

From benthic to pseudoplanktonic life: morphological remodeling of the Triassic crinoid *Traumatocrinus* and the Jurassic *Seirocrinus* during habitat change

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Abstract The pseudoplanktonic driftwood-attached crinoids *Traumatocrinus* (late Ladinian—early Carnian) and *Seirocrinus* (Norian—Toarcian) are compared with their Middle Triassic benthic ancestors of the families Encrinidae and Holocrinidae, respectively. The morphological transformations allow five major adaptations of stalked crinoids for pseudoplanktonic life to be specified within the constraints of the ancestral clades: (1) Lightweight construction to reduce the load of the driftwood, maintaining its buoyancy for as long as possible. This was achieved by pore systems of intercolumnal fossulae and longitudinal tubuli in *Traumatocrinus*, and by a distally tapering column in *Seirocrinus*. (2) Peramorphic lengthening of the column to reach plankton-rich water levels (*Traumatocrinus* and *Seirocrinus*), and the possibility to make the column flexible or stout by mutable connective tissue (*Traumatocrinus*). Different column lengths in a colony of *Traumatocrinus* allowed filtering of a larger water column. (3) Solid and persisting anchoring to the drifting substrate to prevent breakage and detachment from the log by adhesive, anastomosing radicular rootlets in *Traumatocrinus* and—less successful—in *Seirocrinus* by a tuft of flexible cirri. (4) Increasing the length of the food grooves to compensate for the disadvantage of drifting along with the plankton by peramorphic augmentation of endotomously branching arms (both forms). (5) Enlargement of the functional cup by intercalation of tegmental or/and pinnular elements (both forms). Exclusively ligamentary (granosyzygial) brachial articulation made the

Traumatocrinus crown rather inflexible while *Seirocrinus* retained the ancestral flexible muscular articulations. A prerequisite for the pseudoplanktonic lifestyle was the availability of large driftwood logs that became available in late Middle Triassic times after the recovery of large gymnosperms. After 50 Ma, the niche of pseudoplanktonic drifting of stalked crinoids was closed in the Middle Jurassic by the rise of shipsworms.

Keywords Crinoidea · Pseudoplanktonic lifestyle · Habitat change · Functional morphology · Peramorphic heterochrony · Convergency · Evolutionary biology · Triassic · Jurassic · Black shale

Kurzfassung Die pseudoplanktonischen, an Treibholz hängenden Seelilien *Traumatocrinus* (spätes Ladinium bis frühes Karnium) und *Seirocrinus* (Norium bis Toarcium) werden mit ihren mitteltriassischen benthischen Ahnen aus den Familien Encrinidae bzw. Holocrinidae verglichen. Ihre morphologische Umgestaltung zeigt, dass der ererbte Bauplan fünf entscheidende Anpassungen an die pseudoplanktonische Lebensweise erlaubte: (1) Leichtbauweise, um die Auflast des Treibholzes zu reduzieren und dessen Auftrieb so lang wie möglich zu erhalten. *Traumatocrinus* erreichte dies mit einem System von Poren zwischen den Stielgliedern (fossulae), die mit längs verlaufenden Tubuli kommunizieren, *Seirocrinus* mit seinem distal verdünnten Stiel. (2) Heterochrone (peramorphe) Stielverlängerung bei *Traumatocrinus* und *Seirocrinus*, um planktonreiche Wasserschichten zu erreichen, bei *Traumatocrinus* außerdem um den Stiel durch mutables Kollagen wechselnd flexibel oder starr zu machen. Unterschiedliche Stiellängen innerhalb einer Kolonie befähigten *Traumatocrinus* eine größere Wassersäule durchzufiltern. (3) Feste und dauerhafte Verankerung am Treibholz, um Stielbruch und Ablösung

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vom Holz zu verhindern, durch verzweigte Haftwurzeln bei *Traumatocrinus* und—weniger erfolgreich—durch Büschel flexibler Zirren bei *Seirocrinus*. (4) Bei beiden Formen Verlängerung der Nahrungsrinne durch peramorphe Vermehrung der Arme durch endotome Verzweigung und dadurch Ausgleich des nachteiligen Driftens zusammen mit dem Plankton. (5) Bei beiden Formen Vergrößerung des funktionalen Kelchs durch Einschaltung von Elementen der Kelchdecke und/oder der Pinnulae. Durch ausschließlich ligamentäre (granosyzygiale) Verbindung der Armglieder versteifte *Traumatocrinus* die Krone, während *Seirocrinus* die ererbten flexiblen, muskulären Verbindungen beibehielt. Voraussetzung für die pseudoplanktonische Lebensweise war die Verfügbarkeit großer Treibholzstämme, die in der ausgehenden Mitteltrias mit dem Neuaufschwung der Gymnospermen wieder vorhanden waren. Nach 50 Ma schloss sich die Pseudoplankton-Nische für gestielte Crinoiden im Mittleren Jura mit dem Aufstieg der Schiffsbohrwürmer.

Schlüsselwörter Crinoidea · Pseudoplanktonische Lebensweise · Habitatwechsel · Funktionsmorphologie · Heterochronie · Konvergenz · Evolutionsbiologie · Trias · Jura · Schwarzschiefer

Introduction

Fundamental habitat change in a given clade leads to morphological change, however, always within the constraints of the bauplan. Investigating such changes has been one of the major points of Adolf Seilacher's research, explained by fascinating examples from many vertebrate and invertebrate groups, among which echinoderms played an important role. Black shale paleoecology in general and pelagic crinoids in particular have been favorite topics of Dolf Seilacher's research occupying him through decades. Hence, this contribution is dedicated to honor his seminal work.

Columns exceeding 10 m and extraordinarily large crowns with multiple arm branching make the Late Triassic *Traumatocrinus* and the Early Jurassic *Seirocrinus* exceptional crinoids unique to the Phanerozoic. Their all-time size record is splendidly documented by large black shale slabs with complete colonies with countless articulated individuals. Comparable to flower still lifes, some of such slabs are exhibited in the galleries of the world's leading natural history museums as icons of palaeontology, and they are also displayed in scientific and popular books. What makes these crinoids even more fascinating is their inferred pseudoplanktonic lifestyle because there is no extant model for the prerequisites of such a habit.

The first findings of articulated *Seirocrinus* from the Early Jurassic (Toarcian) Posidonia Shale of Württemberg (South Germany) dates back to the early eighteenth century and served the Stuttgart protestant priest Eberhard Friedrich Hiemer as evidence for the diluvianist Deluge theory. He compared the crinoid with the ophiuroid *Gorgonocephalus caputmedusae* and described it as Swabia's Medusan Head (Hiemer 1724; Hölder and Warth 1994). This famous specimen was rediscovered only recently in the collections of the Göttingen Geological Institute (Reich 2010), and it was designated as neotype of *Seirocrinus subangularis* (Miller 1821) by Hunter et al. (2011). A slab of Posidonia Shale measuring 4.5 × 7 m and preserving ~50 exceptionally large specimens with crowns of an average diameter of 80 cm and columns exceeding 15 m was excavated and described by Friedrich August Quenstedt and later exhibited on a wall in the Tübingen Geological Institute (Quenstedt 1868). Unlike other colonies discovered later, the driftwood belonging to the Tübingen slab was not excavated. However, Quenstedt noted that his assistant J. Hildenbrand saved cartloads of matching slabs (Quenstedt 1868, p. 18), which were obviously lost. Subsequently, the seminal collecting and preparation effort of Bernhard Hauff in Holzmaden yielded specimens still attached to bivalve-encrusted driftwood logs. This led several authors to assume a pseudoplanktonic lifestyle for *Seirocrinus* (Walter 1897; Beringer 1926). Their ideas were renewed and corroborated by Seilacher et al. (1968). These authors reconstructed the sinking of the colony to the seafloor from the position of the entangled columns and the position of the crowns with their oral side embedded underneath the columns. The assumption of life in the upper parts of the water column also explained the occurrence of otherwise benthic crinoids in bituminous black shales deposited under dysaerobic to anaerobic bottom conditions. Moreover, the column of *Seirocrinus* is tapering toward the terminal attachment structure and was less flexible in its proximal part. In terms of functional morphology, Seilacher et al. (1968) explained these characters as adaptations to a pseudoplanktonic lifestyle. Revitalization of these ideas caused a scientific controversy. Rasmussen (1977) proposed that *Seirocrinus* discarded the distal column part before it attached to logs on the seafloor. In this argumentation he was influenced by the observation of preformed rupture points at the synostiosal lower nodal facets of the related Isocrinidae, which may shed their distal column parts. However, the pseudoplanktonic lifestyle model for *Seirocrinus* and its sister genus *Pentacrinites* was generally accepted and supported by additional observations of taphonomy and conclusions from functional morphology (Haude 1980, 1981; Simms 1986, 1989, 1999; Hess 1999, 2010; Seilacher and Hauff

2004; Seilacher 2011). A history of the niche of pseudoplanktonic life in the Phanerozoic and its prerequisites was provided by Wignall and Simms (1990).

