needed due to their much longer columns. Instead, to avoid mechanical tilting of the crown, the proximal part of their column is stiffened by radials extending down toward the column (Seilacher & Hauff, 2004). Lastly, both crinoids developed enlarged calyxes (up to

~40 cm in diameter in *Traumatocrinus* and up to ~100 cm in diameter in *Seirocrinus*) and dense filtration fans with many endotomous branches resulting in as many as 600 arm tips (Seilacher & Hauff, 2004), which certainly increased their feeding capacity.

Interestingly, these crinoids preferentially settled the regions of least resistance and more or less free of bark; i.e., the back of a floating log (Fig. 9), which is supposed to be the most efficient place for attachment for tow-net filtrators (Hess, 2010). Furthermore, some recent quantitative simulations have also demonstrated that a single seirocrinid assemblage attached to a large floating log might have lived there for as long as 20 years (Hunter et al., 2020). This seems to be a sufficient time needed to reach maturity

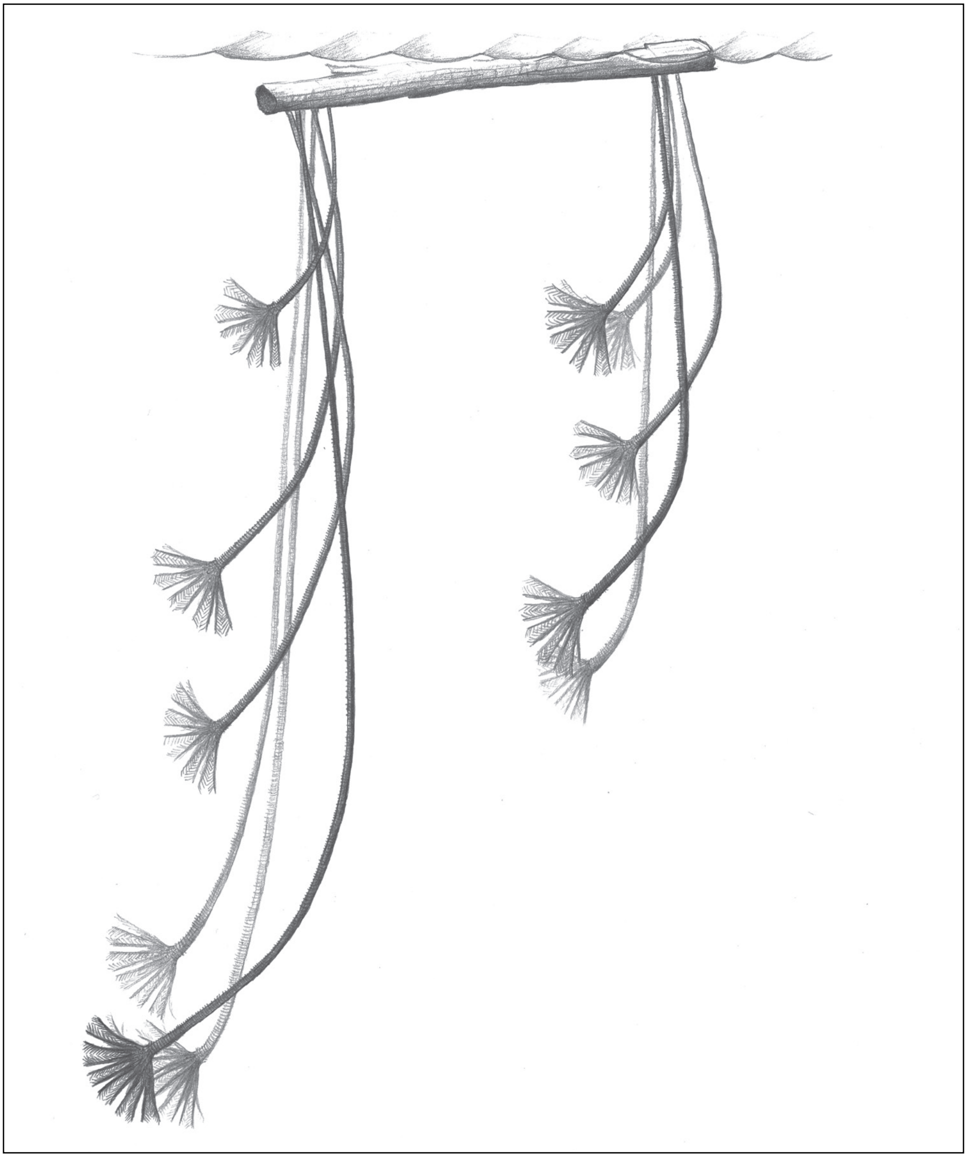

Fig. 9. Life reconstruction of traumatocrinids. Reconstruction: Magdalena Łukowiak (based on Hess, 2010, fig. 7). Width of the calyx ~2.0 cm.

before the log would sink due to wood decay and water infiltration or due to increasing weight from constant settlements of new generations on the same piece of driftwood (or as epizoans to older host specimens). Notably, a remarkable four-generation seirocrinid assemblage has been recently described (Matzke & Maisch, 2019).

Curiously, the vertical velocity gradient between the floating log and the crown suspended below would not work well for the medium to short-stalked pentacrinitids, which are also sometimes preserved associated with driftwood and, thus, are considered to be pseudoplanktonic (Simms, 1999). Seilacher & Hauff (2004) attempted to solve this puzzle by assuming that pentacrinids actively filtered food by using their long and densely packed wing-like cirri, which might have produced currents. Subsequently, Hess (2010) rejected this hypothesis by mentioning that both short and long stalks are known in pentacrinids. Furthermore, the latter author added that isocrinid cirri lack muscles. Indeed, flattened cirri of *Pentacrinites* Blumenbach, 1804 are exclusively comprised of galleried stereom characteristic for ligaments (P. Gorzelak, personal observations). Furthermore, it is worth noting that similar wing-like cirri are also known from the Middle–Late Jurassic benthic isocrinids (e.g., Salamon & Feldman-Olszewska, 2018). A large surface area of driftwood and, consequently, a large force of drag would enhance the tow-net filtration properties of short-stalked pentacrinitids (and juvenile traumatocrinids and seirocrinids); still, this was likely not sufficient to create current flow through the arms. Therefore, as noted by Hess (2010), pseudoplanktonic pentacrinids probably fed by using several mechanisms and sources, including tow-net filtration and capturing of phytoplankton concentrating (and/or reproducing) around the logs or zooplankton moving vertically during diurnal migration.

The co-occurrence of crinoids and logs is also present in Devonian strata. Examples include the Devonian of the United States (Wells 1939, 1941; McIntosh, 1978), Morocco (Webster & Becker, 2009), and Germany (Bohatý & others, 2021). Compared to the Mesozoic occurrences discussed above, the Devonian occurrences are rare and more poorly preserved. Therefore, the paleoecological explanations are more speculative compared to those from the Mesozoic.

CRINOIDS WITH CANTED CROWNS

In most living stalked crinoids (isocrinids), the proximal column bends below the crown enabling inclination of the oral side at an angle or perpendicular to the substratum, which allows for a parabolic or conical suspension-feeding posture. However, in certain stalked crinoids, which are permanently cemented to the substrate, the tilting of the crown is obligate and is achieved by a canted calyx. Among the best known examples of such crinoids are the Permian flexible crinoid *Calycocrinus* Wanner, 1916, as well as fossil and extant cyrtocrinids: *Cyrtocrinus* Jaekel, 1891 [Middle Jurassic–Lower Cretaceous of Europe: Jaekel (1891), Szörényi (1959), Hess (1975), Rasmussen (1978), Hess & Messing (2011), Salamon (2022), and Arendt (1974) indicated that the first occurrence of this taxon was recorded from the Hettangian of France]; *Torynocrinus* Seeley, 1866 [Lower Cretaceous of Europe]; *Salamonicrinus* Trzęsiok, 2015 [Upper Jurassic of southern Poland]; *Ascidicrinus* Hess, Salamon, & Gorzelak, 2011 [Upper Jurassic of southern Poland]; *Hemicrinus* d'Orbigny, 1850, in 1850–1852 [Upper Jurassic–Lower Creatceous of Europe]; *Gammarocrinites* Quenstedt, 1858 [Upper Jurassic of Europe]; and *Neogymnocrinus* Hess, 2006 [Holocene of southwestern Pacific Ocean]. The cups of these cyrtocrinoids are typically spoon-shaped and are comprised of distinctly asymmetric radials fused at a right or almost right angle with an unjoined proximale. Such asymmetry is commonly ascribed as adaptation to a constant unidirectional current (Žitt, 1983). A modern representative of these crinoids – *Neogymnocrinus richeri* (Bourseau, Améziane-Cominardi, & Roux, 1987) commonly lives at great depths (typically between 300 and 500 m of southwestern tropical Pacific Ocean; e.g., Bourseau, Améziane-Cominardi, & Roux, 1987; Hess, 1999b; Hess & Messing, 2011). While feeding, this species displays a combination of the fan and canted posture. Its crown is comprised of five arm rays: four of them radiate outward in a fanlike plane, and the remaining one is strongly reduced in size (Bourseau, Améziane-Cominardi, & Roux, 1987).

CRINOIDS WITHOUT ARMS

A key aspect of the iconic crinoid Bauplan was the extension of the ambulacral system above the theca onto arms. With the arms extended, food particles are captured by tube feet (Meyer, 1982), and respiration also occurs through the tube feet. This extended ambulacral system is a noteworthy departure from most Blastozoa in which the ambulacral system is recumbent along the thecal surface (e.g., blastoids, rhombiferans, and diploporans).

Reduction of arm number was a trend in some eucladids, and total elimination of arms occurred several times in different clades. In some of these clades, ambulacra were recumbent along the theca as in blastozoans (e.g., the Ordovician crinoids *Cornucrinus* Regnèll, 1948 and *Tripatocrinus* Sprinkle, 1973) (Fig. 10). However, in other clades arms and recumbent ambulacra were eliminated, including *Abrachiocrinus* Wanner, 1920 (Permian); *Atremacrinus* Wanner, 1929 (Permian); *Embryocrinus* Wanner, 1916 (Permian); *Parazophocrinus* Strimple, 1963 (Silurian); and *Zophocrinus* Miller, 1891 (Silurian). Many of these taxa have very small thecae (e.g., *Abrachiocrinus*), but others are large (e.g., *Cornucrinus*, *Parazophocrinus*, and *Tripatocrinus*). Those crinoids without exposed ambulacra must have obtained nutrition and oxygen exclusively through epidermal uptake as documented in some living echinoderms (Jangoux & Lawrence, 1982; Flammang, 1996). This is a radical departure from nearly all other crinoids.

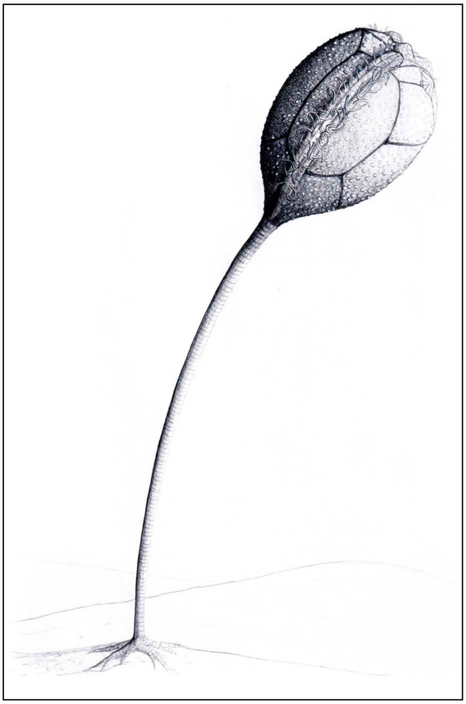

Fig. 10. Life reconstruction of *Tripatocrinus*. Reconstruction: Magdalena Łukowiak (based on Sprinkle, 1973, text-fig. 5). Width of the calyx ~1.0 cm.

CRINOIDS WITH THE HOLDFAST MODIFIED INTO A BULB

Scyphocrinids

Scyphocrinids (Scyphocrinitidae sensu Jaekel, 1918) are a stratigraphically important late Silurian–Early Devonian group of camerate crinoids. These remarkable crinoids are characterized by a relatively large (~40 cm) crown and high (up to about 3 m) stem ending with a bulbous, chambered structure (commonly ~10-20 cm in diameter), the so-called lobolith (Haude, 1972; Haude &

others, 2014). Two basic types of loboliths were described: a cirrus lobolith with many unequal chambers comprised of numerous branching radices, and a plate lobolith with four to seven chambers comprised of two to three layers of thin plates (Haude, 1972; Seilacher & Hauff, 2004; Hess, 2010). Loboliths have confused paleontologists for more than a century. They have been interpreted as: brood-pouches (Haeckel, 1896), genital structures (Jaekel, 1904), holdfasts (Springer, 1917; Ray, 1980; Brett, 1984), parasitic cysts (Haeckel, 1896; Kirk, 1911; Abel, 1920), and buoyancy organs (e.g., Schuchert, 1904; Bather, 1907; Haude, 1972, 1992; Hess, 1999a, 2010; Prokop & Petr, 2001; Seilacher & Hauff, 2004; Haude et al., 2014). The latter interpretation was commonly accepted and adopted in the previous two editions of the Treatise on Invertebrate Paleontology (Ubaghs, 1978; Hess, 2010). It implies that scyphocrinoids were planktonic tow-net filtrators: their floating lobolith (drifting passively either at the water's surface or below it, thus taking advantage of an interface of two water bodies in a stratified sea) was moved along by currents, dragging along the filtration fan, which was suspended below. Arguments used to support a planktonic lifestyle for scyphocrinids include: (1) functional morphology (globular shape and chambered structure of the lobolith implying a hydrostatic function, long stem with dense crown, which are both critical for tow-net filtration), (2) taphonomy (wide geographic distribution of loboliths in different facies, rarely associated with the crown), (3) paradigm approach [noting similarities between buoys and loboliths and recognition of a putative evolutionary trend toward functional optimality (transition from cirrus to plate lobolith)], and (4) theoretical buoyancy calculations of the presumed gas infillings. In a recent paper Gorzelak & others (2020) critically evaluated this hypothesis by synthesizing previous data and providing new evidence from skeletal micromorphology and theoretical biomechanical modeling. The latter authors concluded that these remarkable crinoids were epibenthic rather than planktonic (Fig. 11). The following arguments were invoked to support their statements:

(1) The lobolith was not a perfect air-tight structure; i.e., microstructural adaptations (including internal and external imperforate stereom layers) for preventing gas leaks, ingress of sea water, and/or protecting from destructive solar radiation, wind, high-energy wave action, and storm events are not observed. Noteworthy, both plate and radice network contain open spaces between ossicles.

