

Triassic: the crucial period of post-Palaeozoic crinoid diversification

Hans Hagdorn

Received: 26 July 2010 / Accepted: 24 September 2010 / Published online: 7 December 2010
© Akademie der Naturwissenschaften Schweiz (SCNAT) 2010

Abstract After their near-extinction around the end of the Permian, crinoids recovered during the Triassic and re-occupied almost all ecological niches they had held in Palaeozoic times. Triassic crinoids comprise 33 genera in 12 well-defined families and 5 orders of the subclass Articulata; the systematic position of 4 additional families is unknown. The highest diversity was before the Mid Carnian Wet Intermezzo that caused the extinction of the order Encrinida. Major morphologic changes were connected with the adaptation to various benthic habitats and to pseudoplanktonic and eleutherozoic modes of life. Convergently, the cups of Encrinida and Holocrinida–Isocrinida became cryptodicyclic with large muscular radial facets, arm numbers increased from 5 to more than 300, and the arms of Encrinida became gradually biserial. The Encrinida remained permanently fixed to hardgrounds and acted as frame builders in bioherms. By encrusting bivalve mudstickers some dadocrinids also became secondary soft bottom dwellers. The holocrinid stem evolved preformed rupture points at the lower nodal facets, allowing these crinoids to attach intermittently by cirri. The pseudoplanktonic traumatocrinids evolved extremely long, flexible stems with multiple pore systems and terminal root cirri. Paracomatulids and eocomatulids reduced their stems and adapted to an eleutherozoic mode of life. Somphocrinids miniaturized and remodeled their skeleton towards lightweight construction and adapted to a planktonic life style. After the Triassic no fundamentally novel adaptation

was added. Crinoidal limestones, as common in the Palaeozoic, had their last appearance in Middle Triassic times.

Keywords Crinoids · Triassic · Diversity · Functional morphology · Evolutionary biology · Palaeoecology · Niche adaptation

Introduction

Triassic crinoids gained scientific interest (Agricola 1546) long before their echinoderm nature was known (Rosinus 1719). *Encrinus liliiformis*, the stone lily of the eighteenth century naturalists, was a favorite object in art cabinets. Moreover, crinoidal limestones from the Muschelkalk were named by early stratigraphers using Agricola's term *trochites* (wheelstones) for the cylindrical encrinid columnals. The Trochitenkalk (Schlotheim 1820) has nowadays the rank of a formation. Since then, *Encrinus liliiformis* has become one of the best known crinoids in morphological, palaeoecological and taphonomic respects, and the Trochitenkalk became a model for crinoidal limestone formation. Although several Triassic crinoid species and genera have been added subsequently (for an overview see Biese 1934 and Simms 1990b), their true diversity has long been disregarded, as many taxa were later included into the synonymy of *Encrinus* or *Pentacrinus*. Other taxa are based on poorly preserved and fragmentary material. This is particularly true for the family Isocrinidae, whose Triassic record consists mainly of isolated columnals and cirrals. They are found in Lagerstätten, in which autotomized and subsequently disarticulated distal stem parts have been accumulated.

This is the state of the art as reflected in the crinoid volumes of the Treatise (Moore and Teichert 1978) which

H. Hagdorn (✉)
Muschelkalkmuseum Ingelfingen, Schloss-Str. 11,
74653 Ingelfingen, Germany
e-mail: encrinus@hagdorn-ingelfingen.de

reported only nine genera and five families for the entire Triassic. In the meantime, many publications have increased the number of well-defined taxa. They shed new light on the post-Palaeozoic crinoid phylogeny (Klikushin 1992; Simms 1990a, b; Simms and Sevastopulo 1993; Hagdorn 1995; Simms 1999).