Eventually, it was the discovery of complete individuals of *Traumatocrinus* in the early Late Triassic black shales of the Xiaowa Formation of Southwest China (Lin 2014) that contributed much to a better understanding of the morphological adaptations of *Seirocrinus* to pseudoplanktonic life. Originally described from fragmentary column material from the Hallstatt Limestone of the Austrian Alps (Dittmar 1866) and synonymized with *Encrinus* in the first edition of the Crinoid Treatise (Moore et al. 1978), the morphology of *Traumatocrinus* was described in more detail by Mu (1949) based on intact crowns from Southwest China. The subsequent history of research on *Traumatocrinus* has been documented by Hagdorn et al. (2007) and Hagdorn and Wang (2015). The same endotomous arm branching pattern, the occurrence in black shales, and corresponding taphonomic features induced Hagdorn (1998) to compare *Traumatocrinus* with *Seirocrinus* and to suggest a pseudoplanktonic lifestyle for *Traumatocrinus* too. This assumption was confirmed by findings of large driftwood logs with complete *Traumatocrinus* individuals attached (Hagdorn et al. 2004; Wang et al. 2006, 2008).

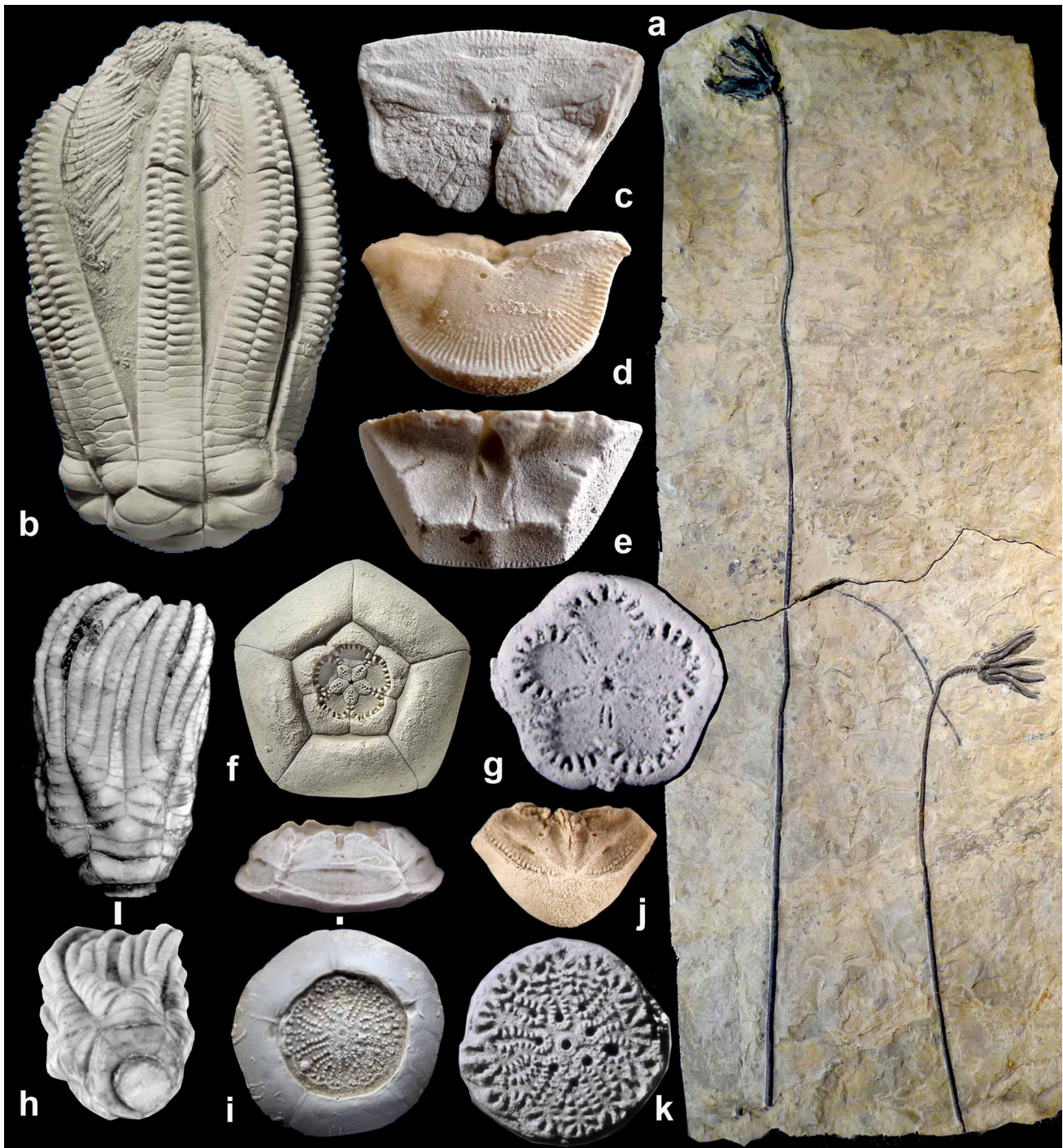
Despite these similarities, the two genera descended from different clades. *Traumatocrinus* is a specialized representative of the Middle Triassic Order Encrinida, while *Seirocrinus* is an offshoot of the Early and Middle Triassic Order Holocrinida and is assigned to the Order Isocrinida, Family Pentacrinidae (Hess 2011). Compared to the widely different characters of their ancestors both genera have an astonishingly similar morphology. These convergencies are explained as heterochronous adaptations caused by habitat change from a benthic lifestyle to pseudoplanktonic drifting on logs (Hagdorn 2011a). Unique and specific morphological characters developed in *Traumatocrinus* and *Seirocrinus* serving for similar functions as required by the habitat change. *Traumatocrinus* provides another example of adaptation to pseudoplanktonic drifting among post-Paleozoic stalked crinoids and, thus, contributes to a better understanding of the functional morphology of *Seirocrinus* and the general requirements for this lifestyle.

Drifting in the water column offers two essential advantages for sessile filter feeders such as crinoids, but it is also connected with serious risks: (1) Buoyancy provided by driftwood keeps the animals in the oxygen- and plankton-rich upper levels of the water column. This enables them to widen their habitats across vast areas by taking advantage of global current systems. Because the

buoyancy of crinoid rafts worked only as long as the log was able to carry the burden of its passengers, weight-saving construction of the crinoids was required. (2) Living high above the seafloor protected the animals from being smothered by storm-induced mud suspensions, the most traumatic and lethal events for crinoids living in shallow water. Hence, the ability to hermetically close the crown is not essential. In contrast to a benthic crinoid in a suitable environment that is permanently supplied with plankton, a pseudoplanktonic crinoid is drifting with the plankton. Other driftwood dwellers, e.g., barnacles, bivalves, or tunicates are active filter feeders, creating their own current for food supply. Because crinoids are passive suspension feeders, pseudoplanktonic representatives required morphological adaptations to compensate for this disadvantage.

Morphology of *Seirocrinus* and its sister genus *Pentacrinites* is well known from classic descriptions (e.g., Quenstedt 1868; Beringer 1926; Simms 1989), and functional morphology and habitat adaptation have been analysed by Seilacher et al. (1968), Haude (1980, 1981), Seilacher and Hauff (2004), Seilacher (2011), and Hess (2010). In contrast to the Early Jurassic *Seirocrinus subangularis*, no complete colonies are known of the Norian/Rhaetian *Seirocrinus klikushini* from North Siberia (Simms 1989). Hence, *Seirocrinus subangularis* has been chosen as representative of the genus in the present paper. However, the focus is on the less well-known *Traumatocrinus*, newly described on the basis of isolated and articulated material from Southwest China by Hagdorn and Wang (2015). For illustrations of *Seirocrinus*, the reader is referred to the literature cited.

The *Traumatocrinus* material under study comprises intact individuals and disarticulated ossicles from the early Late Triassic Xiaowa Formation of Guizhou and Yunnan (South China), which show the articulation facets, as well as complete colonies in their original attachment to driftwood. The material is kept in the Yichang Institute of Geology and Mineral Resources (YIGMR), the Wolonggong Museum of Guanling County, and the Muschelkalkmuseum Ingelfingen (MHI). The Chinese *Traumatocrinus* specimens have been collected in the Xinpu area, Guanling County (Guizhou Province, South China). Additional columnal material from Afghanistan has been donated to the Muschelkalkmuseum by V. G. Klikushin, St. Petersburg. Encrinids and holocrinids shown in Figs. 1 and 2 are also kept in MHI unless otherwise indicated. As for *Seirocrinus*, a closer look was taken at specimens in the Stuttgart Natural History Museum, the Urweltmuseum Hauff Holzmaden, and the Tübingen University Museum. The terminology follows Hess (2011).