(2) The overall morphology is similar to many benthic crinoids but is different from taxa thought to be pseudoplanktonic tow-net filtrators, which developed much longer stems and denser filtration fans. Notably, theoretical calculations imply that the tow-net mode of feeding of scyphocrinoids would be highly ineffective because of small relative velocities between the towed filter and the ambient water.

3) Numerous examples of epibionts preferentially encrusting the proximal side of loboliths (including epibenthic platyceratid gastropods and bryozoans) are known, which certainly might have affected the buoyancy of scyphocrinoids (e.g., Hess, 1999a).

4) Loboliths are commonly preserved unsorted and with the collar (proximal part) upward as indicated by the geopetal structures (for details see Ray, 1980).

5) Both lobolith types occur independently in different lineages within scyphocrinitids and marhoumacrinids (Prokop & Petr, 1992), and there is no evidence for so-called cosmopolitan distribution of particular species (Prokop & Petr, 1987) or that stratigraphically lower units yielded cirrus loboliths, while younger ones bear plate loboliths.

Based on the current state of knowledge, it seems that scyphocrinids were epibenthic and their loboliths acted as modified holdfasts. The bulbous and hollow structure of the lobolith, along with its distally positioned microspines, served as adaptations for living in unconsolidated substrata, with an analogy to iceberg- and snowshoe-like strategies. Like modern isocrinids (Fig. 1.1), scyphocrinoids might have extended the distal portion of the stalk along the bottom for stability (Fig. 11). As a consequence, the free-lying lobolith may have been advantageous during crinoid dislodgement induced by storms. Noteworthy, even with this recumbent posture, scyphocrinoids could have risen to the highest epifaunal tier during the Paleozoic, which enabled them to inhabit diverse environments, including those with unfavorable bottom (e.g., low-oxygenated) conditions.

CRINOIDS WITH HIGHLY MODIFIED COLUMNAL SHAPES RESULTING IN EXCEPTIONAL FLEXURE

Crinoid columnals may be circular, elliptical, pentagonal, pentastellate, pentalobate, tetragonal, or trilobate in cross section. Among Mississippian crinoids, Baumiller & Ausich (1996) demonstrated that various morphological modifications of columns with circular columnals had no effect on

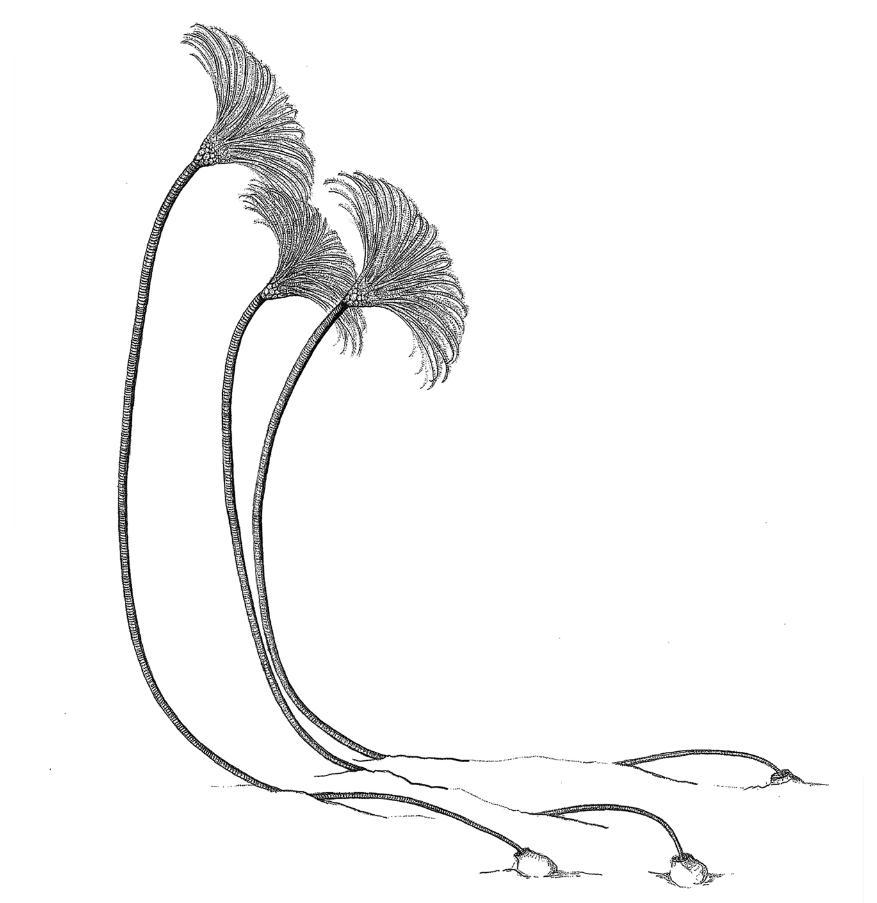

Fig. 11. Life reconstruction of scyphocrinids. Reconstruction: Magdalena Łukowiak (based on Gorzelak & others, 2020, fig. 9). Width of the calyx ~1.0 cm.

the maximum column flexibility. Instead, flexibility in the column was dictated by maximum stretching of ligamentary tissue. Exceptions include columns with elliptical columnals, such as those in the Platycrinitidae, Bourgueticrinidae, Myelodactylidae, Ammonicrinidae, and Camptocrinidae. In crinoids with cylindrical columns (circular columnals), articulations between adjoining columnals typically occur around the entire columnal facet along a crenularium. The percentage of the columnal width engaged in this articulation varies depending on the relative widths of the crenularium versus the areola. Flexure of a crinoid column with a circular crenularium can occur in any direction. Functionally, this articulation operates as a third-class lever (Baumiller & Ausich, 1996). The fulcrum is a short segment of the outer crenularium margin coincident with the direction of bending, and the amount of movement on this fulcrum is a function of the limit of ligament stretching at the opposite end of the articulation (Baumiller & Ausich, 1996). Of course, total column flexure is much greater because it would reflect the added flexure between columnals along the entire column. The bending restriction imposed on circular columns is broken in two ways: 1, circular columnals with a perilumen; and 2, columns with elliptical columnals. Crinoids with elliptical columnals and articular ridge operate as a first-class lever (Donovan, 1988), and many functional interpretations have been proposed.

Planispirally coiled columns

Three clades asynchronously evolved a planispirally coiled column comprised of elliptical columnals with fulcral ridges aligned on both sides of columnals. These include the Myelodactylidae (Ordovician to Silurian disparids), *Ammonicrinus* Springer, 1926a in the Calycocrinidae (Devonian flexibles), and Camptocrinidae (Mississippian to Permian camerates) (Fig. 11–13). Each interation of this extreme departure from the crinoid Bauplan was accomplished slightly differently, but the overall result was the same: a crinoid with a column that could enroll around the crown when in a closed, non-feeding posture. *Ammonicrinus* is discussed in detail below.

Ammonicrinidae

Devonian crinoids of the calycocrinid genus *Ammonicrinus* (Flexibilia) are distinctive in having a xenomorphic stem comprised of distal barrel-shaped columnals and the median-proximal crescent-shaped columnals articulated synarthrially yielding the so-called lateral columnal enclosure extensions (LCEE) (Bohatý, 2011) (Fig. 12). This unusual column enabled ammonicrinids to planispirally coil and enclose the short-armed

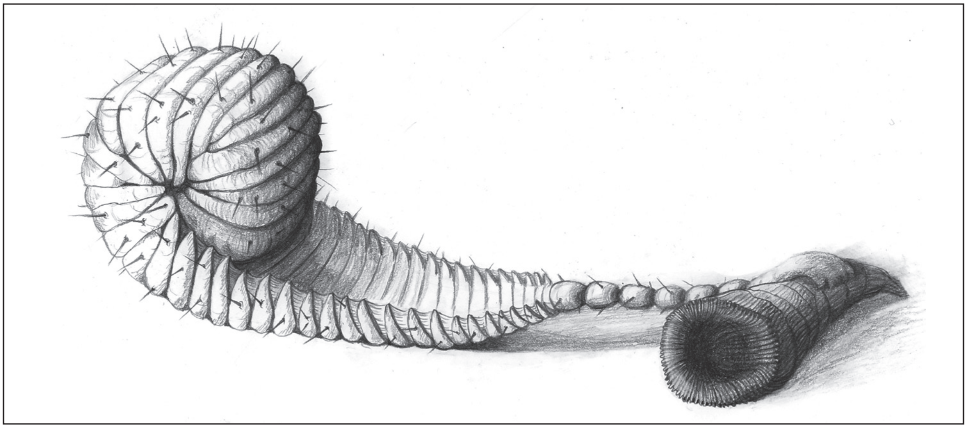

Fig. 12. Life reconstruction of an ammonicrinid. Reconstruction: Magdalena Łukowiak (based on Bohatý, 2011, fig. 7). Width of the median columnal ~1.0 cm.

crown (Fig. 13.2). Another unique feature of this crinoid is that spines are articulated to echinoid-like tubercles on the columnal latera (Haude, 1980).

Owing to this bizarre morphology, the mode of life of ammonicrinids has become the subject of controversy (e.g., Springer, 1926a; Krause, 1927; Ubaghs, 1952; Piotrowski, 1977). Typical erect feeding posture to even a planktonic lifestyle for these crinoids were suggested by several researchers, but these remain speculative. Bohatý (2011), based on integrated sedimentologic and functional morphology analyses, suggested that these crinoids were soft-bottom dwellers, feeding in low-velocity currents. More specifically, the latter author distinguished three facies-controlled morphotypes: exposed, encased, and settler-type. The first type comprises the geologically oldest forms in which the stem tapers as it approaches the crown, so that it was laterally not covered by the LCEE, but rather elevated up from the substratum. The second type encompasses specimens with well-developed LCEE in the proxistele and mesistele enabling extensive coiling (Fig. 12). These crinoids are supposed to have laid on the soft bottom attaching to hard objects with a holdfast. The third type includes forms with a much-reduced column dististele, which were attaching to empty shells laying on the bottom.

Because ammonicrinids were living in habitats with low-velocity currents, it has been proposed that they fed through a self-produced water flow mediated by partial opening and closing of the stem (Bohatý, 2011). This process might have been controlled by stiffening and relaxation of non-muscular mutable collagenous tissues (MCT) located in the two ligamentary facets on the opposite sides of synarthrial articulation. However, the conversion from stiff to soft of MTC proceeds rather slowly (Ribeiro & others, 2011). Gorzelak, Głuchowski, & Salamon (2014) showed that the peripheral areas on each side of the surface of elongated LCEE in some median columnals of ammonicrinids have microstructure unexpectedly resembling the fine labyrinthic stereom of some modern crinoids, which is commonly associated with muscle attachment. These microstructural data, combined with other morphologic features (i.e., the presence of a transverse ridge) and

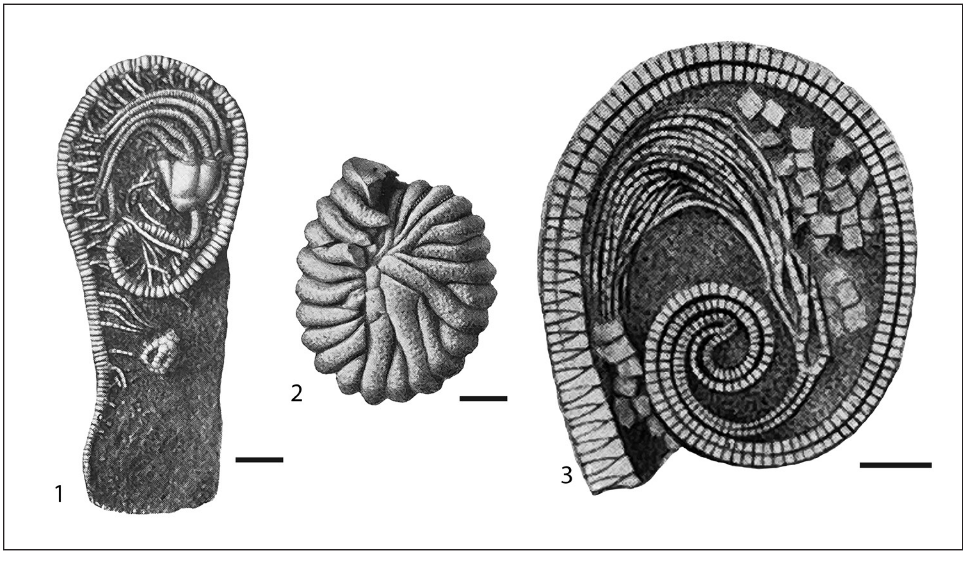

Fig. 13. Crinoids with planispirally coiled column, all scale bars = 5 mm. 1, *Camptocrinus cirrifer* Wachsmuth & Springer, 1897 (from Springer, 1926a, pl. 8, fig. 4). 2, *Ammonicrinus wanneri* Springer, 1926 (from Springer, 1926a, pl. 6, fig. 5). 3, *Myelodactylus extensus extensus* Springer, 1926 (from Springer, 1926a, pl. 3, fig. 7).

evidence from taphonomy (coiled preservation consistent with post-mortem flexure behavior of muscle-bearing skeletal parts of modern echinoderms), may suggest that these crinoids might have contained muscles in their column. This fact is quite surprising because muscles in modern crinoids are only present in their arms, thus ammonicrinids would represent the only instance known of a crinoid having a muscle-bearing stem. Nonetheless, it must be pointed out that even if ammonicrinids indeed possessed muscles, the stem-pumping mode of feeding suggested for these crinoids would have had a high energetic cost. Indeed, such a mode of active feeding has never been observed in modern crinoids. Rather, it seems that the ability to enclose the crown in ammonicrinids was not connected with feeding but with protection against predators or increased water turbulence due to storm activity. In any case, development of muscles in their column would be crucial to allow effective and rapid planispiral closing. Indeed, although modern crinoids may bend their stalks thanks to the presence of ligaments, the ligamentary contraction was shown to be an order of magnitude slower than contraction of muscles (Motokawa et al., 2004). Notably, *in situ* observations showed that some modern stalked crinoids can bend their stalk and reestablish an upright posture on a timescale of days (Veitch, 2022).