Due to Hans Hess's experience and effort, the Articulata volume of the revised Crinoid Treatise has been finished and awaits publication (Hess 2010a). It includes all post-Palaeozoic crinoids and lists 33 Triassic genera in 12 well-defined families and 5 orders; the systematic position of 4 additional families is uncertain (Fig. 1). Unlike the 1978 Treatise that assigned Encrinidae (with only one valid genus) to the subclass Inadunata, this clade is now regarded as a separate order Encrinida of the subclass Articulata and

comprises the families Encrinidae, Dadocrinidae, Traumatocrinidae, and Ainigmacrinidae. The true diversity of Triassic crinoids is probably even broader, because there are new finds from the early Carnian Cassian Formation of the Dolomites (Italy) and from the middle Carnian Hanwang Formation of Sichuan (Central China) that still await description.

The present paper is based on the classification that Hans Hess used in the new Treatise. It does not deal with the Palaeozoic ancestors and their extinction (Simms and Sevastopulo 1993), nor with the Early Triassic echinoderm bottleneck, which has only recently been summarized by Twitchett and Oji (2005). Its aim is rather to give a preliminary and concise overview of radiations and morphodynamics during the Triassic recovery, in particular (1)

Indusian	Olenekian 3	Anisian 30				Ladinian 17		Carnian 25		Norian 14			Rhaetian 10	Stage	Genus	species number	Family species number	Order species number
		Aegean 2	Bithynian 9	Pelsonian 9	Illyrian 18	Fassanian 6	Longobardian 15	Juvalian 24	Tuvanian 7	Lacian 9	Alaunian 7	Sevatian 14						
	3	1	2	2	2	1	1								<i>Holocrinus</i>	10	Holo- crinidae	15
			1												<i>Moenocrinus</i>	1		
				1											<i>Eckicrinus</i>	1		
					1										<i>Tollmannicrinus</i>	3		
			1												n. gen. <i>Dadocrinidae</i>	1	Dado- crinidae	24
		1	3												<i>Dadocrinus</i>	3		
				1											<i>Carnallicrinus</i>	1		
			2	4	6	1	1	1							<i>Encrinus</i>	9	En- crinidae	15
				1				1							<i>Chelocrinus</i>	3		
					1			1							<i>Cassianocrinus</i>	1		
								2							<i>Zardincrinus</i>	2		
								1							<i>Ainigmacrinus</i>	1	Ainigmacr. 1	17
								1	1						<i>Traumatocrinus</i>	2	Traumatocrinidae 3	
								1							<i>Vostocovacrinus</i>	1		
															<i>Pentacrinites</i>	2	Pentacri- nitidae	4
															<i>Seiocrinus</i>	1		
															<i>Eocomatula</i>	1		
				1				4	1						<i>Tyrolocrinus</i>	5	Iso- crinidae	12
				1				1							<i>Balanocrinus</i>	3		
									1						<i>Singularocrinus</i>	2		
										1					<i>Laevigatocrinus</i>	1		
										1					n. gen. „ <i>Isocrinus</i> “ <i>propinquus</i>	1		
															<i>Paracomatula</i>	1	Paracomat. 1	
					1										<i>Bangtoupocrinus</i>	1	Bangtoupocri- nidae	4
					2										<i>Silesiacrinus</i>	2		
															n. gen. <i>Millericrinida</i>	1	fam. indet. 1	
															<i>Axicrinus</i>	1	Axicrinidae 1	8
															<i>Somphocrinus</i>	1	Somphocrinidae 7	
															<i>Ossicrinus</i>	1		
															<i>Osteocrinus</i>	5		
															<i>Lanternocrinus</i>	1	Lanternocr. 1	12
															<i>Nasutocrinus</i>	2		
															<i>Leocrinus</i>	5	Leocrinidae Quinyanocr.	
															<i>Quingyanocrinus</i>	1		
															<i>Tulpacrinus</i>	2	Tulpacrin. fam. indet.	
															<i>Bihatocrinus</i>	1		