The ancestors: the Middle Triassic Encrinidae and Holocrinidae

Traumatocrinus and *Seirocrinus* are Late Triassic offshoots of the Middle Triassic Encrinidae and Holocrinidae, respectively. They preserve specific characters of their ancestors, which were passive filter feeding benthic

organisms occupying higher tiers in their habitats. As Hagdorn (2011a) pointed out, a first radiation after the end-Permian extinction occurred in early Middle Triassic—or even in late Early Triassic times resulting in two different modes of substrate attachment: (1) permanent attachment by elements of the terminal column modified as discoid or incrusting holdfasts and (2) temporary attachment by cirri,

Fig. 1 Encrinidae. **a–g** *Encrinus liliiformis* Lamarck, 1801; Upper Muschelkalk, Trochitenkalk Formation, Anisian. **a** Almost complete individual, however devoid of holdfast, with proximal column bent; length of larger individual 132 cm; smaller individual with incomplete column; Alverdisen (Lower Saxony); MHI 2135. **b** Crown with 10 biserial arms; arms slightly splayed due to sediment upload; Schwäbisch Hall-Steinbach (Germany); MHI 1043/1; height 8 cm. **c** Proximal brachial with muscular articulation and aboral marginal ridges; Crailsheim-Wollmershausen (Germany); MHI 2131/1; width 9.2 mm. **d** Zygosynostosal distal facet of axillary with aboral marginal ridges; Crailsheim-Wollmershausen (Germany); MHI 2131/2; width 9.0 mm. **e** Radial in oblique proximal-adoral view showing zygosynostosal interrarial facets and basal-radial facets with marginal ridges; Crailsheim-Wollmershausen (Germany); MHI 1877/1; width 12.5 mm. **f** Aboral view of cryptodicyclic cup with infrabasal, basal, and radial circlets showing subcircular column pit with short marginal ridges; Crailsheim-Wollmershausen (Germany); MHI 1214/1; width 16.0 mm; (from Hagdorn 2011a). **g** Proximal nodal showing blueprinted pattern of column pit; Crailsheim-Wollmershausen (Germany); MHI 2131/3; width 5.7 mm. **h, j** *Cassianocrinus varians* (Münster, 1841). **h** Juvenile crown with 39 arms, endotomous arm branching commencing at second axillary of outer arms, echelon arrangement of arms; Cassian Formation, Carnian; St. Kassian, Dolomites (Italy); Naturhistorisches Museum Wien 1865/IX/130; height 21.5 mm; (from Hagdorn 2004). **j** Muscular facet of axillary with marginal ridges; Pachcardia Tuffite, Ladinian; Seiser Alpe, Dolomites (Italy); MHI 2132/1; width 5.9 mm. **i, k** *Zardinicrinus granulatus* (Münster, 1834) Cassian Formation, Carnian; Dolomites (Italy). **i** Cup in aboral and lateral view, showing muscular radial facet, wide column pit with proximal columnals with granosyzygial columnal facet covering basals completely; Naturhistorisches Museum Wien NHMW 2006 z 0265/0005; width 12 mm; (from Hagdorn 2011a). **k** Granosyzygial proximal columnal with five tubuli within granule loops; Bayerische Staatssammlung für Paläontologie und Geologie München SNSB-BSPG 1877 X 1023; width 6 mm; (from Hagdorn 2011b)

flexibly articulated to nodals. The first mode was attained by the Order Encrinida, the second by the Order Holocrinida and its descendants in the Order Isocrinida. However, there are additional differences between these clades, which are summarized below.

The well-known Muschelkalk sea lily *Encrinus liliiformis* is selected here as a typical representative of the Family Encrinidae. This crinoid reached a height of 1.5 m, with a column of discoid to cylindrical elements (Fig. 1a). While the distal and medial column was stout enough to keep the animal upright, the proximal column was flexible and is commonly bent. This allowed the arms to be oriented with their aboral side toward the plankton bearing current for downstream feeding (Seilacher et al. 1968; Dynowski 2015). In the crown, a wide bowl-shaped circlet of radials and a tight closure of neighbouring proximal arms provided enough space for the functional cup (Fig. 1b, f), bordered by a flexible tegmen of granular plates. Muscular articulations allowed active tilting of the arms at the radials (Fig. 1e), at the axils (axillary second primibrachials), and at a few proximal secundibrachials (Fig. 1c). Due to ligamentary articulations, the biserial parts of the arms were inflexible (Fig. 1b). However,

muscular articulation between the first pinnular and its brachial allowed tilting of the pinnules and limited spreading to provide a filtration fan. The ability of *Encrinus liliiformis* to close its arms and pinnules tightly has been interpreted as an adaptation to active filtering of very small particles by means of ciliary currents (Jefferies 1989). Such an adaptation would make sense in a palaeo-community of diverse crinoid clades with different arm and pinnular structures adapted to different food size. However, in the monospecific crinoid palaeo-community of the Upper Muschelkalk Trochitenkalk Formation, tiers of different elevations up to 150 cm above the seafloor were occupied intraspecifically by individuals of *Encrinus liliiformis* with different column lengths. Additional filter feeders collecting normal-sized particles were not present in these tiers. Hence, the tight arm closure rather served to prevent influx of suspended sediment into the filtration system during storms occurring frequently in the Muschelkalk sea. For these reasons the interpretation suggested by Jefferies (1989) is intriguing but not convincing.

The *Encrinus* pattern was improved by peramorphic repetition of isotomous arm branching resulting in the 20 arms of *Chelocrinus* (Hagdorn 1982). Additional, endotomous branching is seen in the late Ladinian and early Carnian *Zardinicrinus* and *Cassianocrinus* (Fig. 1h; Hagdorn 2011a, b). Encrinids were able to close their crown up to the tips of the arms against sediment influx (Fig. 1b). To achieve this, the arm tips of *Chelocrinus* and other taxa with more than 20 arms are recurved (Fig. 1h). The weak point of the Encrinidae was breakage of the column because re-attachment was impossible. The inflexible arms would not allow that a detached crown adopted a secondary feeding position, with the mouth directed upward toward the plankton rain (Baumiller et al. 2008). Column breakage was commonly caused by storms as indicated by individuals with their distal stems broken (Linck 1954, 1965; Hagdorn 1978).

Holocrinids and the Middle Triassic isocrinids have pentagonal to stellate or cylindrical columns with cirriferous nodals (Fig. 2a–e), and the cirri enabled the animals to attach to a variety of substrates. Their taphonomic record is indicative of preformed rupture points at the lower nodal facets, ensuring that the column terminated with a set of cirri after shedding of distal parts (Baumiller and Hagdorn 1995). For this reason, the ancestral holocrinid symplectial facet between nodal and infranodal was remodeled in the isocrinids to a smooth cryptosymplexy or synostosis with short ligament fibers. The proximal columns of living isocrinids are continuously growing by addition of newly formed nodals and internodals and are shortened by shedding of the terminal parts at the synostosal lower nodal facets (Oji 1989). The taphonomic record indicates that this was already the case in the holocrinid column (Fig. 2d, e;