To sum up, ammonicrinids were likely plate-encased soft-bottom dwellers having the ability to enclose their crowns in response to the external stimuli such as predators or storms. Their echinoid-like spines, in addition to their potential role in stabilization on muddy bottoms, might have also constituted an anti-predatory adaptation.

Myelodactylidae and Camptocrinidae

The potential functional morphology of the Myelodactylidae and the Camptocrinidae has not recently been as thoroughly considered as *Ammonicrinus.* However, multiple hypotheses have been put forward for myelodactylids (Fig. 13.3) (see discussion in Donovan & Sevastopulo, 1989; Seilacher & McClintock, 2005; Donovan, 2006, 2016; Rozhnov, 2021). The morphology of columnals is well documented (e.g., Springer, 1926a; Willink, 1980; and Donovan & Franzén-Bengston, 1988), and both are generally regarded to have had an erect posture with an open column and the crown in a down-current position (e.g., Donovan & Sevastopulo, 1989) (Fig. 14). The only stereom that has been identified in columnal facets of the Myelodactylidae and the Camptocrinidae (Fig. 13.1) is galleried stereom that presumably housed ligamentary tissue (Donovan & Sevastopulo, 1989; Baumiller & Ausich, 1996). Thus, the motion of the column coiling and uncoiling must have been much slower than that interpreted for *Ammonicrinus* (Gorzelak & others, 2014). Although the muscle-controlled snap coiling hypothesis (Seilacher & MacClintock, 2005) seems unlikely, a ligamentary-controlled coiling mechanism is a potential model that could be applied.

The *Gilbertsocrinus* column

Gilbertsocrinus Phillips, 1836 has a column articulation with a perilumen that functionally approaches a first-class lever system. The perilumen is a raised articular surface that surrounds the lumen (Fig. 15.1), and it is raised higher than the peripheral crenularium. Rather than the fulcrum, the outer crenularium in columnals with this morphology acts like a door stop to limit the amount of bending between two adjoining columnals. Columns with perilumen articulations between adjoining columns have exceptional flexibility. The best documented example of *Gilberstocrinus* is *Gilbertsocrinus tuberosus* (Lyon & Casseday, 1859), and some examples of columns in this crinoid are wrapped around the column of another crinoid or tied in knots (Lane, 1973; Riddle, Wulff, & Ausich, 1988; Baumiller & Ausich, 1996; Hollis & Ausich, 2008) (Fig. 16.1). This highly flexible column and other unique aspects of *Gilbertsocrinus* morphology suggests that the paleoecology of *Gilberstocrinus* was very different than in typical crinoids (see further discussion below). Other crinoids had perilumens (e.g., Moore & Jeffords, 1968, pl. 21), and it is reasonable to assume that the columns of these crinoids also had exceptional column flexibility.

A helically coiled column

Elliptical columnals also evolved in the Platycrinitidae (Devonian to Permian) (Donovan & Lewis, 1999) and the Bourgueticrinidae (Cretaceous to present) (Donovan, 1996). In contrast to the myelodactylids, ammonicrinids, and camptocrinids, the articular ridges on opposing facets of a single platycrinitid or bourgueticrinid columnal were either aligned or not aligned. If not aligned, the column was helically spiraled (Fig. 15.2, 15.3, 17). In platycrinitids, the helically spiraled column occurred along the entire column or along all but the few immature columnals immediately below the aboral cup. In contrast, a helically spiraled column is present only in the distal portion of the bourgueticrinid column. The degree of offset of articular ridges on

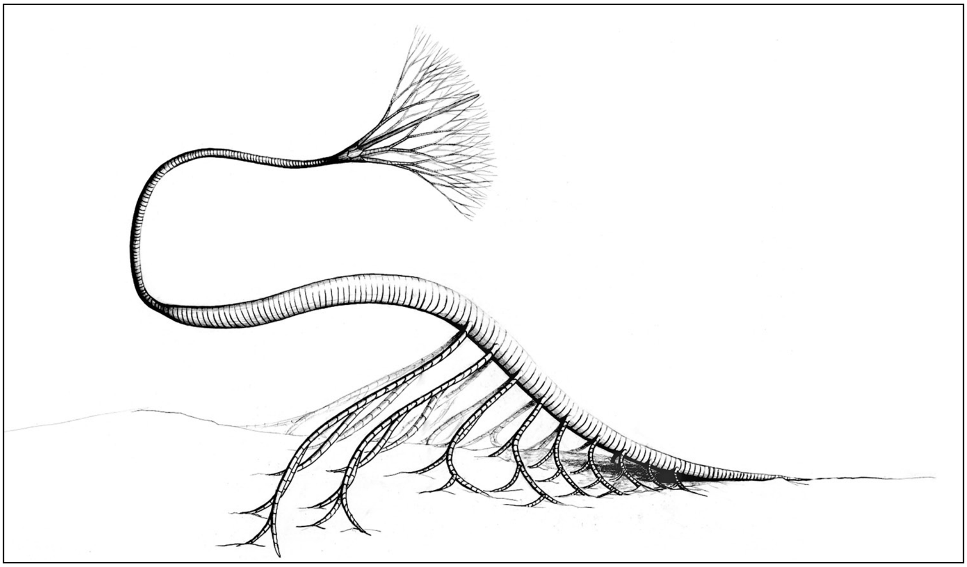

Fig. 14. Life reconstruction of *Crinobrachiatus brachiatus* (Hall, 1852). Reconstruction: Magdalena Łukowiak (based on Donovan & Sevastopulo, 1989, text-fig. 3 and Rohznov, 2021, fig. 8). Width of the calyx ~0.3 cm.

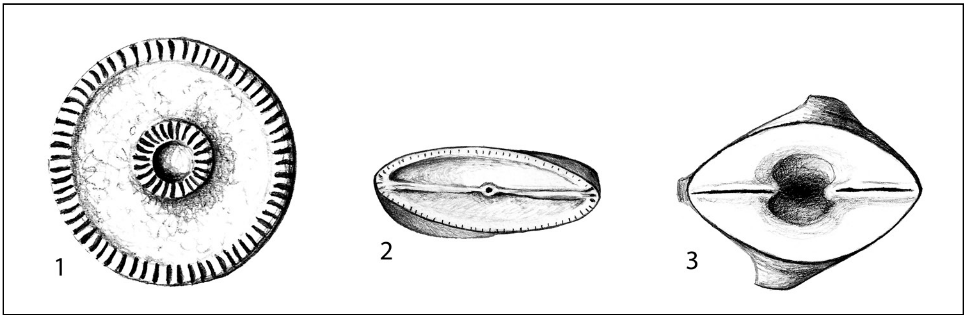

Fig. 15. Columnal facet of highly flexible crinoid columns. 1, *Gilbertsocrinus* sp. Width of the columnal ~1.0 cm; 2, *Platycrinites* sp. Width of the columnal ~1.0 cm; 3, *Bourgueticrinus danicus* Nielsen, 1913. Width of the columnal ~0.5 cm. Reconstruction: Magdalena Łukowiak (based on Ubaghs, 1978, fig. 55.3, 56.2, 56.3, respectively).

opposing sides of a single column range from a few degrees to 180°. Preservation of helically spiraled columns clearly demonstrate that this column style greatly increases column flexibility (Baumiller & Ausich, 1996; Hess & others, 1999 (note the cover image)) (Fig. 17). Further, Riddle (1989) examined particle movement in laminar flow around cylindrical versus helically spiraled pluricolumnals. In the latter example, a dye stream passed along one-half volution around the column and was directed obliquely upward in a diffuse cloud. Thus, it is possible that a helically spiraled column produced a feeding advantage by redirecting water closer to the sediment-water interface

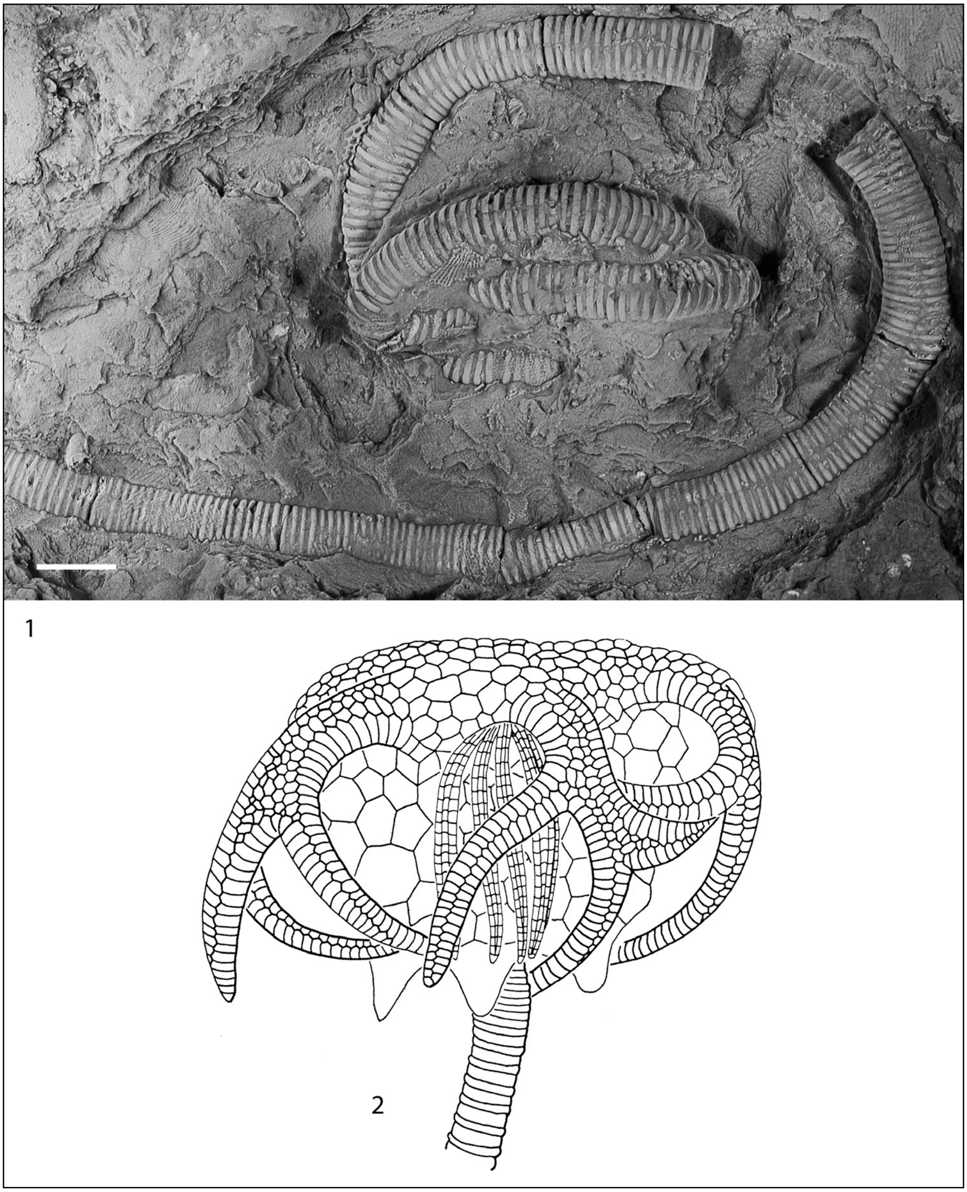

Fig. 16. *Gilbertsocrinus tuberosus* Lyon & Casseday, 1859. 1, coiled column, OSU 50395, scale bar = 1 cm 2, reconstruction of a crown and proximal column (from Van Sant & Lane, 1964, fig. 35).

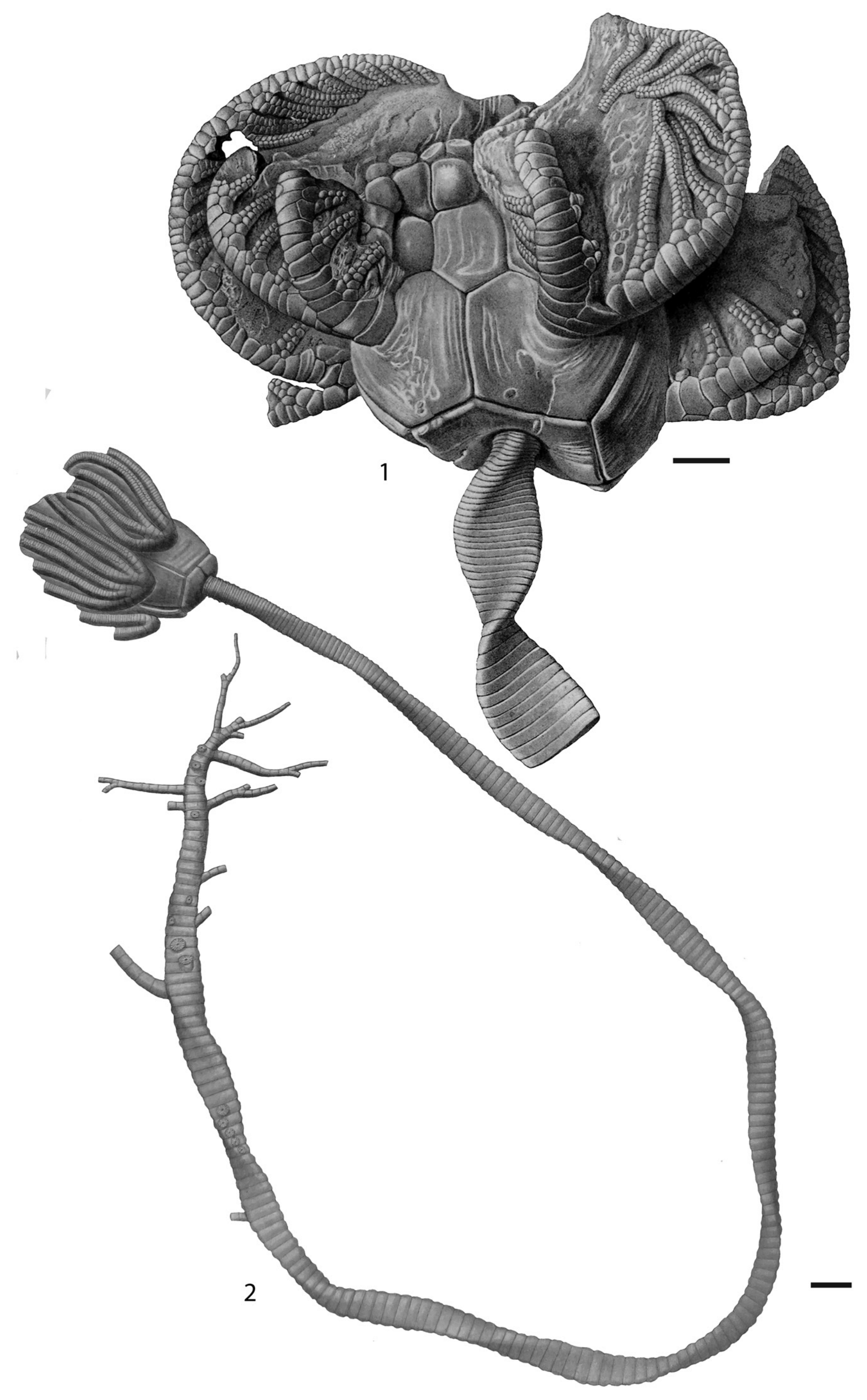

Fig. 17. Crinoids with helically spiraled column. 1, *Eucladocrinus pleurovimenus* (White, 1862), scale bar = 1 cm (from Wachsmuth & Springer, 1897, pl. 74, fig.1). 2, *Platycrinites* s.l. *regalis* (Hall, 1861), scale bar = 0.5 mm (from Wachsmuth & Springer, 1897, pl. 72, fig.1).

with a higher density of particulate organics up toward the arms. If this was the case, perhaps a feeding advantage was in part a factor in the longevity of both clades.