Fig. 1 Triassic crinoid diversification. Genus and higher taxonomic units are based on Hess (in press). Numbers indicate valid species as referenced in the Appendix. Artefacts may originate from the limited fossil record. Conservation Lagerstätten with diverse crinoid palaeocommunities such as the Anisian Muschelkalk or the late Ladinian/early Carnian Cassian Formation may be overrepresented compared to early Ladinian or early Norian sediments that have yielded relatively few crinoids. Moreover, the diversity of Isocrinidae recorded in countless nominal “*Isocrinus*” species based on isolated columnals (Simms 1990a, b) is certainly higher than in this chart. The species concept of *Osteocrinus* (ca. 15 nominal species) and of the benthic microcrinoids is also based on isolated sclerites showing minimal differences, many of which may have resulted from the

etching process during preparation. In this paper 5 well characterized *Osteocrinus* species were selected. Nominal species attributed to the parataxonomic genus *Entrochus* were excluded. A distinct faunal change caused by the “Mid Carnian Wet Intermezzo” is indicated by the extinction of order Encrinida, while Isocrinida and Millericrinida persisted into the Norian and later Mesozoic. Thus, four Triassic benthic crinoid associations can be distinguished (cf. Fig. 11), (1) an Early Triassic Holocrinida association of extremely low diversity, (2) a diverse Middle Triassic Holocrinida/Encrinida association, (3) an early Late Triassic Isocrinida/Encrinida association, (4) a late Late Triassic Isocrinida/Millericrinida association. The major turnover happened in Carnian times after the overall Triassic diversity had reached its peak

crinoid diversity through the Triassic stages and substages, (2) character evolution and functional morphology with a focus on convergent adaptations, (3) ecological niches. With regard to the entire class Echinodermata, post-Palaeozoic radiation has been dealt with by Simms (1990a), Hagdorn (2000) and Twitchett and Oji (2005). Due to their poor fossil record and fragmentary preservation, the Quingyanocrinidae (Stiller 2000) and the Triassic microcrinoid families Tulipacrinidae, Lanternocrinidae and Leocrinidae (Kristan-Tollmann 1990) have also been excluded. They are taken into account, however, in the diversity chart (Fig. 1).

Evolutionary trends and morphodynamics

The fossil record of the less derived Early and Middle Triassic crinoids contains a set of ancestral characters shared by the orders Holocrinida and Encrinida. Probably, these characters were already present in a Late Palaeozoic or Early Triassic “proto-Articulata” (Fig. 2) that is still to be found among advanced cladids (Simms and Sevastopulo 1993). The characters of this hypothetical ancestor should include:

1. a dicyclic cup with circles of infrabasals (visible in lateral view), basals, and radials;
2. no anal plate;
3. muscular distal radial facets;
4. double axial canal in radials and proximal arms;
5. the arms branching at the second, axillary primibrachial with muscular facets;
6. proximal arms uniserial but distally becoming biserial with wedge-shaped brachials;
7. muscular and ligamentary articulations in proximal arms;
8. muscular and ligamentary articulations in distal arms;
9. brachials pinnulate, with the second pinnular longer than the first;
10. proximal stem pentagonal, distally becoming circular;
11. proximal nodals with cirri;
12. terminal discoid holdfast.

8. ligamentary articulations in distal arms;
9. brachials pinnulate, with the second pinnular longer than the first;
10. proximal stem pentagonal, distally becoming circular;
11. proximal nodals with cirri;
12. terminal discoid holdfast.