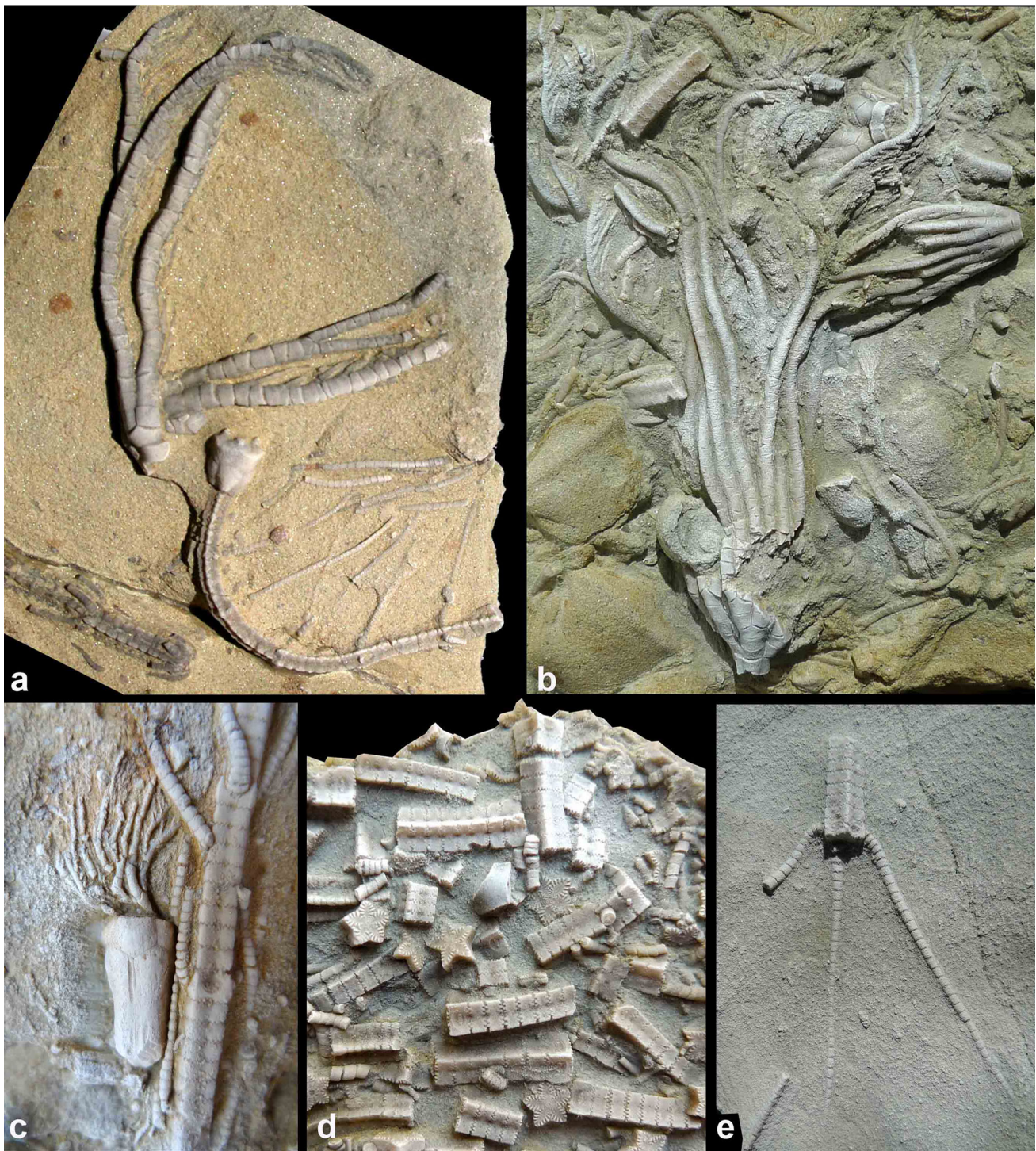


Fig. 2 Holocrinidae **a–e** *Holocrinus dubius* (Goldfuss, 1831); Lower Muschelkalk, Udelfangen Formation, Anisian; Ralingen-Kersch (Germany) (**a**, **b**, **d**, **e**), Rüdersdorf Formation, Anisian; Rüdersdorf (Germany) (**c**). **a** Cup with arms detached; arms with wide-spaced pinnules, some arms bifurcating; columns with cirri; MHI 1276/18; height of picture detail 35 mm. **b** Three crowns, two of them detached from cup (autotomized), arms with muscular articulations, flexible;

MHI 1276/5; height of picture detail 55 mm. **c** Crown with high cone-shaped cup and arms in early stage of regeneration; column of another individual; MHI 1256/2; height of picture detail 30 mm. **d** Partly disarticulated columns, preferentially broken at preformed rupture points of lower nodal facets; MHI 1276/7; height of picture detail 28 mm. **e** Column broken at lower nodal facet, with cirri attached; MHI 1276/6; height of picture detail 38 mm

Hagdorn and Baumiller 1998). The holocrinid cup is dicyclic and high barrel-shaped, with small radial facets directed upward (Fig. 2a, c). The 10–15 uniserial arms with alternating ligamentary and muscular articulations were flexible and actively movable but unable to (tightly) close the crown (Fig. 2a, b). According to the taphonomic record, holocrinids were able to discard their complete arms and to regenerate them subsequently (Fig. 2a–c; Hagdorn and Baumiller 1998). The radial facets with muscular articulation in the cups of cryptodicyclic isocrinids and pentacrinids were wider and directed obliquely outward, thus giving space for additional arm branching and fan-like widening of the arms. As Baumiller et al. (2008) pointed out, isocrinids detached from their columns are able to actively attain a mouth-upward position allowing continued filter feeding.

Remodeling of *Traumatocrinus* and *Seirocrinus* in adaptation to a pseudoplanktonic lifestyle

Adaptation to the new lifestyle required morphological remodeling. It is fascinating to understand these changes within the constraints and the potential of the echinoderm bauplan in general and the bauplan of their immediate Middle Triassic ancestors as described above. A major tool of remodeling is based on the study of peramorphic heterochrony.

Crown

Compared to their ancestors, the crowns of *Traumatocrinus* and *Seirocrinus* grew to much larger size by peramorphic amplification of the endotomously branching arms (Fig. 3a). *Traumatocrinus* has 20 isotomously branching, biserial major arms. During ontogeny (Hagdorn and Wang 2015) the arm number continuously increased by endotomous branching, yielding more than 500 smaller but still biserial armlets, which may additionally bifurcate in their distal parts. All brachials are granosyzygial and pinnulate after the second branching. Granosyzygies (Fig. 3b, c; Hagdorn and Wang 2015) differ from comatulid or millericrinid syzygies with simple ridges by the presence of strings of granules forming loops with intermittent furrows. The armlets are arranged in an inward directed echelon form giving the crown a shape comparable to a plicate coffee filter. Thus, the aboral surface of the crown is enlarged and allows more space for the armlets. The echelon form of the endotomous arms was already present in the benthic *Cassianocrinus varians*, one of the inferred ancestors of *Traumatocrinidae* (Fig. 1h; Hagdorn 2004). The tips of the major arms and the armlets end flush, leaving the distal side of the crown open, thus permanently

exposing the pinnule combs to the water body. In contrast, *Encrinus* was able to close its arms up to the tips to keep out suspended sediment particles.

An adult *Encrinus liliiformis* crown 12 cm in height has ten free arms, ~10 cm long, with roughly 100 brachials per arm, and each brachial bears a 15 mm long pinnule (Fig. 1b). This adds to a food groove length of 1.6 m per arm, and of 16 m in total. In a *Traumatocrinus* crown of similar size (Fig. 3a) the 20 major arms have ~200 low brachials, each bearing a 15 mm long pinnule; additionally, each of about 25 armlets in a major arm comprises roughly 100 brachials with a 10 mm long pinnule. This adds up to a food groove length of 112 m per ray and 560 m in total. Hence, the food groove length of the *Traumatocrinus* crown is increased by a factor of 35. In this calculation, bifurcations of the distal armlets (Fig. 4a) are not even considered. In large individuals of *Traumatocrinus* with a crown height of up to 20 cm, this figure is correspondingly larger. The ratio of food groove length of *Holocrinus* compared to *Seirocrinus* or *Pentacrinites* is increased by comparable factors. In relation to the size increase of crowns of pseudoplanktonic crinoids during ontogeny, the morphological cup is occupying an increasingly smaller part. However, such allometric growth during ontogeny is common in articulate crinoids (Hagdorn and Schulz 1996; Hagdorn 2011a).

Cup—The morphological cup of a crinoid is the place where the first brachials and the nodals are formed (‘nodal factory’, Seilacher 2011). Among the Anisian encrinids, the slightly depressed infrabasal/basal circlet occupies a relatively small part of the bowl shaped cup, and the basals are not completely inside the columnal pit where the nodals are formed (Fig. 1f). Hence, the encrinid column diameter is much smaller than the cup diameter. The pentalobate to subcircular, marginally crenulated, column pit acts as a blueprint for the crenulate pattern of the proximal nodals (Fig. 1g).

In contrast, the infrabasal/basal circlet of *Traumatocrinus* occupies almost the entire width of the cup. Its aboral (lower) side is a circular, planar surface with radiating rows of granules alternating with radial grooves (fossulae), and five deeper interbasal furrows (Fig. 3e, f). The granule rows are in granosyzygial contact with corresponding granule rows of the last-formed nodal, and the fossulae are opening in circular pores visible from outside. Hence, the (aboral) lower surface of the infrabasal/basal circlet acts as reproduction matrix producing wide nodals with the corresponding granosyzygial pattern. As demonstrated in “Column and attachment”, the five interbasal furrows are connected with five tubes that run longitudinally through the proximal column. It may be hypothesized that these tubes contained long strings of mutable connective tissue (MCT) connecting cup and column tightly but flexibly.