OTHER BIZARRE CRINOIDS

Other Morphological Outliers

The crinoids discussed above are examples of significant departure from the typical crinoid Bauplan that iteratively evolved in different clades at different times. Other crinoids also evolved significant morphological departures, but these morphologies evolved only one time or in a single clade and have received relatively little study devoted to understanding their functional adaptations. A few examples are discussed below.

Gilbertsocrinus Phillips, 1836

As noted above, *Gilbertsocrinus* is a Middle Devonian to Mississippian diplobathrid camerate. It has a highly modified columnal morphology that resulted in a highly flexible column, as discussed above. In addition to the unusual column, the crown of *Gilbertsocrinus* was also unique. The otherwise flat or very low bowl-shaped tegmen had hollow, plated, tubular appendages that extend outward or downward from the tegmen margin (Fig. 16.2). These appendages could be as long as the height of the calyx, and they branched two or more times. Also, rather than erect arms, *Gilbertsocrinus* had short, narrow, branching arms that are typically preserved hanging downward between the tegmen appendages and the calyx.

Because some *Gilbertsocrinus* are wrapped around the column of another crinoid, at least some individuals were secondary tierers (Bottjer & Ausich, 1987). Also, the combination of highly unusual arms, tegmen, and column suggest an alternative autecology compared with typical crinoids, but the autecology of *Gilbertsocrinus* has not been studied.

Crotalocrinites Austin & Austin, 1843

Crotalocrinites is a paleobiogeographically widespread Silurian crinoid with unique arms. Each arm branched numerous times, but all brachials within a single arm are fused laterally to adjacent brachials (Fig. 18.1). Each arm with laterally linked brachials form a very fine meshwork. Brett (1984) briefly discussed *Crotalocrinites*. Although the fluid dynamics of this arm morphology has not been modeled, it seems unlikely that much fluid flowed through meshwork of fused arms. If true, food particle capture was very different from most other crinoids.

Petalocrinidae

The Petalocrinidae (Ordovician to Silurian) is a paleogeographically widespread family that had unique arms with the brachials of an arm fused together into a single large plate (Ausich, Mao, & Li, 2019). The arms in *Petalocrinus* Weller & Davidson, 1896 were flat and trianglular with the ambulacra only on the oral side of the fused arm (Fig. 18.2, 18.3). *Sinopetalocrinus* Mu & Lin, 1987 had fused arms of various shapes, and ambulacra were present on both the oral and aboral side of the arms. In *Spirocrinus* Mu & Wu, 1974, the single arm plate was an elongated cylinder, and the ambulacra spiraled around the arm. Assuming the column of *Petalocrinus* bent with the current, which is typical for crinoids, particle capture must have occurred only in eddying currents on the down-current side of the arms (Rubenstein & Koehl, 1977). Mao & others (2015) speculated that *Spirocrinus* may have been adapted to a habitat with a multidirectional current regime, such as the infrastructure within a reef.

Crinoids with obligate recumbent arms

A few camerate crinoids evolved obligate recumbent arms. Examples include *Barrandeocrinus* Angelin, 1878 (Silurian) (Fig. 19.2); *Amphoracrocrinus* Moore & Strimple, 1969 (Fig. 19.1); and *Artaocrinus* Ausich & Kammer, 2009. In *Barrandeoc-*

rinus the arms form a subspherical structure that encloses the calyx. Arms branch once, and brachials and pinnules of each arm form an elongated, enclosed prismatic chamber that is subtriangular in shape (Fig. 19.3). It is unclear whether the distal tips of arms could open and expose the ambulacra so that Fig. 19.2 represents a trauma posture. Alternatively, Fig. 19.2 could be the feeding posture for *Barrandeocrinus.* Based on preservation, the pinnules do not appear to have been cemented into this shape, so it is possible that the pinnules along the arms spread open while the arms remained in an obligate recumbent posture, which would have exposed the ambulacra on the outside of the structure. Ubaghs (1978) and Brett (1984) briefly discussed the potential autecology of *Barrandeocrinus*; but without fluid dynamic studies, one can only speculate on the feeding mode of this Silurian crinoid.

Amphoracrocrinus, *Artaocrinus*, some species of *Macrostylocrinus* Hall, 1852, *Strimplecrinus* Broadhead, 1981, and other crinoids had obligate recumbent arms. The arms of *Amphoracrocrinus* conformed to the calyx shape (Fig. 19.1), and the arms of *Artaocrinus* formed more of a globular shape. In both cases, the ambulacra would have been oriented on the outside of the recumbent arms, and feeding was presumably by inertial impact on the exposed tube feet.

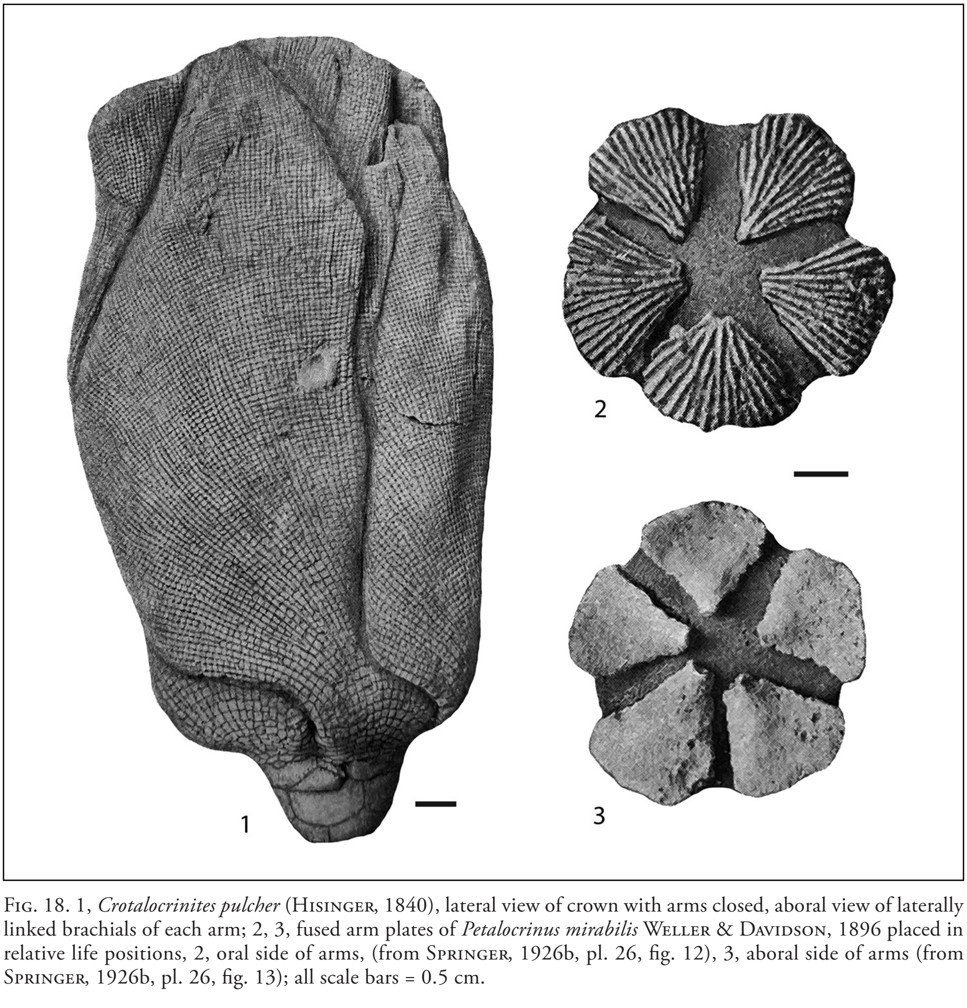

Fig. 18. 1, *Crotalocrinites pulcher* (Hisinger, 1840), lateral view of crown with arms closed, aboral view of laterally linked brachials of each arm; 2, 3, fused arm plates of *Petalocrinus mirabilis* Weller & Davidson, 1896 placed in relative life positions, 2, oral side of arms, (from Springer, 1926b, pl. 26, fig. 12), 3, aboral side of arms (from Springer, 1926b, pl. 26, fig. 13); all scale bars = 0.5 cm.

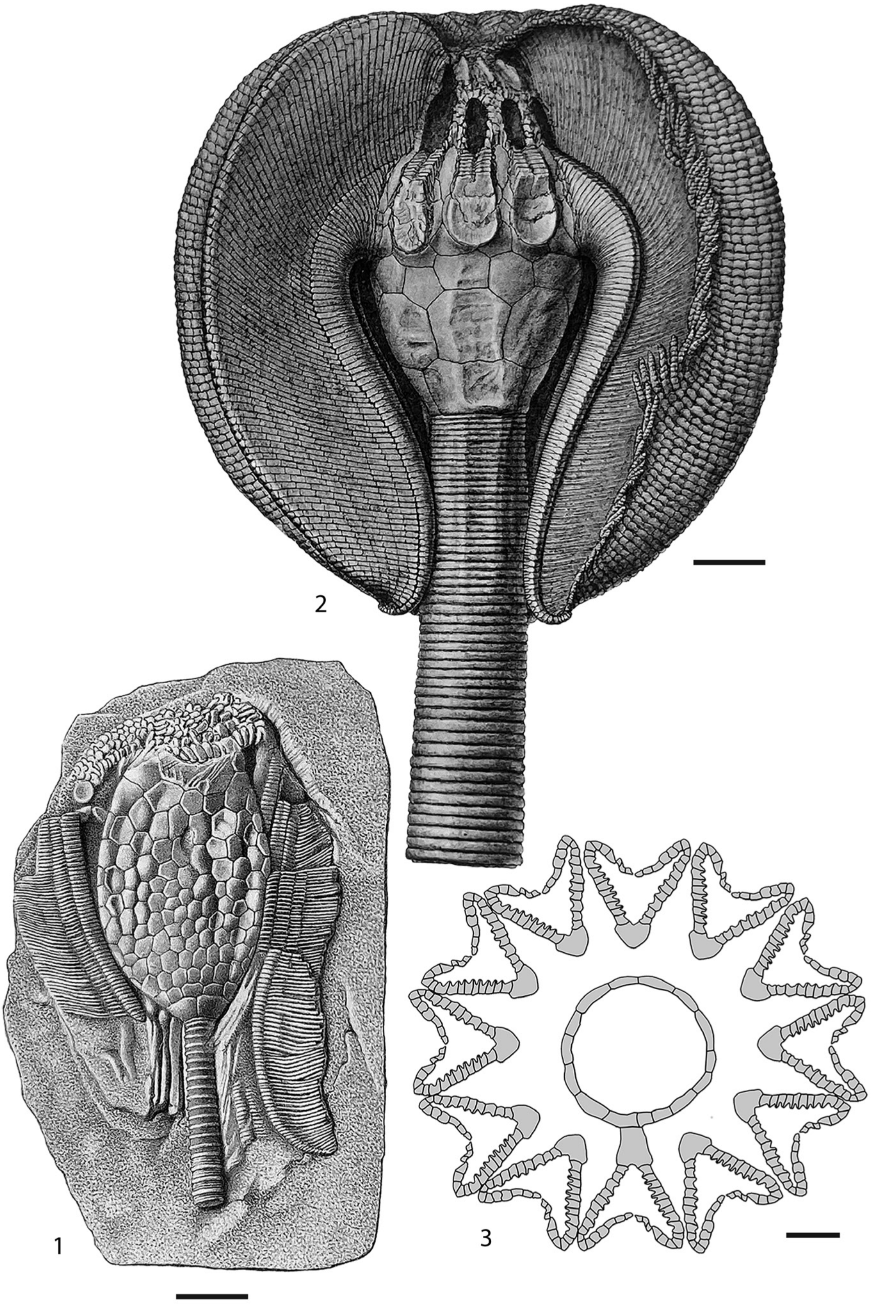

Fig. 19. Crinoids with recumbent arms, all scale bars = 5.0 mm. 1, *Amphoracrocrinus amphora* (Wachsmuth & Springer, 1897), the arms are absent from the front of this specimen, but arms are preserved that extend distally along the column (from Wachsmuth & Springer, 1897, pl. 80, fig. 5). 2, 3, *Barrandeocrinus sceptrum* Angelin, 1878, 2, Specimen with the three forward arms cut away (from Wachsmuth & Springer, 1897, Pl. 8, fig.1); 3, Horizontal cross section through crown illustrating circular calyx in the center surrounded by recumbent arms, redrawn from Ubaghs (1978, fig. 273.1e).

Only hypotheses are given above for the mode of food capture in *Barrandeocrinus, Amphoracrocrinus*, and *Artaocrinus.* Although models would be a challenge to build, fluid dynamic study in either a flume tank or using computational fluid dynamics are needed to better understand the feeding behavior of these most interesting crinoids.