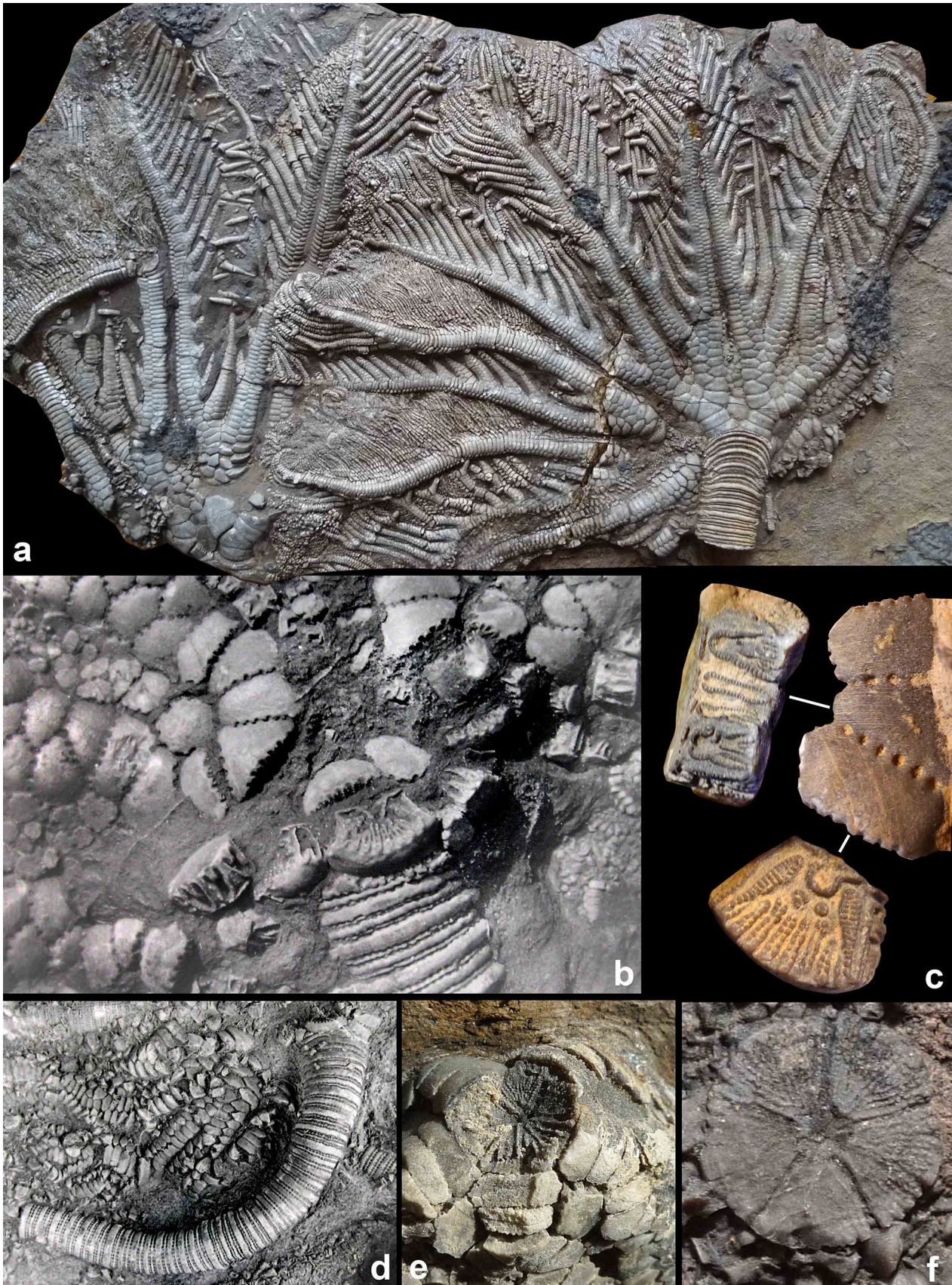


Fig. 3 *Traumatocrinus* Wöhrmann, 1889. Crown and cup. **a, b, d–f** Xiaowa Formation, Carnian; Guanling County (Guizhou Province, South China). **a** Crowns and proximal column of adult individual in bell (lateral) preservation; arms rays with four isotomously branching major arms and additional endotomously branching armlets; all arms biserial, pinnulated, distally with aboral spines; between proximal arms interbrachial plating; MHI 1882/5; height of picture 115 mm. **b** Radial circlet with radial facets inclined outward; radial facets granosyzygial; note fossulae openings along interbrachial sutures; detail of slab MHI 1850; height of picture detail 37 mm (from Hess 2011). **c** Three thick-plated proximal brachials (in the centre axillary) showing granosyzygial articulations, also at lateral articulations; fossulae openings along sutures; Zhuganpo Formation, Ladinian; MHI 2128; width of lower facet 4.5 mm; (from Hagdorn and Wang 2015). **d** Proximal column of semiadult individual with cup, arms disarticulating; columns distally tapering; detail of slab MHI 1854; width of picture detail 45 mm. **e** Cup and proximal arms of juvenile individual in aboral view, note large interradian extending between radials; details of slab MHI 2127; width of picture detail 13 mm. **f** Basal circlet in aboral view with five deep fossulae that meet the five infrabasals; detail of slab MHI 1677/9; width of picture detail 8 mm; (from Hagdorn and Wang 2015)

However, such cup morphology was basically achieved by the immediate ancestor, the benthic encrinid *Zardinicrinus*, whose radial facet is still muscular (Fig. 1i; Hagdorn 2011a, b). The nodals of *Seiocrinus* (and *Pentacrinites*) were formed in a relatively narrow columnal pit which was strengthened by aboral extensions of the basals, stabilizing the fragile contact between column and cup, and by a protective tuft of cirri (Seilacher and Hauff 2004: fig. 2C, 7; Seilacher 2011).

Arms—In *Traumatocrinus* all brachial articulations are of the unique granosyzygial type. The fossulae are opening in equidistant circular pores along the aboral suture lines in many adult individuals (Fig. 3b, c). Granosyzygies may have originated from synostosal articulations with faint marginal ridges that occur in advanced encrinids, e.g., between basals and radials (Fig. 1e), and primibrachials 1 and 2 (Fig. 1d). However, ancestral muscular articulations between radials and first primibrachials and between axillary second primibrachials and first secundibrachials were likewise remodeled to uniform granosyzygies. However, in advanced encrinids marginal ridges may also occur along the aboral side of muscular articulations (Fig. 1c, j). Hence, the uniform granosyzygies in the *Traumatocrinus* arm are derived from both ligamentary and muscular ancestral articulations.

The *Traumatocrinus* crown devoid of muscular articulations—apart from the pinnule sockets—must have been rather inflexible. Hypothetically, the ligament connecting the granosyzygial ossicles was of MCT, allowing the animal to maintain the bell-shaped and strongly plicate crown. In contrast to the syzygies of comatulids that acted as preformed rupture points, the *Traumatocrinus* granosyzygies had to maintain tensile strength to preclude loss of

arms. This is confirmed by the taphonomic record that yielded no evidence of detached and isolated arms or individuals with regenerating arms. Hence, the pseudo-planktonic lifestyle in higher water levels does not require autotomy as a stress reaction triggered by mud suspensions among their benthic ancestors.

The endotomous arm branching pattern of *Traumatocrinus* amazingly corresponds with the ideal layout of harvesting transportation roads in banana plantations as demonstrated by Cowen (1981). Based on the example of the camerate crinoid family Melocrinidae that optimized their food gathering and transporting mechanisms by evolutionary adaptation between Late Ordovician and Late Devonian times, he raised the question why this pattern has not become dominant among crinoids. As an explanation, he considered the rigidity of the camerate crown as the most likely prerequisite, a characteristic “uncommon among other crinoids”. As discussed above, the replacement of all muscular articulations by granosyzygies in the *Traumatocrinus* arm provided the rigidity suggested by Cowen. The time span of 5–10 Ma in the late Ladinian and early Carnian for this change was much less than the time needed by the Melocrinidae. This was possibly due to the rapid evolutionary habitat change of the Triassic Crinoidea after the end-Permian crisis (Hagdorn 2011a). However, Melocrinidae from the Devonian of New York have been found associated with fossil logs and may also have been pseudoplanktonic as suggested by Wells (1947) and McIntosh (1978). For additional evidence of pseudo-planktonic lifestyles by attachment to driftwood among Palaeozoic crinoids, see Hess (2010).

The aboral sides of *Traumatocrinus* arms are tightly closed so that not even small particles found their way into the folded crown (Fig. 4a). If so, *Traumatocrinus* did not present a screen-like filter fan like living crinoids but rather collected food on the leeside where back currents flushed particles through the open distal end of the crown. The folded aboral surface may have helped to channel the current to the leeside of the crown. However, this inference has to be proven by experimental analyses of current regime models as performed by Dynowski (2015) for *Encrinus liliiformis* and living crinoids. A velcro effect of coupled rows of neighboring pinnules by ciliary adhesion, hypothesized by Seilacher and Hauff (2004, Fig. 4) may have strengthened the aboral closure of the arms. In addition, the large aboral spines observed in the distal parts of the medial to distal armlets of adult crowns (Fig. 3a) could have acted as a grid or lattice to prevent coarse particles reaching the pinnular combs inside the crown.

If this assumption is correct, food particles entered the space between the densely packed pinnule combs of arms and armlets through the wide distal opening on the lee side of the crown. In contrast to other crinoids, the distal



◀ **Fig. 4** *Traumatocrinus* Wöhrmann, 1889. Arms and pinnules. Xiaowa Formation, Carnian; Guanling County (Guizhou Province, South China). **a** Arms of semiadult crown, initial arm branching isotomous then changing to endotomous pattern; note axillary spines at bifurcating distal armllets, pinnulation of major arm; detail of slab MHI 1850; width of picture detail 82 mm. **b** Distal part of pinnules, pinnularia with distal spines; minute granules in food groove of proximal pinnularia (left upper corner); detail of MHI 1881/2 (Fig. 3a); width of picture detail 7.5 mm; (from Hagdorn and Wang 2015). **c** Distal arms with fur of spine-shaped distal pinnularia; detail of slab MHI 1677/4; width of picture detail 29 mm

pinnulars of *Traumatocrinus* are devoid of a food groove but have long, blade-like extensions or spines, and the terminal pinnular is reduced to a spine (Fig. 4b, c). These pinnulars produce the spiny fur observed around the tegmen of specimens preserved in oral aspect (Fig. 4c). This fur was exposed by the living crinoid toward the reverse current on the leeside. However, without a food groove, and; hence, without tube feet, the distal pinnules were unable to seize food particles but rather acted as sieves that excluded larger particles to enter the food gathering inner part of the pinnular combs. As no other post-Palaeozoic crinoid has such pinnules, one may conclude that they served for gathering small food particles.

Tegmen—Food particles were transported along the food grooves from the medial and proximal pinnules to the armllets, then to the major arms and finally to the cup. Surprisingly, neither ambulacral food grooves nor a mouth could be observed on the tegmina. Hence, the food grooves of the major arms should have entered the cup at the margins of the tegmen, but here, too, ambulacrals cannot be observed. However, where the free arms join the tegmen, small areas with tiny granules covered by circular pores occur (Hagdorn and Wang 2015: fig. 6a, a'). In contrast to the finely granulated flexible tegmen of Encrinidae, the tegmen of *Traumatocrinus* is paved by polygonal plates and extends into the space between the proximal arms as far as to the interradianal suture. These interbrachial and interradianal plates close the enlarged functional cup between the fan-like, widening arms (Fig. 3a, b, e). Interradianal plates have not been observed in Encrinidae, but they occur already in juvenile *Traumatocrinus* of the *Encrinus* growth stage of less than 10 mm crown length (Hagdorn and Wang 2015: fig. 9a, b).

It was the general similarity with *Seirocrinus* and *Pentacrinites* that induced Hagdorn (1998) to assume a pseudoplanktonic lifestyle for *Traumatocrinus*. After the extinction of the Encrinida in mid-Carnian times, *Pentacrinites* and *Seirocrinus* changed their habitat from benthic to pseudoplanktonic. This was the second occupation of the niche presented by driftwood suitable for crinoids (Hagdorn et al. 2007; Hagdorn 2011a). The most spectacular adaptation of the remodeled crowns was the transition

from the ancestral holocrinid isotomous branching to the endotomous pattern, convergently developed with *Traumatocrinus*. The holocrinid offshoots closed the gaps between the proximal arms by incorporating tegminal plates and proximal pinnules (Simms 1989) and by encapsulation of the enlarged functional cup. In contrast to *Traumatocrinus*, the articulations of the uniserial brachials still correspond to those of the ancestral Holocrinidae. However, pentacrinid articulations are exclusively muscular, each brachial bearing a pinnule. Hence, pinnulation is as dense as in *Traumatocrinus* (Seilacher and Hauff 2004: fig. 2B). In contrast, the arms remained flexible and could be moved actively; in addition, the aboral side of the *Seirocrinus* crown was not closed but allowed conventional, downstream food gathering. As there is no evidence of a morphological change of pinnules as in *Traumatocrinus*, one may consider *Seirocrinus* and *Pentacrinites* as unspecialized plankton feeders.

Column and attachment

Remodeling the column of their benthic ancestors was as far-reaching for pseudoplanktonic life as remodeling the crown. In a benthic crinoid the basic function of its column is to elevate the crown above the seafloor and to anchor the animal against hydraulic pressure. Hence, column length is limited. For a pseudoplanktonic lifestyle, lengthening of the column must have been advantageous. This is indicated by column lengths of more than 11 m for *Traumatocrinus* (Hagdorn and Wang 2015) and of up to 20 m for *Seirocrinus* (Hess 1999). Because breakage of the column would cause lethal sinking of the crinoid to the seafloor, attaining sufficient tensile strength and flexibility, protection from breakage, and efficient attachment to the floating substrate were prerequisites.

The column of *Traumatocrinus* is characterized by a unique system of two levels of porosity, which induced its first author Alfons von Dittmar (1866) to propose *Porocrinus*, an unfortunate preoccupied name. In its proximal and medial parts, the column is perforated by a system of interconnected tubes, the intercolumnar fossulae, and the longitudinal tubuli. The fossulae open in equidistant circular pores arranged along the intercolumnar sutures (Fig. 5a). The openings of the tubuli are visible on columnal articulation facets and in longitudinal sections of the column (Fig. 5c, d). The nodals, which can be identified only in the proximal column, are devoid of cirri and are slightly higher and wider than the internodals (Fig. 5a, c, f). Hence, the number of internodals per noditaxis cannot be counted in the medial and distal column. Below the crown, the column of adult individuals is bent like the handle of a walking stick and considerably wider than more distally. The columnal articular facets have multiradiate

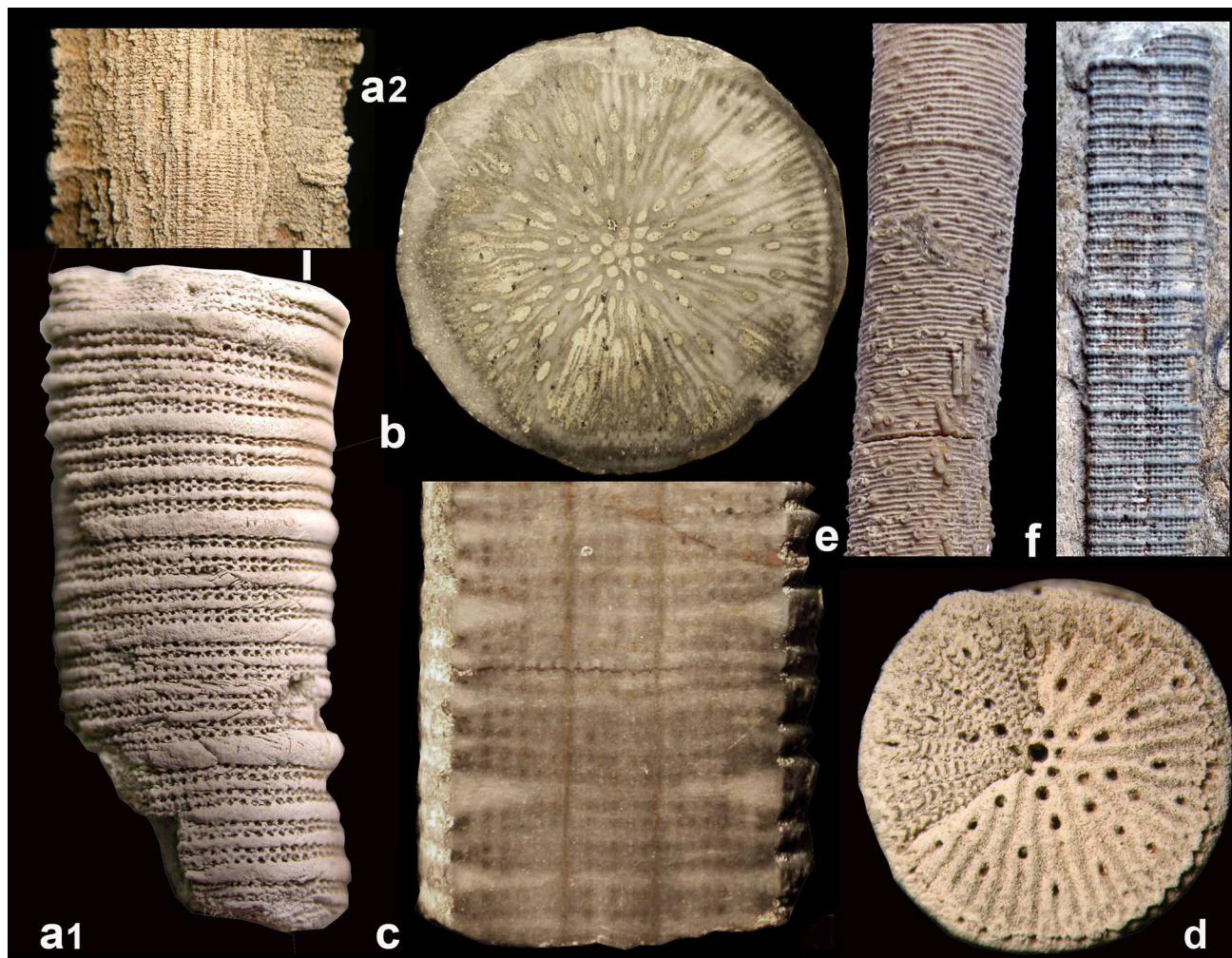


Fig. 5 *Traumatocrinus* Wöhrmann, 1889. Column. **a, d–h** From a karstified bedding plane of uppermost Zhuganpo Formation, Ladinian; **e, f** Xiaowa Formation, Carnian; Guanling County (Guizhou Province, South China); **b, c** Carnian, Basin of River Šela-i-Khodjapalur (Herat Province, Afghanistan). (**a1**) Pluricolumnal of proximal column with nodals and series of two orders of internodals; external side showing openings of intercolumnar fossulae, internal side etched by humic acid (**a2**) exposing longitudinal tubuli; note thickened rims of nodals; MHI 1880/2; length of pluricolumnal 25.5 mm (from Hess 2011). **b** Polished cross section of pluricolumnal showing intercolumnar fossulae and series of tubuli; five primary