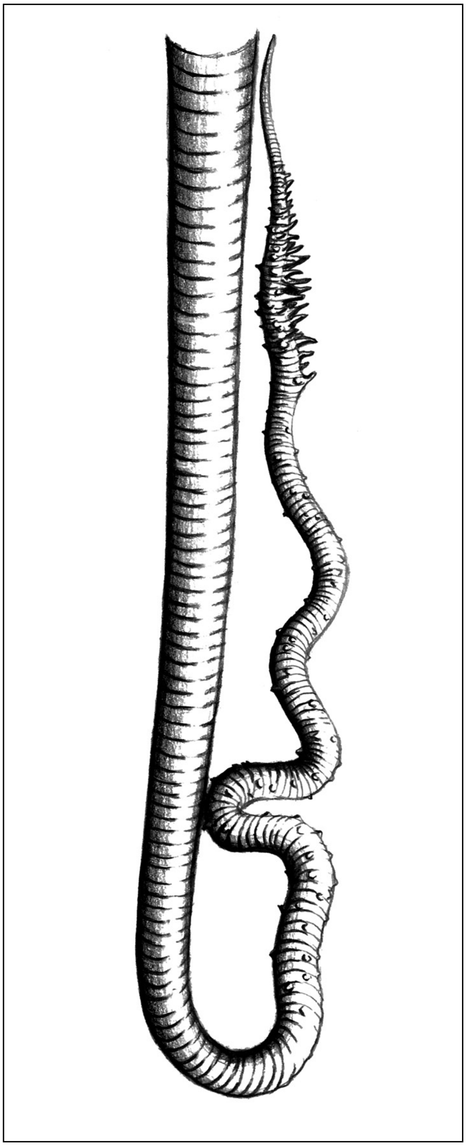

Fig. 20. Columnal of *Trombonicrinus* (col.) Donovan & others, 2018. Reconstruction: Magdalena Łukowiak (based on Donovan & others, 2018, fig. 1). Max. width of column ~1.0 cm.

Other Unusual Crinoids

In addition to deviations from typical column morphology that increased column flexibility (discussed above), crinoids evolved other atypical columns. As discussed above, the cross-sectional shape of crinoid columnals may be circular, elliptical, pentagonal, pentastellate, pentalobate, tetragonal, or trilobate. Columns may also be homeomorphic (all columnals along the column have the same morphology), heteromorphic (columnals of different height and/or width along the column) or xenomorphic (column divided along the column into three distinct sections: proxistele, mesistele, and dististele). Further, columnals may be holomeric (each columnal one calcite plate) or pentameric (each columnal comprised of five plates) to trimeric (each columnal comprised of three plates) (Moore & Jeffords, 1968; Ubaghs, 1978). An example of the latter is *Bodacrinus* Donovan, 1986.

However, the columnals of some crinoids have morphologies that deviate from this otherwise wide range of morphologies. These include crinoids with columnals with large, elongated protruding nodes (e.g., *Hyperexochus* (col.) *immodicus* Moore & Jeffords, 1968) or the so-called brickwork of plates surrounding an otherwise typical column (*Tetrabrachiatus* Termier & Termier, 1958; see Lane, 1979). Another departure from a typical column is *Annulocrinus* (col.) Donovan, 1995, in which the calcite is very narrow and surrounds a very wide lumen.

Among the most unusual crinoid columns is the Devonian *Trombonicrinus* (col.) Donovan & others, 2018. *Trombonicrinus* (col.) has a 180° turn approximately halfway along its height (Fig. 20). The dististele is considerably thinner than the proxistele and is characterized by short pseudoradices, which were presumably for attachment (Donovan & others, 2018). The 180° turn takes place in the mesistele, and the proxistele is more than twice as wide as the dististele. Donovan & others (2018) speculated that the dististele was attached and grew downward along an upright object before making a 180° turn bend so that the proxistele would elevate the crow above the sediment-water interface.

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REFERENCES

Abel, Othenio. 1920. Lehrbuch der Paläozoologie. Gustav Fischer. Jena. 1–523, 700 fig.

Abel, Othenio. 1927. Lebensbilder aus der Tierwelt der Vorzeit. Gustav Fischer. Jena. 1–714, 507 fig.

Angelin, Nils Peter 1878. Iconographia crinoideorum in stratis Sueciae Siluricis fossilium. Samson & Wallin. Holmiae, 1–62, 29 pl.

Arendt, Yuri A. 1968. Novye dannye o rannemelovykh krinoideyakh Kryma [New information about Early Cretaceous crinoids of the Crimea]. Byulleten' Moskovskogo obshchestva ispytatelei prirody, otdelenie geologii 43(5):156–157.

Arendt, Yuri A. 1970. Morskie Lilii Gipokrinidy [Crinoids Hypocrinidae]. Trudy Paleontologicheskogo Instituta, Akademia Nauk SSSR, 128:1–220.

Arendt, Yuri A. 1974. Morskie lilii. Tsirtokrinidy (Sea lilies, Cyrtocrinids). Akademia Nauk SSSR, Trudy Paleontologicheskogo Instituta, number 144:1–251, 37 pl.

Ausich, William I. 1980. A model for niche differentiation in Lower Mississippian crinoid communities. Journal of Paleontology 54:273–288.

Ausich, William I. 1984. Calceocrinids from the Early Silurian (Llandoverian) Brassfield Formation of southwestern Ohio. Journal of Paleontology 8:1167–1185, 12 fig.

Ausich, William I. 1986. Palaeoecology and history of the Calceocrinidae (Palaeozoic Crinoidea). Palaeontology 29:85–99, 6 fig.

Ausich, William I. 2022. The calceocrinid puzzle. *In* Contributions from the Museum of Paleontology Papers. University of Michigan. Special Volume 34(8):103–122, 15 fig. [https://deepblue.lib.umich.edu/handle/2027.42/172912].

Ausich, William I., & D. J. Bottjer. 1982. Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. Science 216:173–174, 1 fig. [DOI: 10.1126/science.216.4542.173].

Ausich, William I., Carlton E. Brett, Hans Hess, & Michael J. Simms. 1999. Crinoid form and function. *In* H. Hess, W. I. Ausich, C. E. Brett, & M. J. Simms, eds., Fossil Crinoids. Cambridge University Press. Cambridge. p. 3–30, fig. 4–51.

Ausich, William I., & Thomas W. Kammer. 2009. Generic concepts in the Platycrinitidae Austin and Austin, 1842 (Class Crinoidea). Journal of Paleontology 83:694–717, 3 fig. [DOI:10.1666/08-107.1].

Ausich, William I., Ying-Yan Mao, & Ycai-Hua Li. 2019. Fusion or hypertrophy?: The unusual arms of the Petalocrinidae (Ordovician-Devonian; Crinoidea). Journal of Paleontology 93:966–970, 3 fig. [http://dx.doi.org/10.1017/jpa.2019.22].

Austin, Thomas, & Thomas Austin Jr. 1843–1847. A monograph on recent and fossil Crinoidea, with figures and descriptions of some recent and fossil allied genera. vol. 1, 2, p. 1–32, pl. 1–4, frontispiece (1843); vol. 3, p. 33–48, pl. 5–6 (1844); vol. 4, p. 49–64, pl. 7–8 (1845); vol. 5, p. 65–80, pl. 9–10 (1846); vol. 6–8, p. 81–128, pl. 11–16 (1847); 128 p., 16 pl. London and Bristol.

Bather, Francis A. 1896b. On *Uintacrinus*: a morphological study. Zoological Society of London, Proceedings 1895:974–1003, 13 fig.

Bather, Francis A. 1907. The discovery in West Cornwall of a Silurian crinoid characteristic of Bohemia. Royal Geological Society of Cornwall, Transactions 13:191–197, 4 fig.

Baumiller, Tomasz K. 1997. Crinoid functional morphology. Paleontological Society Papers 3:45–68, 9 fig.

Baumiller, Tomasz K., & William I. Ausich. 1996. Crinoid stalk flexibility: Theoretical predictions and fossil stalk postures. Lethaia 29:47–59, 10 fig.

Benyoucef, Madani, Bruno Ferré, Bartosz J. Płachno, Imad Bouchemla, & Mariusz A. Salamon. 2022. Crinoids from the Ouarsenis Massif (Algeria) fill the Lower Cretaceous (Berriasian and Valanginian) gap of northern Africa. Annales de Paléontologie 108:102555, 6 fig. [https://doi.org/10.1016/j.annpal.2022.102555].

Blumenbach, Johann F. 1802–1804. Abbildungen naturhistorischer Gegenstände, part 7, 10:1–4 , 1 pl.

Bohatý, Jan. 2011. Revision of the flexible crinoid genus *Ammonicrinus* and a new hypothesis on its life mode. Acta Palaeontologica Polonica 56:615–639, 15 fig., [DOI: http://dx.doi.org/10.4202/app.2010.0020].

Bohatý, Jan, William I. Ausich, & Ralph T. Becker. 2021. Frasnian crinoid associations of the Prüm Syncline (Eifel, Rhenish Massif, Germany) – biostratigraphic framework and macrofossil assemblages. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 312:31–83, 13 fig. [http://dx.coi.org/10.1127/njgpa/2024/1200].

Bottjer, D. J., & William I. Ausich. 1987. Phanerozoic development of tiering in soft substrata suspension-feeding communities. Paleobiology 12:400–420, 4 fig.

Bourseau, Jean-Pierre, Nadia Améziane-Cominardi, & Michael Roux. 1987. Un crinoïde pédonculé nouveau (Echinodermes), représentant actuel de la famille jurassique des Hemicrinidae: *Gymnocrinus richeri* nov. sp. des fonds bathyaux de

Nouvelle-Calédonie (S.W. Pacifique). Comptes Rendus de l'Académie des Sciences Paris, 305, série III:595–599, 11 fig., 16 pl.

Breimer, Albert, & Gary N. Lane. 1978. Ecology and paleoecology. *In* Raymond C. Moore & Curt Teichert, eds., Treatise on Invertebrate Paleontology, Part T., Echinodermata 2, vol. 1. The Geological Society of America & The University of Kansas Press. Boulder & Lawrence. p. 316–347, 9 fig.

Breimer, Albert, & Gary D. Webster. 1975. A further contribution to the paleoecology of fossil stalked crinoids. Koninklijke Nederlandes Akademie van Wetenschappen, Proceedings (series B) 76:249–167.

Brett, Carlton E. 1981. Systematics and paleoecology of Late Silurian (Wenlockian) calceocrinid crinoids from New York and Ontario. Journal of Paleontology 55:145–175, 5 pl.

Brett, Carlton E. 1984. Autecology of Silurian pelmatozoan echinoderms. *In* M. G. Bassett & J. D. Lawson, eds., Autecology of Silurian organisms. Special Papers in Palaeontology 32:87–120.

Broadhead, Thomas W. 1981. Carboniferous camerate crinoid subfamily Dichocrininae. Palaeontographica, Abt. A 176: 81–157, 5 fig.

Brodacki, Michał. 2006. Functional anatomy and mode of life of the latest Jurassic crinoid *Saccocoma*. Acta Palaeontologica Polonica 51:261–270, 6 fig.

Brower, James C. 1966. Functional morphology of Calceocrinidae with description of some new species. Journal of Paleontology 40:613–634, 75 pl.

Brower, James C. 1977. Calceocrinids from the Bromide Formation (Middle Ordovician) of southern Oklahoma. Oklahoma Geological Survey Circular 78:28 p., 4 pl.

Brower, James C. 1985. Ontogeny and functional morphology of two Ordovician calceocrinids. *In* Keegan & O'Conner, eds., Echinodermata. Proceedings of the Fifth International Echinoderm Conference Galway. Rotterdam. A.A. Balkema. 13–18, 8 fig., 4 pl.

Brower, James C. 1990. Ontogeny and phylogeny of the dorsal cup in calceocrinid crinoids. Journal of Paleontology 64:300–318, 13 fig.

Clark, Austin Hobart. 1909. New genera and higher groups of unstalked crinoids. Proceedings of the Biological Society of Washington. 22:173-178.

Dacqué, Edgar. 1921. Vergleichende biologische Formenkunde der fossilen niederen Triere. Bornträger. Berlin. 1–770, 247 fig.

David, Jérôme, Michel Roux, Charles G. Messing, & Nadia Améziane. 2006. Revision of the pentacrinid stalked crinoids of the genus *Endoxocrinus* (Echinodermata, Crinoidea), with study of environmental control of characters and its consequences for taxonomy. Zootaxa 1156:1–50.

Donovan, Stephen K. 1986. A new genus of inadunate crinoid with unique stem morphology from the Ashgill of Sweden. Palaeontology 29:235–242, 4 fig., 1 pl.

Donovan, Stephen K. 1986-1995. Pelmatozoan columnals from the Ordovician of the British Isles. In three parts. Monograph of the Palaeontographical Society, London 138(568):1–68 [1986], 142(580):69–114 [1989], 149(597), 115–193[1995].

Donovan, Stephen K. 1988. Functional morphology of synarthrial articulations in the crinoid stem. Lethaia 21:169–175, 5 fig.

Donovan, Stephen K. 1992. Scanning EM study of the living cyrtocrinid *Holopus rangii* (Echinodermata, Crinoidea) and implications for its functional morphology. Journal of Paleontology 66:665–675, 12 fig.

Donovan, Stephen K. 1996. Comparative morphology of the stems of the extant bathycrinid *Democrinus* and the Upper Palaeozoic platycrinitids (Echinodermata, Crinoidea). Bulletin of the Mizunami Fossil Museum 23:1–27, 5 fig., 11 pl.

Donovan, Stephen K. 2006. Comment. Crinoid anchoring strategies for soft-bottom dwelling (Seilacher & MacClintock, 2005). Palaios 21:397–399, 4 fig. [DOI: 10.2110/palo.2006.P06-3].

Donovan, Stephen K. 2016. Problematic aspects of the form and function of the stem in Palaeozoic crinoids. Earth-Science Reviews 154:174–182.

Donovan, Stephen K., & Christina Franzén-Bengston. 1988. Myelodactylid crinoid columnals from the Lower Visby Beds (Llandoverian) of Gotland. Geologiska Förenigen i Stockholm Förhandlingar 110:69–79, 4 fig.

Donovan, Stephen K., & David N. Lewis. 1999. An epiobiont and the functional morphology of the column of a platycrinitid crinoid. Yorkshire Geological Society, Proceedings 52:321–323.

Donovan, Stephen K., & David L. Pawson. 2008. A new species of the sessile crinoid Holopus d'Orbigny from the tropical western Atlantic, with comments on holopodid ecology (Echinodermata: Crinoidea: Holopodidae). Zootaxa 1717:31–38, 3 fig.