tubuli around central canal; MHI 1885/1; width 20 mm; (from Hess 2011). **c** Polished longitudinal section of pluricolumnal showing two tubuli and countless fossulae; MHI 1885/2; height of picture detail 16 mm. **d** Granosyzygial facet with rows of chevron-shaped granules, overlain by thin fragmentary nascent internodals with fossulae of different length ending in longitudinal tubuli; note granule string bifurcations regularly commencing at a tubulus. MHI 1880/4; width 6.8 mm (from Hess 2011). **e** Pluricolumnal of distal column with buds of radicular root cirri; MHI 1882/2; width 19 mm. **f** Flattened pluricolumnal of proximal column, showing longitudinal breaking edge; MHI 1881/1; width of pluricolumnal 11.5 mm

rows of granules or very short crenulae arranged as sets of chevrons; these granosyzygial articulations are astonishingly similar to the brachial articulations. The number of granule rows is increasing toward the margin by bifurcation and intercalation. The fossulae are running from their marginal openings toward the center and connecting with the longitudinal tubuli, each vertical row of fossulae entering the same tubulus. This feature is most clearly seen in 3-D MicroCT scans (Dynowski et al. 2013). The oldest (primary) set of five tubuli surrounding the central canal in radial position is connected with the oldest fossulae that

originate from the five interbasal fossulae (Figs. 3, 5d). Columns wider than 12 mm have up to six series of tubuli. In the distal column, no tubuli are present.

Hagdorn et al. (2007) hypothesized the presence of long, parallel strings of MCT in the tubuli, thus preventing torsion of the column and allowing alternating stiffening and relaxation of the column. This would have enabled the animal to actively move its crown. This hypothesis is corroborated by taphonomy, because *Traumatocrinus* columns are preserved either in loosely curved strings or straight (Hagdorn et al. 2004, 2005; Hagdorn and Wang

2015). With such mobility, it is not necessary to assume that wind-driven logs drifted faster than the current and that the crinoids deployed a tow-net-style filter fan for feeding, as proposed by Seilacher and Hauff (2004). The model of the *Traumatocrinus* column producing its own motion would still be working effectively if the float was drifting in deeper waters below wind influence. As demonstrated by Hagdorn et al. (2007) a colony with different column lengths could filter a larger volume than a colony with uniform column lengths drifting at a given depth. Assuming the same age of the individuals in the colony, as indicated by equal crown size, intracolony competition could be avoided by differential growth rates of the columns. This would correspond to the intraspecifically different tiers of elevation observed in the benthic *Encrinurus liliiformis*, however, in an inverted way.

Basically, *Traumatocrinus* column growth corresponds to the pattern of its encrinid ancestors by (1) nodal production in the column pit (2) production of series of internodals throughout the column and (3) accretionary growth. Columnals produced in the small column pit of juveniles migrated distally and grew by lateral accretion, becoming wide and low discoid like a coin. The newly formed nodals and internodals of adults in the bent proximal column are wider than columnals after the bending (Fig. 3d). Hence, nodal production in the column pit must have ceased at a certain point. As far as nodals and internodals can be distinguished, a noditaxis comprised up to eight columnals. Hence, individual column length must have been controlled by peramorphic production of additional internodals.

Moreover, soft tissue of less density within the pore systems compared to the mineralized stereom reduced the weight of the crinoids and, hence, the load of the driftwood. Such weight-reducing construction is proven in the taphonomic record by proximal columns compressed and fractured under sediment load (Fig. 5f). In terms of functional morphology, composite material and structure of the *Traumatocrinus* column resembled palm tree stems and their flexibility and strength. However, decrease of density was certainly not the primary function, as the pore systems were already present in *Zardinicrinus*, the benthic ancestor of *Traumatocrinus* (Fig. 1k).

In contrast to its benthic holocrinid ancestors, the *Seirocrinus* column was rather stiff in its proximal part and, due to tapering, more flexible near its attachment area (Seilacher et al. 1968; Haude 1980, 1981; Seilacher and Hauff 2004: fig. 2A). The extreme length is caused by unlimited production of internodals between two nodals (more than 1000 according to Seilacher 2011). However, in the terminal column cirriferous nodals are closely spaced to strengthen attachment of the crinoid by a tuft of cirri. As pseudoplanktonic animals need lifelong attachment,

Seirocrinus and *Pentacrinites* had to abandon infranodal rupture inherited from their holocrinid ancestors; hence, they rather strengthened their cirrus-based attachment structure.

Traumatocrinus modified the encrinid terminal discoid or incrusting holdfast to a terminal attachment area of several centimeters in length by the distal columnals. This column segment was closely agglutinated to the surface of the substrate by countless segmented, cirrus-like radicular rootlets originating from circular buds with multiradiate facets (Fig. 5d). The rootlets are irregularly anastomosing comparable to the anchoring roots of ivy, and they may merge to a crust that covers neighboring areas of the substrate (Fig. 6a, b). A well-preserved piece of driftwood with a *Traumatocrinus* root shows parts of the wood surface coated by crinoidal callus (Fig. 6c). The taphonomic record of many logs indicates a preferred attachment position at either end of the log, avoiding the presence of bark. Such attachment facilitated a fixation that could be continuously adjusted or repaired. Hence, detached individuals of *Traumatocrinus* are less common than in *Seirocrinus* with their weaker attachment (e.g., Seilacher and Hauff 2004: Fig. 2A). On driftwood with *Traumatocrinus* no bivalve epibionts have been observed, although small incrusting oyster-like bivalves occur in the Xiaowa Formation black shales on larger ammonoids and on driftwood free of crinoids. Possibly, the callus crust of living crinoids with its epithelium cover prevented settlement of bivalve larvae or other epibionts, thus keeping the substrate afloat longer. If such a crust covered larger areas of the log surface, it may also have retarded soaking, hence, prolonging drifting time.

Compared to their holocrinid benthic ancestors, *Seirocrinus* and *Pentacrinites* maintained attachment by means of true cirri that were rather grasping than clinching or gluing. For this purpose, densely spaced nodals at the terminal column of *Seirocrinus* provided a tuft of cirri (Seilacher and Hauff 2004; Seilacher 2011). However, cirrus attachment was certainly less efficient than radicular attachment as indicated by the fossil record. In terms of evolutionary biology, the inherited constraints of temporary attachment by cirri were more favorable to benthic life than to pseudoplanktonic life. On the other hand, benthic crinoids tightly and permanently attached to the substrate by a holdfast were unable to re-attach after column fracture, a disadvantage beneficial to their pseudoplanktonic descendants.

Taphonomy and paleoecological conclusions

As demonstrated by Haude (1980) for *Seirocrinus*, there seems to be a comparable relation of driftwood size and number and/or size of *Traumatocrinus* individuals