Donovan, Stephen K. & George D. Sevastopulo. 1989. Myelodactylid crinoids from the Silurian of the British Isles. Palaeontology 32:689–710, 2 pl.

Donovan, Stephen K., Johnny A. Waters, & Mark S. Pankowski. 2018. Form and function of the strangest crinoid stem: Devonian of Morocco. Journal of Palaeontology 137:205–210.

Eckert, James D. 1984. Early Llandovery crinoids and stelleroids from the Cataract Group (Lower Silurian), southern Ontario, Canada. Royal Ontario Museum Life Sciences, Contributions 137:1–83, 10 pl.

Eckert, James D., & Carlton E. Brett. 1985. Taxonomy and palaeoecology of the Silurian myelodactylid crinoid *Crinobrachiatus brachiatus* (Hall). Royal Ontario Museum Life Sciences, Contributions 141:1–15, 2 pl.

Ettensohn, Frank R. 1975. The autecology of *Agassizocrinus lobatus*. Journal of Paleontology 49:1044–1061, 8 fig., 2 pl.

Ettensohn, Frank R. 1980. *Paragassizocrinus* systematics, phylogeny and ecology. Journal of Paleontology 54:978–1007, 8 fig., 2 pl.

Ettensohn, Frank R. 1981. A case for substrate influence on infrabasal-cone morphology of two Paleozoic stemless crinoid genera from eastern Kentucky. Southeastern Geology, 22:169–175.

Ettensohn, Frank R. 1984. Unattached Paleozoic stemless crinoids as environmental indices. Geobios, Special Memoir 8:63–68, 1 fig.

Flammang, Patrick. 1996. Adhesion in echinoderms. *In* Michel Jangoux & John M. Lawrence, eds., Echinoderm Studies Volume 5. Rotterdam. A.A. Balkema. 1–60, 8 fig., 4 pl.

Gale, Andrew S. 2016. Roveacrinida (Crinoidea, Articulata) from the Santonian–Maastrichtian (Upper Cretaceous) of England, the US Gulf Coast (Texas, Mississippi) and southern Sweden. Papers in Palaeontology 2:489–532, 18 fig., [doi:10.1002/ spp2.1050].

Gale, Andrew S. 2023. Microcrinoids (Roveacrinidae) from the Middle–Upper Cenomanian Grey Chalk Subgroup, Dover (Kent, United Kingdom: biostratigraphy and re-evaluation of cup structure in roveacrinids. Acta Geologica Polonica 73:685–705, 9 fig., 6 pl. [DOI: https://doi.org/10.24425/agp.2022.143598]

Gervais, F.L.P., 1835. *In* Cuvier, M. R. (Director), Dictionnaire d'Histoire Naturelles. Paris, Le Normant; Strasbourg. F. G. Levrault 3: 49, 1 pl.

Gislén, Torsten. 1924. Echinoderm studies. Zoologisk Bidrag från Uppsala 9:330 p., 349 fig.

Gorzelak, Przemysław, Edward Głuchowski, & Mariusz A. Salamon. 2014. Reassessing the improbability of a muscular crinoid stem. Scientific Reports 4:6049, 8 fig. [DOI: https://doi.org/10.1038/srep06049].

Gorzelak, Przemysław, Edward Głuchowski, Tomasz Brachaniec, Magdalena Łukowiak, & Mariusz A. Salamon. 2017. Skeletal microstructure of uintacrinoid crinoids and inferences about their mode of life. Palaeogeography, Palaeoclimatology, Palaeoecology 468:200–207, 5 fig. [https://doi.org/10.1016/j.palaeo.2016.12.012].

Gorzelak, Przemysław, Dorota Kołbuk, Mariusz A. Salamon, Magdalena Łukowiak, William I. Ausich, & Tomasz K. Baumiller. 2020. Bringing planktonic crinoids back to the bottom: Reassessment of the functional role of scyphocrinoid loboliths. Paleobiology 46:104–122, 10 fig. [https://doi.org/10.1017/pab.2019.36].

Gorzelak, Przemysław, Janiszewska Katarzyna, Hoşgör İzzet, & & Mariusz A. Salamon. 2025. Microstructural design of the stalk in the crinoid *Seirocrinus* supports its pseudoplanktonic lifestyle. Scientifc 15, 31418: [DOI: https://doi.org/10.1038/s41598-025-16412-8]

Grewingk, Constantin Casper A. 1867. Über *Hoplocrinus dipentas* und *Baerocrinus ungerni*. Dorpat, Archiv Naturkunde Liv-, Ehst- und Kurlands, (series 1) 4:100–114, 1 pl.

Grimmer, John C., & Nicholas D. Holland. 1990. The structure of a sessile, stalkless crinoid (*Holopus rangii*). Acta Zoologica 71:61–67, 9 fig.

Grinnell, Georg B. 1876. On a new crinoid from the Cretaceous formation of the West. American Journal of Science and Arts (series 12) 3:81–83, 1 pl.

Guensburg, Thomas E. & James Sprinkle. 1992. Rise of echinoderms in the Paleozoic evolutionary fauna: Significance of paleoenvironmental controls. Geology 20:407–410.

Haeckel, Ernst. 1896. Systematische Phylogenie. Entwurf eines natürlichen Systems der Organismen auf grund ihrer Stammesgeschichte. Theil 2. Wirbellose Thiere. G. Reimer. Berlin. 1–720.

Hagdorn, Hans. 2016. From benthic to pseudoplanktonic life: Morphological remodeling of the Triassic crinoid *Traumatocrinus* and the Jurassic *Seirocrinus* during habitat change. Paläontologische Zeitschrift 90:225–241, 6 fig. [https://doi.org/10.1007/s12542-016-0285-9].

Hall, James. 1852. Palaeontology of New York, vol. 2, containing descriptions of the organic remains of the lower middle division of the New-York system. Natural History of New York. D. Appleton & Co. and Wiley & Putnam. Boston, Gould, Kendall, & Lincoln. 6:362 p., 84 pl.

Hall, James. 1858. Crinoids of New York [in advance of Palaeontology of New York, vol. 3]. The American Journal of Arts and Science (series 2) 25:277–279.

Hall, James. 1860. Observations upon a new genus of Crinoidea. *Cheirocrinus, in* Appendix F. Contributions to Palaeontology, 1858 & 1859. Thirteenth Annual Report of the Regents of the University of the State of New York, on the Condition of the State Cabinet of Natural History, and the Historical and Antiquarian Collection Annexed thereto, State of New York in Senate Document 89:121–124, 80 fig.

Haude, Reimund. 1972. Bau und Funktion der *Scyphocrinites*-Lobolithen. Lethaia 5:95–125, 21 fig. [https://doi.org/10.1111/j.1502-3931.1972.tb00844.x].

Haude, Reimund. 1980. Constructional morphology of the stems of Pentacrinitidae, and mode of life of *Seirocrinus*. *In* Michel Jangoux, ed., Proceedings of the European Colloquium on Echinoderms, Brussels, 3–8 September 1979. A.A. Balkema. Rotterdam. p. 17–23

Haude, Reimund. 1992. Scyphocrinoiden, die Bojen-Seelilien im hohen Silur-tiefen Devon. Palaeontographica Abteilung A 222:141–187, 17 fig., 8 pl.

Haude, Reimund, Maria G. Corriga, Carlo Corradini, & Otto H. Walliser. 2014. Bojen-Seelilien (Scyphocrinitidae, Echinodermata) in neudatierten Schichten vomoberen Silur bis untersten Devon Südost-Marokkos. *In* Frank Wiese, Mike Reich, & G. Arp, eds., "Spongy, slimy, cosy & more": Commemorative volume in celebration of the 60th birthday of Joachim Reitner. Göttingen Contributions to Geosciences 77:129–145, 13 fig., [doi:10.3249/webdoc-3924].

Hess, Hans. 1975. Die fossilen Echinodermen des Schwizer Juras. Veröffentlichungen aus dem Naturhistorischen Museum Basel 8:1–130, 57 fig. 48 pl.

Hess, Hans. 1999a. Scyphocrinitids from the Silurian-Devonian Boundary of Morocco. *In* H. Hess, W. I. Ausich, C. E. Brett, & M. J. Simms, eds., Fossil Crinoids. Cambridge University Press. Cambridge. p. 93–102, fig. 108–113.

Hess, Hans. 1999b. Upper Jurassic Solnhofen Plattenkalk of Bavaria, Germany. *In* H. Hess, W. I. Ausich, C. E. Brett, & M. J. Simms, eds., Fossil Crinoids. Cambridge University Press. Cambridge. p. 216–224, fig. 217–223.

Hess, Hans. 1999c. *Uintacrinus* Beds of the Upper Cretaceous Niobrara Formation, Kansas, USA. *In* H. Hess, W. I. Ausich, C. E. Brett, & M. J. Simms, eds., Fossil Crinoids. Cambridge University Press. Cambridge. p. 225–232, fig. 224–229.

Hess, Hans. 2002. Remains of saccocomids (Crinoidea: Echinodermata) from the Upper Jurassic of Southern Germany. Stuttgarter Beiträge zur Naturkunde (Serie B) 329:1–57, 15 fig., 11 pl.

Hess, Hans. 2006. Crinoids from the Lower Jurassic (Pliensbachian) of Arzo, southern Switzerland. Schweizerische paläontologische Abhandlungen 126:1–143, 29 fig. 29 pl.

Hess, Hans. 2010. Part T (revised), vol. 1, chap. 19: Paleoecology of pelagic crinoids. Treatise Online 16:1–33, 23 fig. [https://doi.org/10.17161/to.v0i0.4086].

Hess, Hans. 2015. Roveacrinids (Crinoidea) from the mid-Cretaceous of Texas: ontogeny, phylogeny, functional morphology and lifestyle. Swiss Journal of Palaeontology 134:77–107, 20 fig. [https://doi.org/10.1007/s13358-015-0076-z].

Hess, Hans, & Walter Etter. 2011. Life and death of *Saccocoma tenella* (Goldfuss). Swiss Journal of Geosciences, Special Issue: Proceedings of the 5th International Symposium on Lithographic Limestone and Plattenkalk 104:99–106, 8 fig. [https://doi.org/10.1007/s00015-011-0059-z].

Hess, Hans, & Charles G. Messing. 2011. Treatise on Invertebrate Paleontology Part T, Echinodermata 2 Revised, Vol. 3 Revised, Chapter 16. *In* Paul Seldon, ed., William I. Ausich (Coordinating Author). The University of Kansas. Lawrence, Kansas. p. 1–261, 112 fig.

Hess, Hans, William I. Ausich, Carlton E. Brett, & Michael J. Simms. 1999. *Fossil Crinoids*. Cambridge University Press. Cambridge. p. 1–275, 238 fig.

Hess, Hans, Mariusz A. Salamon, & Przemyslaw Gorzelak. 2011. Late Jurassic–Early Cretaceous (Tithian–Berriasian) cyrtocrinids from south-eastern Poland. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 269:119–128, 2 fig. [doi:10.1127/0077-7749/2011/0143].

Hisinger, Wilhelm 1840. Anteckinger i Physik och Geognosie under resor uti Sverige och Norrige, Sjunde Haflet. Uppsala. p. 15, 45, 64–65, 72 fig.

Hollis, Kathleen A., & William I. Ausich. 2008. The holdfast of *Gilbertsocrinus* (Mississippian, Crinoidea). Canadian Journal of Earth Sciences 45:135–140.

Hoyal, Cuthill, J. F., & Aaron Hunter. 2020. Fullerene-like structures of Cretaceous crinoids reveal topologically limited skeletal possibilities. Palaeontology 63:513–524, 4 fig. [https://doi.org/10.5061/dryad.cc1v570].

Hunter, Aaron W., David Casenove, Celia Mayers, & Emily G. Mitchell. 2020. Reconstructing the ecology of a Jurassic pseudoplanktonic raft colony. Royal Society Open Science 7:200142, 4 fig. [https://doi.org/10.1098/rsos.200142].

Hyman, Libbie H. 1955. The Invertebrates: Echinodermata. The Coelomate Bilateria, 4th ed. McGraw-Hill Book Co. New York. p. 1–763, 280 fig.

Jaekel, Otto. 1891. Ueber Holopocriniden mit besonderer Berücksichtigung der Stramberger Formen. Zeitschrift der Deutschen geologischen Gesellschaft 44:619–696, 13 fig., 6 pl.

Jaekel, Otto. 1892. Ueber Plicatocriniden, *Hyocrinus* und *Saccocoma*. Zeitschrift der Deutschen geologischen Gesellschaft 44:619–696, 13 fig., 6 pl.

Jaekel, Otto. 1904. Über sogenannte Lobolothen. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 56:59–63, 11 fig.

Jaekel, Otto. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3:1–128, 114 fig.

Jagt, John W. M. 1999. Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeastern Netherlands and northeastern Belgium. Part 1, Introduction and Stratigraphy; Part 2, Crinoids. Scripta Geologica 116:1–255, 50 fig., 46 pl.

Jagt, John W. M. 2005. The youngest pelagic crinoids (latest Maastrichtian, the Netherlands). Bulletin of the Geological Society of Denmark 52:133–139, 3 fig. [https://doi.org/10.37570/bgsd-2005-52-10].

Jangoux, Michel, & John M. Lawrence, eds., 1982. Echinoderm Nutrition. A.A. Balkema. Rotterdam. p. 1–700. [https://doi.org/10.1201/9781003078920].

Kesling, Robert V., & James P. Siegler. 1969. *Cunctocrinus*, a new Middle Devonian calceocrinid crinoid from the Silica Shale of Ohio. University of Michigan Museum of Paleontology Contributions 22:339–360, 13 fig., 1 pl.

Kirk, Edwin. 1911. The structure and relationships of certain eleutherozoic pelmatozoa. US National Museum, Proceedings 141:137 p., 11 pl. [https://doi.org/10.5479/si.00963801.41-1846.1].

Kitazawa, Kota, Tatsuo Oji, & Michinari Sumamura. 2007. Food composition of crinoids (Crinoidea: Echinodermata) in relation to stalk length and fan density: Their paleoecological implications. Marine Biology 152:959–968, 3 fig.

Krause, Paul G. 1927. Über *Ammonicrinus* aus dem Mitteldevon der Eifel. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 79:448–456, 1 pl.

Lamarck, Jean-Baptiste Pierre Antoine de M. de. 1816. Histoire naturelle des animaux sans vertèbres, vol 2. Published by the author. Paris. p. 1–568.

Lane, N. Gary. 1973. Paleontology and paleoecology of the Crawfordsville fossil site (Upper Osagian. Indiana). California University Publications in the Geological Sciences 99, p. 1–141, 21 pl.

Lane, N. Gary. 1979. Upper Permian crinoids from Djebel Tebaga, Tunisia. Journal of Paleontology 50:240–244, 1 pl.

Lane, N. Gary, & George D. Sevastopulo. 1981. Growth and systematic revision of *Kallimorphocrinus astrus*, a Pennsylvanian microcrinoid. Journal of Paleontology 56:244–259, 7 fig., 3 pl.

Lane, N. Gary, & George D. Sevastopulo. 1982. Microcrinoids from the Middle Pennsylvanian of Indiana. Journal of Paleontology 56:103–115, 3 pl.

Linné, Carl [Linnaeus, Carolus]. 1767. Systema naturae, 12th ed., vol. 1, number 2. Laurentius Salvius. Holmiae. p. 533–1327.

Loriol, Perceval de. 1882–1889. Paléontologie française, Série 1, Animaux invertébrés. G. Masson. Paris. Terrain jurassique, vol. 11, Crinoïdes, part 1 (1882–1884) p. 1–627, 121 pl.; part 2 (1884–1889) p. 1–580, pl. 122–229.

Lyon, Sydney S., & Simon A. Casseday. 1859. Description of nine new species of Crinoidea from the Subcarboniferus rocks of Indiana and Kentucky. American Journal of Science (series 2) 28:233–246.

Macurda, David B., Jr., & David L. Meyer. 1974. Feeding posture of modern stalked crinoids. Nature 247:394–396, 1 fig.

Manni, Riccardo, Umberto Nicosia, & Livia Tagliacozzo. 1997. *Saccocoma*, a normal benthonic stemless crinoid: An opportunistic reply within muddominated facies. Palaeopelagos 7:121–132, 5 fig.

Männil, Raimund M. 1959. New representatives of the genus *Hoplocrinus* from the Middle Ordovician of Estonia. Scientific Notes of Tartu State University 75:82–97.

Mao, Ying-Yan, Jih-Pai Lin, Cai-Hua Lin, & William I. Ausich. 2015. Chinese origin and radiation of the Palaeozoic crinoid family Petalocrinidae. Palaeoworld 24:445–453, fig. 3. [doi:j.palwor.2-14.12.007].

Matzke, Andreas T., & Michael W. Maisch. 2019. Palaeoecology and taphonomy of a *Seirocrinus* (Echinodermata: Crinoidea) colony from the early Jurassic Posidonienschiefer Formation (Early Toarcian) of Dotternhausen (SW Germany). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 291:89–107, 7 fig. [doi:10.1127/njgpa/2019/0791].

McIntosh, George C. 1978. Pseudoplanktonic crinoid colonies attached to Upper Devonian (Frasnian) logs. Geological Society of America, Abstracts with Programs 10:453.

Messing, Charles G., William I. Ausich, & David L. Meyer. 2021. Feeding and arm postures in living and fossil crinoids. Treatise on Invertebrate Paleontology Part T, Echinodermata 2, Vol. 1 Revised, Chapter 16. *In* Paul Seldon & William I. Ausich, eds., and William I. Ausich (Coordinating Author). Treatise Online, 150, The University of Kansas. Lawrence, Kansas. p. 1–47 p., 24 fig. [https://journals.ku.edu/treatiseonline].

Messing, Charles G., David L. Meyer, Ulrike E. Siebeck, Lars S. Jermiin, David I. Vaney, & Greg W. Rouse. 2004. A modern, soft-bottom, shallow-water tropical crinoid fauna, with a comparison between living *Comatula rotalaria* and fossil *Uintacrinus socialis* (Echinodermata: Crinoidea). *In* Thomas Heinzeller & James H. Nebelsick, eds., Echinoderms: München. A.A. Balkema. Rotterdam. p. 596–597, [doi:10.1007/s00338-005-0076-3].

Meyer, David L. 1982. Food and feeding mechanisms: Crinozoa. *In* Michel Jangoux & James M. Lawrence, eds., Echinoderm nutrition. A.A. Balkema. Rotterdam. p. 25–42.

Meyer, David L., & Donald B. Macurda Jr. 1977. Adaptive radiation of comatulid crinoids.

Paleobiology 3:74–82, 4 fig.

Meyer, David L., & Christopher G. Maples. 1995. *Uintacrinus* as a bottom dweller: evidence from taphonomy. Geological Society of America, Abstracts with Programs 27:113.

Meyer, David L., & Clare V. Milsom. 2001. Microbial sealing in the biostratinomy of *Uintacrinus* Lagerstätten in the Upper Cretaceous of Kansas and Colorado. Palaios 16:535–546, 6 fig. [DOI: https://doi.org/10.2307/35156270].

Meyer, David L., Clare V. Milsom, & A J. Webber. 1999. *Uintacrinus*: A riddle wrapped in an enigma. Geotimes 44:14–16.

Miller, John S. 1821. A natural history of the Crinoidea or lily-shaped animals, with observations on the genera *Asteria*, *Euryale*, *Comatula*, and *Marsupites*. C. Frost. Bristol. p. 1–150, 50 pl.

Miller, Samuel A. 1891. Palaeontology. Advance sheets, Indiana Department of Geology and Natural Resources. 17th Annual Report. p. 1–103, 20 pl.

Milsom, Clare V. 1994. *Saccocoma*: A benthic crinoid from the Jurassic Solnhofen Limestone, Germany. Palaeontology 37:121–129, 4 fig.

Milsom, Clare V. 1999. Rovings of the roveacrinids. *In* Maria D. Candia Carnevali, F. Bonasoro, eds., Echinoderm Research 1998. A.A. Balkema. Rotterdam. p. 339.

Milsom, Clare V., Michael J. Simms, & Andrew S. Gale. 1994. Phylogeny and palaeobiology of *Marsupites* and *Uintacrinus*. Palaeontology 37:595–607, 3 fig.

Moore, Raymond C. 1962. Revision of Calceocrinidae. University of Kansas Paleontology Contributions, Echinodermata Article 4:1–40, 17 fig., 4 pl.

Moore, Raymond C., & J. D. Ewers. 1942. A new species of *Synbathocrinus* from Mississippian rocks of Texas, description and ontogeny. Denison University Bulletin, Journal of Scientific Laboratories 37:92–106.

Moore, Raymond C., & Russell M. Jeffords. 1968. Classification and nomenclature of fossil crinoids based on studies of dissociated parts of their columns. The University of Kansas Paleontological Contributions 4:1–186, 28 pl., 6 fig.

Moore, Raymond C., & F. B. Plummer. 1940. Crinoids from the Upper Carboniferous and Permian of Arkansas, Oklahoma, and Texas. Texas University Bulletin 3945:1–468, 78 fig., 21 pl.

Moore, Raymond C., & Harrell L. Strimple. 1969. Explosive evolutionary differentiation of unique group of Mississippian-Pennsylvanian camerate crinoids (Acrocrinidae). University of Kansas Paleontological Contributions, Paper 39:1–44, 24 fig.

Moore, Raymond C., & Curt Teichert, eds. 1978. Treatise on Invertebrate Paleontology Part T, Echinodermata 2, The University of Kansas Press. Lawrence, Kansas. p. 1–1027, 619 fig.

Motokawa, Tatsuo, Osamu Shintani, & Rüdiger Birenheide. 2004. Contraction and stiffness changes in collagenous arm ligaments of the stalked crinoid Metacrinus rotundus (Echinodermata). Biological Bulletin 206:4–12, 8 fig.

Mu, En-Zhi, & Chao-Hsiung Lin. 1987. Petalocrinidae from the Silurian of Shiqian District, Guizhou. Bulletin of the Nanjing Institute Geology and Palaeontology, Academica Sinica 12:1–122 p., 8 pl.

Mu, En-Zhi, & Y-R. Wu. 1974. Crinoid sections. In A handbook of the stratigraphy and paleontology in southwest China. Nanjing Institute of Geology and Palaeontology, Academia Sinica 1–455, 202 pl.

Nielsen, K. Brünnich. 1913. Crinoderne i Danmarks Kridtaflejringer. Danmarks geologisk undersøgelse (series 2) 26:1–120, 34 fig. 12 pl.

d'Orbigny, Alcide. 1837. Mémoire sur une seconde espèce vivante de la familie des Crinoïdes ou Encrines, servant de type au nouveau genre Holope (Holopus). Magasin de Zoologie (7ème année) 10:1–8, 3 pl.

d'Orbigny, Alcide. 1850–1852. Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés, faisant suite au Cours élémentaire de paléontologie et de géologie stratigraphiques. Masson. Paris. vol. 1 (1849 [1850]):394 p.; vol. 2 (1850 [1852]):427 p.; vol. 3 (1852):196 p. + table alphabétique et synonymique des genres et des espèces, p. 1–189.

Owen, David D., & Benjamin F. Shumard. 1852. Descriptions of seven new species of crinoidea from the subcarboniferous of Iowa and Illinois. Journal of the Academy of Natural Sciences of Philadelphia (series 2) 2:89–94.

Philips, John. 1836. Illustration of the geology of Yorkshire, or, A description of the strata and organic remails, Part 2, the mountain limestone districts. John Murray. London. p. 1–253, 25 pl.

Piotrowski, Andrzej. 1977. Genus *Ammonicrinus* Crinoidea, from the Middle Devonian of the Holy Cross Mountains, Poland. Acta Palaeontologica Polonica 22:205–219, 6 fig.

Prokop, Rudolf J., & Vaclav Petr. 1987. Marhoumacrinus legrandi, gen. et sp. n. (Crinoidea, Camerata) from Upper Silurian – lowermost Devonian of Algeria. Sborník Národního Muzea v Praze 43:1–14, 11 fig.

Prokop, Rudolf J., & Vaclav Petr. 1992. A note on the phylogeny of scyphocrinitid crinoids. Acta Universitatis Carolinae, Geologica 1–2:31–36, 2 fig.

Prokop, Rudolf J., & Vaclav Petr. 2001. Remarks on palaeobiology of juvenile scyphocrinitids and marhoumacrinids (Crinoidea, Camerata) in the Bohemian uppermost Silurian and lowermost Devonian. Journal of the Czech Geological Society 46:259–268, 3 fig.

Quenstedt, Friedrich August. 1852. Handbuch der Petrefactenkunde, 1st ed. Laupp. Tübingen. p. 1–729, 62 pl.

Quenstedt, Friedrich August. 1858. Der Jura. Laupp. Tübingen. p. 1–842, 99 pl.

Ramsbottom, William Henry C. 1952. Calceocrinidae from the Wenlock Limestone of Dudley. Bulletin of the Geological Survey of Great Britain, vol. 4, p. 33–48, pl. 4–5.

Rasmussen, H. Wienberg. 1961. A Monograph on the Cretaceous Crinoidea. Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter 12:1–428, 60 pl.

Rasmussen, H. Wienberg. 1978. Articulata. In Raymond C. Moore & Curt Teichert, eds., Treatise on Invertebrate Paleontology, Part. T, Echinodermata 2, vol. 3. Geological Society of America & University of Kansas Press. Boulder & Lawrence. p. 813–928, fig. 549–616.

Ray, Bradley S. 1980. A study of the crinoid genus Camarocrinus in the Hunton Group of Pontotoc County, Oklahoma. Baylor Geological Studies 39:1–16, 26 fig.

Regnéll, Gunnar 1948. Swedish Hybocrinida (Crinoidea Inadunata Disparata; Ordovician–Lower Silurian). Arkiv för Zoologi, vol. 40, number 9, p. 1–27, 4 pl.

Rhodes, Donald C., & Larry F. Boyer. 1982. The effects of marine benthos on physical properties of the sediments. In Peter L. McCall, & Michael J. S. Tevesz, eds., Animal-Sediment Relations. Plenum. New York. p. 3–52, 14 fig.

Ribeiro, Ana R., Alice Barbaglio, Cristiano D. Benedetto, Cristina C. Ribeiro, Iain C. Wilkie, Maria D. C. Carnevali, & Mário A. Barbosa. 2011. New insights into mutable collagenous tissue: Correlations between the microstructure and mechanical state of a sea-urchin ligament. PloS One 6:e24822, 10 fig. [DOI: https://doi.org/10.1371/journal.pone.0024822].

Richards, Karl J. 1990. Physical processes in the benthic boundary layer. Philosophical Transactions of the Royal Society of London A, 331:3–13, 7 fig.

Riddle, Steven W. 1989. Functional morphology and paleoecological implications of the platycrinitid columnal (Echinodermata, Crinoidea). Journal of Paleontology 63:889–897, 2 fig. [https://doi.org/10.1017/S0022336000036581].

Riddle, Steven W., Julia I. Wulff, & William I. Ausich. 1988. Biomechanics and stereomic microstructure of the *Gilbertsocrinus tuberosus* column. In R. D. Burke, P. V. Mladenov, P. Lambert, & R. L. Parsley, eds., Echinoderm Biology. A.A. Balkema. Rotterdam. p. 641–648, 8 fig.

Ringueburg, Elihu N. S. 1889. The Calceocrinidae: A revision of the family, with descriptions of some new species. New York Academy of Sciences 4:388–408, 2 pl.

Rouse, Greg W., Lars S. Jermiin, Nerida G. Wilson, Igor Eeckhaut, Deborah Lanterbecq, Tatsuo Oji, Craig M. Young, Teena Browning, Paula Cisternas, Lauren E. Helgen, Michelle Stuckey, & Charles G. Messing. 2012. Fixed, free, and fixed: The fickle phylogeny of extant Crinoidea (Echinodermata) and their Permian–Triassic origin. Molecular Phylogenies and Evolution 66:161–181, 5 fig. [https://doi.org/10.1016/j.ympev.2012.09.018].

Rozhnov, Sergey V. 1985a. Hybocrinea, a new subclass of crinoids. Dolk Add. Naul SSSR 280(4):1012–1015.

Rozhnov, Sergey V. 1985b. Morphology, symmetry, and systematic position of hybocrinid crinoids. Paleontological Journal 2:4–6.