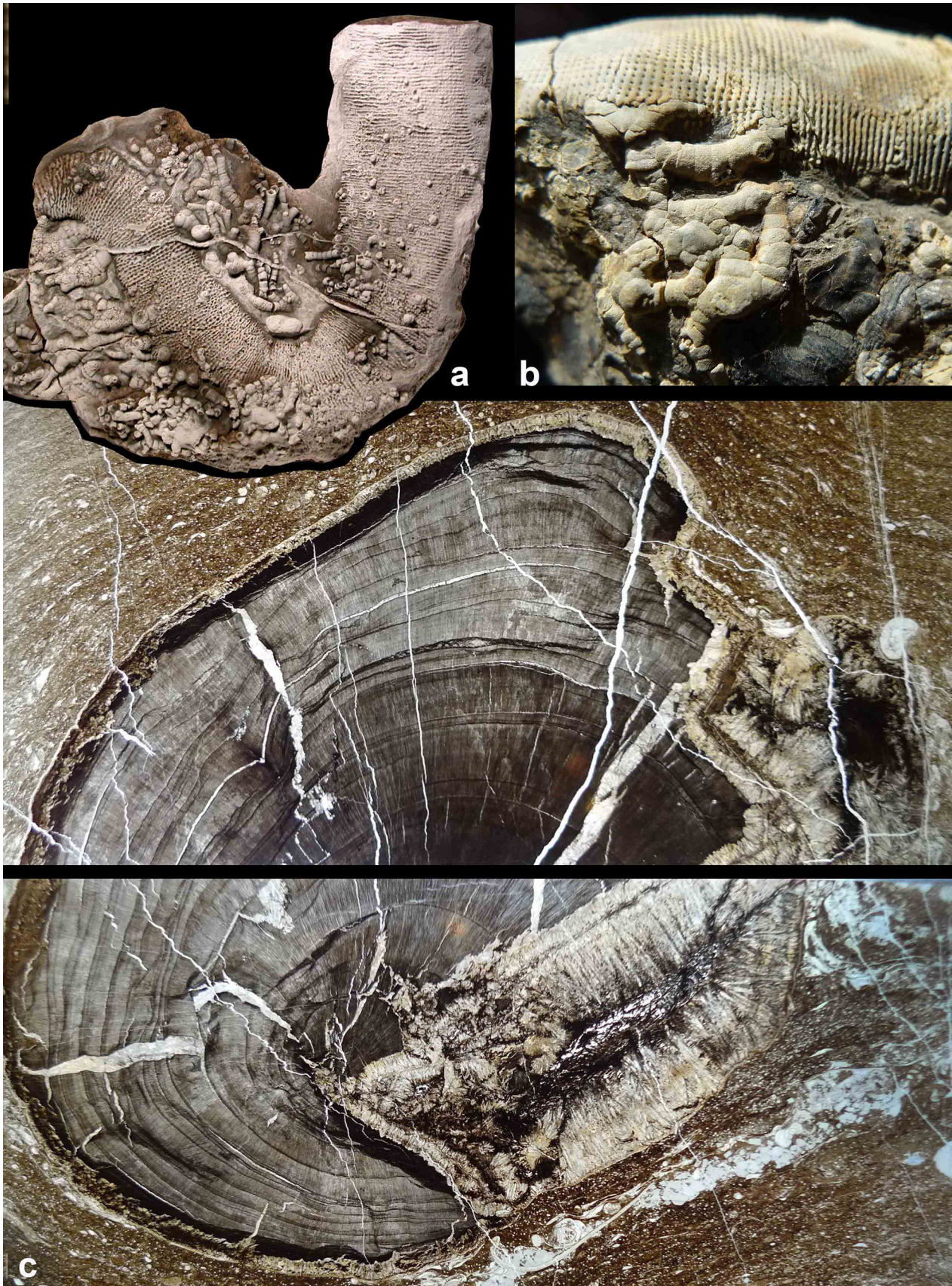


Fig. 6 *Traumatocrinus* Wöhrmann, 1889. Attachment structures. **a–c** Xiaowa Formation, Carnian; Guanling County (Guizhou Province, South China). **a** Distal column bent at angle of $\sim 50^\circ$, opposite side was attached to driftwood; countless irregularly anastomosing radicular cirri enlarging attachment area; articulation facets of additional rootlets (root cirri) pointing outward, not contacting the wood substrate; MHI 1882/1; height 57 mm (from Hess 2011). **b** Distal column with anastomosing radicular root cirri covering and invading gaggatized driftwood; MHI 2133/1; width of picture 25 mm. **c** Thin section of driftwood log (in two parts) with *Traumatocrinus* root attached invading into heartwood and covering driftwood surface; MHI 2134; width 12 cm; thin sections produced by B. Leipner-Mata, GeoZentrum Nordbayern der Universität Erlangen

attached. Small driftwood pieces always have small crinoids because of an unfavorable relation of buoyancy and load capacity (Hagdorn and Wang 2015: fig. 10d). Medium-sized logs of approximately 1 m are commonly crowded by densely settled, semiadult *Traumatocrinus* at both ends of the log (Hagdorn and Wang 2015: fig. 10b–c). Really large individuals with column lengths exceeding 10 m are only found on large logs of several meters in length. Thus, the lifespan of driftwood-attached pelagic crinoids is necessarily limited by the drifting time of the logs. Haude (1980) explained drifting conditions, inferred drifting time, load capacity, and sinking conditions of logs.

Unfortunately, we cannot refer to an Extant model for a better understanding of driftwood-attached crinoids because this ecological niche was closed at the end of the Early Jurassic. The last representative of the Family Pentacrinidae, the Bathonian *Pentacrinites dargniesi*, has reverted to benthic life (Hess 1999). *Traumatocrinus* was the first post-Paleozoic crinoid switching from benthic to pseudoplanktonic life in late Ladinian/early Carnian times. Hence, this niche, which existed for roughly 50 Ma from late Ladinian to Toarcian, was occupied twice: first by encrinid offshoots, and, after their decline in mid-Carnian times, again by holocrinid offshoots in Norian times (Hagdorn et al. 2007). According to these authors, the drifting time of wood in marine environments was reduced by the rise of shipworms so that the time for growth and reproduction of the crinoids became too short.

This poses the question of how *Traumatocrinus* may have reproduced. *Traumatocrinus* could have produced a large number of planktotrophic larvae that were spread by currents over vast areas and attached themselves to driftwood of any size. The chance to find a suitable piece of driftwood in a vast ocean was increased by high production of larvae. Such *r*-strategy of reproduction was probably more favorable than producing a smaller number of lecithotrophic offspring settling on the driftwood in the vicinity of the parents with the danger of overloading the raft. The fossil record indicates that the *r*-strategy was more likely for *Traumatocrinus* because individuals on a

log are roughly of the same size—with column lengths of adults varying as explained above. However, in *Seirocrinus* colonies, juvenile individuals are commonly attached to the proximal columns of adults to take advantage of their long columns, supporting lecithotrophic reproduction.

In contrast to benthic crinoids that were dispersed to suitable habitats exclusively by larvae, pseudoplanktonic crinoids could expand their habitat also as adults drifting through the seas attached to logs. This is shown by the fossil record of *Traumatocrinus* across the Palaeo-Tethys, from the type region in the classic Hallstatt Limestone of the Eastern Alps (Austria) through Slovakia, Romania, Iran, Afghanistan, the Himalayas, South China, and as far East as the Island of Timor (for locality data see Hagdorn et al. 2007). Its sister genus, *Vostocovacrinus*, inhabited the Boreal realm of the Triassic world. Hence, such global distribution is likely due to dispersion of driftwood by oceanic currents in addition to larval dispersion.

Conclusions

A prerequisite for a pseudoplanktonic lifestyle of stalked crinoids was the availability of suitable driftwood. After the Late Paleozoic decline of forests documented by a rapid decrease of gymnosperm pollen and a sudden increase of fungi at the Permian/Triassic boundary ('fungal spike'; Looy 2000), this niche opened in the late Middle Triassic. The niche was subsequently occupied by the encrinid offshoot *Traumatocrinus* in the late Ladinian, and, after the decline of the Order Encrinida in the mid Carnian, a second time by the holocrinid descendant *Pentacrinites* and *Seirocrinus* (Hagdorn et al. 2007).

A comparison of the morphological transformations of *Seirocrinus* and *Traumatocrinus* allows the top adaptations for pseudoplanktonic life of stalked crinoids to be specified within the constraints of the encrinid and the holocrinid clades:

- Lightweight construction to reduce the load on the driftwood, maintaining its buoyancy as long as possible. This was achieved by pore systems of intercolumnal fossulae and longitudinal tubuli in *Traumatocrinus*, and by a distally tapering column in *Seirocrinus*.
- Peramorphic lengthening of the column to reach plankton-rich water levels (*Traumatocrinus* and *Seirocrinus*), and construction of both a flexible and stout column by MCT (*Traumatocrinus*). Different column lengths in a colony of *Traumatocrinus* allowed filtering of a larger water body.
- Solid and persisting anchoring to the drifting substrate to prevent breakage and detachment from the log (better in *Traumatocrinus* than in *Seirocrinus*).

- Increasing the length of the food grooves to compensate for the disadvantage of drifting along with the plankton by peramorphic augmentation of endotomically branching arms (both forms).
- Enlargement of the functional cup by intercalation of tegminal or/and pinnular elements (both forms).
- Among articulate crinoids, and compared to *Pentacrinites* and *Seirocrinus* with similar lifestyle, *Traumatocrinus* developed unique morphologies. Most remarkable are the complex pore structures of the column and the ligamentary granosyzygies between the brachials, even including the articulation between radials and first primibrachials.

Epilogue

If a human being could have dived into the Late Triassic tropical Palaeo-Tethys Ocean, he would have been overwhelmed by the majestic sight of a floating log carrying a freight of hundreds of crinoids drifting through the crystal-clear water. This would have been an attraction incomparable to anything else seen today. One may bewail that such a vision remains a matter of imagination only. Fortunately, visitors to natural history museums all over the world may admire wall-filling slabs of black shale with rafts of flower-like fossils whose long columns carry delicate crowns. It is such fascination that encourages palaeontologists to investigate the mysteries of forgotten underwater worlds.

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