Rozhnov, Sergey V. 2021. Two coils in the morphology of Myelodactylids (Crinoidea, Disparida): The morphogenetic basis of their formation and adaptation potential. Paleontological Journal 55:993–1012. [https://doi.org/10.1134/S0031030121090124]

Rubenstein, Daniel I., & Mary A. R. Koehl. 1977. The mechanisms of filter feeding: Some theoretical considerations. American Naturalist 111:981–994, 2 fig.

Salamon, Mariusz A. 2019. A new prospect in crinoid (Crinoidea, Echinodermata) research: An example from the Lower Jurassic of Montenegro. Carnets de Geologie 12:211–220, fig. 3. [doi:10.4267/2042/70491].

Salamon, Mariusz A. 2022. Kimmeridgian-Hauterivian crinoidal assemblages from the Bakony Mountains (Transdanubian Range, Hungary). *In* István Főzy, ed., Fauna, biostratigraphy, facies and paleotectonic evolution of the Late Jurassic–Early Cretaceous formations in the Bakony Mountains (Transdanubian Range, Hungary). Institute of

Geosciences, University of Szeged. Hungary. p. 433–453, 1 fig., 2 pl.

Salamon, Mariusz A., & Anna Feldman-Olszewska. 2018. Crinoids (Crinoidea, Echinodermata) from the Middle Jurassic (Callovian) of eastern Poland: A case study from the Żebrak IG 1 borehole. Annales Societatis Geologorum Poloniae 88:273–283, 3 fig.. [DOI: https://doi.org/10.14241/asgp.2018.020].

Salamon, Mariusz A., & Przemysław Gorzelak. 2017. Epizoan encrustation on *Marsupites testudinarius* – additional argument favoring an epifaunal mode of life of uintacrinoids? Annales de Paléontologie 103:217–221, 1 fig. [DOI: https://doi.org/10.1016/j.annpal.2017.05.002].

Salamon, Mariusz A., Tomasz Brachaniec, Karolina Paszcza, Dorota Kołbuk, & Przemysław Gorzelak. 2023. The role of mass extinction events in shaping the body-size dynamics of fossil crinoids. Palaeogeography, Palaeoclimatology, Palaeoecology, 622:111593, 7 fig. [doi:10.1016/j.palaeo.2023.111593]

Schmidt, Wilhelm E. 1934. Die Crinoideen des Rheinischen Devons. I. Teil: Die Crinoideen des Hunsrückschiefers. Abhandlung der Preussischen Geologischen Landesanstalt 163:1–149, 34 pl.

Schneider, Heinz L. 1989. Zur Morphologie und Ontogenese von *Roveacrinus geinitzi* n. sp. (Crinoidea, Oberkreide). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 178:167–181, 5 fig.

Schneider, Heinz L. 1995. Crinoidea (Roveacrinidae) aus dem Unter-Turon in Wüllen (Münsterländer Kreidebecken/Nordrhein–Westfalen). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 198:35–46, 3 fig.

Schuchert, Charles. 1904. On siluric and devonic Cystidea and *Camarocrinus*. Smithsonian Miscellaneous Collections 47:201–272, 44 pl.

Seely, Harry G. 1866. Notice of *Torynocrinus* and other new and little-known fossils from the Upper Greensand of Hunstanton, commonly called the Hunstanton Red Rock. Annals and Magazine of Natural History (series 3) 17:173–183.

Seilacher, Adolf, & Rolf B. Hauff. 2004. Constructional morphology of pelagic crinoids. Palaios 19:3–16, 12 fig. [https://doi.org/10.1669/0883-1351(2004)019<0003:CMOPC>2.CO;2].

Seilacher, Adolf, & Copeland MacClintock. 2005. Crinoid anchoring strategies for soft-bottom dwelling crinoids. Palaios 20:224–240, 18 fig. [doi:io.2iio/Paio.2o].

Semenov, Nikolai K., S. Sergey Terentyev, Georgi Mirantsev, & Sergey V. Rozhnov. 2021. A new hybocrinid genus (Echinodermata, Crinoidea) from the Middle Ordovician of Ladoga Glint on the Volkhov River. Paleontological Journal 55(1):54–63, 5 fig., 2 pl.

Simms, Michael J. 1986. Contrasting lifestyles in Lower Jurassic crinoids: A comparison of benthic and pseudopelagic Isocrinida. Palaeontology 29:475–493, 5 fig.

Simms, Michael J. 1999. *Pentacrinites* from the Lower Jurassic of the Dorset Coast of Southern England. *In* H. Hess, W. I. Ausich, C. E. Brett, & M. J. Simms, eds., Fossil Crinoids. Cambridge University Press. Cambridge. p. 177–182, 3 fig.

Smith, Andrew B. 1980. Stereom microstructure of the echinoid test. Special Papers in Palaeontology 25:1–81, 20 fig., 23 pl.

Springer, Frank. 1901. *Uintacrinus*: Its Structure and Relations. Harvard College, Museum of Comparative Zoology, Memoir 25:1–89, 8 pl.

Springer, Frank. 1917. On the crinoid genus *Scyphocrinus* and its bulbous root *Camarocrinus*. Smithsonian Institution 2440:1–74, 19 fig., 9 pl.

Springer, Frank. 1926a. Unusual forms of fossil crinoids. Proceedings of the United States National Museum 67:1–137, 26 pl.

Springer, Frank. 1926b. American Silurian Crinoids. Smithsonian Institution 2872:1–239, 33 pl.

Sprinkle, James. 1973. *Tripatocrinus*, a new Hybocrinid crinoid based on disarticulated plates from the Antelope Valley Limestone of Nevada and California. Journal of Paleontology 47:861–882, 4 fig.

Steenstrup, Johannes Japetus S. 1847. Über Korallen in der Faksöer Kreide, *Moltkia* and *Cyathidium*. *In* G. A. Michaelis & H. F. Scherk, (eds.), Amtlicher Bericht über die 24. Versammlung Deutscher Naturforscher und Aerzte in Kiel 1846. Akademische Buchhandlung. Kiel. p. 148–150.

Strimple, Harold L. 1963. Crinoids of the Hunton Group. Oklahoma Geological Survey Bulletin 100:1–169, 30 fig., 12 pl.

Struve, Wolfgang. 1957. Ein Massengrab kreidezeitlicher Seelilien. Die *Uintacrinus*-Platte des Senckenberg-Museums. Natur und Volk 87:361–373.

Syverson, Val J., Charles G. Messing, Karl Stanley, & Tomasz K. Baumiller. 2015. Growth, injury, and population dynamics in the extant cyrtocrinid Holopus mikihe (Crinoidea, Echinodermata) near Roatán, Honduras. Bulletin of Marine Sciences 91:47–61, 4 fig. [https://doi.org/10.5343/bms.2014.1061].

Szörényi, Erzsébet. 1959. Les *Torynocrinus* (Crinoïdes) de Crétacé inférieur de la Hongrie. Acta Geologica a Magyar Tudományos Akadémia Földtani Közlönye 6:231–271, 4 pl.

Trzęsiok, Dawid. 2015. Crinoids (Crinoidea, Echinodermata) from the Štramberk-type limestones of Poland. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 276:155–172, 3 fig. [doi:10.1127/njgpa/2015/0472].

Ubaghs, Georges. 1952. *Ammonicrinus* Springer, Crinoidea Flexibilia du Dévonien moyen d'Allemagne. Senckenbergiana 33:203–226, 4 fig.

Ubaghs, Georges. 1978. Skeletal morphology of fossil crinoids. *In* R. C. Moore & C. Teichert, eds. Treatise on Invertebrate Paleontology. Part T, Echinodermata 2, vol. 1. Geological Society of America & University of Kansas Press. Boulder, Colorado and Lawrence, Kansas. p. 58–216, 4–184 fig.

Ulrich, Edward O. 1886. Remarks upon the names *Cheirocrinus* and *Calceocrinus*, with descriptions of three new generic terms and one new species. Minnesota Geological and Natural History Survey, Annual Report 14:105–113, fig. 3.

Van Sant, Jan F., & N. Gary Lane. 1964. Crawfordsville (Indiana) crinoid studies. University of Kansas Paleontological Contributions, Article 7:1–136, 8 pl.

Veitch, M. A. 2022. Reflecting the Past in the Present: How Studying Living Crinoids Sheds Light on Their Fossil Record. Ph.D. thesis. University of Michigan. 1–187, 41 fig.

Wachsmuth, Charles, & Frank Springer. 1897. The North American Crinoidea *Camerata*. Harvard College Museum of Comparative Zoology, Memoir 20:1–897, 83 pl.

Walker, Kenneth R., & Robert K. Bambach. 1974. Feeding by benthic invertebrates: Classification and terminology for paleoecological analysis. Lethaia 7:67–78, 2 fig.

Wanner, Johannes. 1916. Die Permischen echinodermen von Timor I. Teil. Paläontologie von Timor 11:1–329, 19 fig.

Wanner, Johannes. 1920. Ueber einige palaeozoische Seeigelstacheln (*Timorocidaris* gen. nov. und *Bolboporites* Pander). Koninklijke Nederlandse Akademie van Wetenschappen Amsterdam Wis en Natuur, Proceedings 28:797–813, 2 fig., 15 pl.

Wanner, Johannes. 1929. Die Krinoiden-Gattung *Holopus* im Lichte der Paläontologie. Paläontologische Zeitschrift 11:318–330, 8 pl.

Webber, Andrew J., David L. Meyer, & Claire V. Milsom. 2008. New observations on taphonomy and paleoecology of *Uintacrinus socialis* Grinnell (Crinoidea; Upper Cretaceous). *In* W. I. Ausich, & G. D. Webster, eds., Echinoderm Paleobiology. Indiana University Press. Bloomington. p. 92–113, 13 fig.

Webby, Barry D., Florentin Paris, Mary L. Droser, & Ian G. Percival, eds., 2004. The Great Ordovician Biodiversification Event. Columbia University Press. New York. 1–484, 140 fig.

Webster, Gary D., & R. Thomas Becker. 2009. Devonian (Emsian to Frasnian) crinoids of the Dra Valley, western Anti-Atlas Mountains, Morocco. Geological Society of London, Special Publications 314:131–148, 5 fig. [https://doi.org/10.1144/ SP314.7].

Weller, Stuart, & Alfred D. Davidson. 1896. *Petalocrinus mirabilis* (n. sp.) and a new American fauna. Journal of Geology 4:166–173, 6 fig., pl. VI, VII.

Wells, John W. 1939. Association of crinoids with *Callixylon* in the lower Ohio Shate. Palaeobiologica 7:105–110, 2 fig.

Wells, John W. 1941. Crinoids and *Callixylon*. American Journal of Science 239:454–456.

White, Charles A. 1862. Description of new species of fossils from the Devonian and Carboniferous rocks of the Mississippi Valley. Boston Society of Natural History Journal 9:8–33.

Willink, Robert J. 1980. A new coiled-stemmed camerate crinoid from the Permian of eastern Australia. Journal of Paleontology 54:15–34.

Wilson, Mark A., Timothy J. Palmer, Thomas E. Guensburg, Charles D. Finton, & Larry E. Kaufman. 1992. The development of an Early Ordovician hardground community in response to rapid sea-floor calcite precipitation. Lethaia 25:19–34.

Wöhrmann, Sidney von. 1889. Die Fauna der sogenannten Cardita- und Raibler-Schichten in den Nordtiroler und den bayerischen Alpen. Jahrbuch der Geologischen Reichsanstalt, 39:181–258, 6 pl.

Worthen, Amos H., 1882. Descriptions of fifty-four new species of crinoids from the Lower Carboniferous limestones and Coal Measures of Illinois and Iowa. Illinois State Museum of Natural History, Bulletin 1:3–38.

Žítt, Jiří. 1983. Spoon-like crinoids from Štramberk (Lower Cretaceous, CSSR). Sborník Národního muzea v Praze (Acta Musei Nationalis Pragae) 39B:69–114, 13 fig., 12 pl.

Zittel, Karl Alfred von. 1876–1880. Handbuch der Palaeontologie, Band 1, Palaeozoologie, Abt. 1. R. Oldenbourg. München & Leipzig. 1–765, 557 fig.

ABOUT THE AUTHORS

Przemysław Gorzelak, Ph.D., D.Sc., received his M.Sc. in Paleontology in 2008 from the Faculty of Earth Sciences at the University of Silesia (Poland). He went on to earn his Ph.D. in 2011 and his habilitation in 2019 at the Institute of Paleobiology of the Polish Academy of Sciences, where he is currently serving as Deputy Director for Research.

Dr. Gorzelak has extensive editorial experience. Since 2019, he has been a Subject Editor for Scientific Reports. He also served as Associate Editor of Acta Palaeontologica Polonica (2015–2020) and, since 2022, has been an Associate Editor of the Journal of Paleontology. Between 2019 and 2024, he was a member of both the Polish Young Academy of the Polish Academy of Sciences (PAS) and the Committee of Geological Sciences of PAS.

His research focuses on paleoecology, functional morphology, and biomineralization of both modern and fossil echinoderms, with a particular emphasis on crinoids.

Professor Mariusz A. Salamon, received his M.Sc. in Palaeontology in 1998 at the Faculty of Earth Sciences at the University of Silesia (Poland). He went on to earn his Ph.D. in 2003, habilitation in 2011, both at the Faculty of Earth Sciences at the University of Silesia. In 2020 he received the title of professor from the President of the Republic of Poland.

Mariusz A. Salamon has extensive editorial experience. Since 2015, he has been an associate editor for Annales Societatis Geologorum Poloniae. Prof. Salamon also served as associate editor of Geoscience Notes (2012–2014). He is the recipient of numerous national and international scholarships and awards, including from the Foundation for Polish Science. In 2020, he was awarded the Medal of Merit for Polish Geology.

His research focuses on taxonomy, paleoecology, paleobiology, and functional morphology of Mesozoic crinoids. Prof. Salamon also deals with prey-predator interactions in the context of the Mesozoic marine revolution.

William I. Ausich, Academy Professor, The Ohio State University, Columbus, Ohio. He received his B.S. (1974) in Geology from the University of Illinois, and A.M. (1976) and Ph.D. (1978) in Geology from Indiana University. He was a faculty member at Wright State University (1978-1984), The Ohio State University (1984-2013), and now an Academy Professor (2013-present) at The Ohio State University. He has received several teaching and research awards and has extensive editorial experience, including Interim Editor-in-Chief for the Treatise (2020-2022). His research has primarily focused on the community paleoecology of Paleozoic benthic communities and the paleoecology, phylogeny, systematics, and evolutionary paleoecology of crinoids.