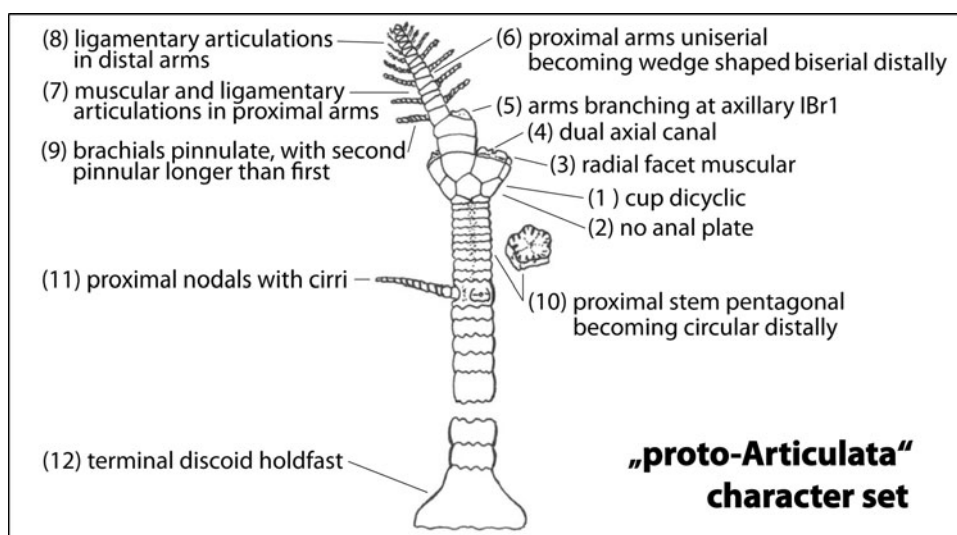
During the Triassic, most of these characters underwent significant changes. Thereby, the morphospace expanded with the derived character sets being distinctive for the more advanced later clades. Ancestral features, however, may be preserved in juveniles. Examples are the uniserial arms in advanced encrinids or rudimentary cirri in some encrinids, or even discoid holdfasts in extant comatulids. The living *Proisocrinus* has retained a holdfast even in the adult stage and reduced the cirri to the proximal stem.

The rich fossil record of the Encrinida and the less continuously documented lineage leading from Holocrinida to Isocrinida provides a more detailed view of this change. As the morphological remodeling was connected with niche splitting, Mesozoic crinoid phylogeny opens a fascinating field of convergent morphological changes. This has been demonstrated by Seilacher and Hauff (2004) and Hagdorn et al. (2007) who compared the convergent adaptation of Pentacrinitidae and Traumatocrinidae to driftwood-dwelling.

Remodeling of the cup

The dicyclic cup with the infrabasals visible in side view is a constant character among all Anisian holocrinids (Fig. 7) and in an unidentified, generically uncertain, five-armed dadocrinid (see Appendix; Fig. 8a). In *Dadocrinus*, the dicyclic cup may be present in parts of a population

Fig. 2 Reconstruction of the hypothetical “proto-Articulata”



(*Dadocrinus grundeyi*; Fig. 4a) or not at all (*Dadocrinus gracilis*, *Dadocrinus kunischi*). Holocrinids have a barrel-shaped or cylindrical, dicyclic cup with extremely thick plates and a narrow lumen (Figs. 3, 5a). The zygosynostial basal-radial and interradial facets make the holocrinid cup inflexible. In dadocrinids, the basals and radials of the conical cup are synostosomal with deep ligament pits and are much thinner and thus enclose a wider lumen. In both groups, the radial facets are directed upwards (perpendicular to the long axis). However, the small holocrinid radial facets cause a constriction between cup and arms that must have been fragile and sensitive to the autotomy of complete arms. Accordingly, the holocrinid fossil record has yielded many specimens with regenerating arms, as well as crowns with all arms autotomized (Hagdorn and Baumiller 1998).

In the middle Anisian 20-armed dadocrinid *Carnallicrinus*, formerly attributed to the Encrinidae, the cup has become a low cone with the infrabasals concealed in the stem pit and with long basals still visible in side view (cryptodicyclic cup; Fig. 4b). The radials are much wider than in other dadocrinids and their facets are directed obliquely outward. Thus, there is more space for the proximal arm fan, which has become much wider at the level of the second branching (secundibrachial 2).

The same trend can be observed in the family Encrinidae. The earliest known encrinids already have a cryptodicyclic, low bowl-shaped cup with the basals visible in side view (*Encrinus brahli*, *E. robustus*) and the radial facets are directed obliquely outwards. In *E. liliiformis* (Fig. 4c) as well as in the 20-armed *Chelocrinus schlotheimi* and *Ch. cassianus*, the basals are largely within the stem pit and only

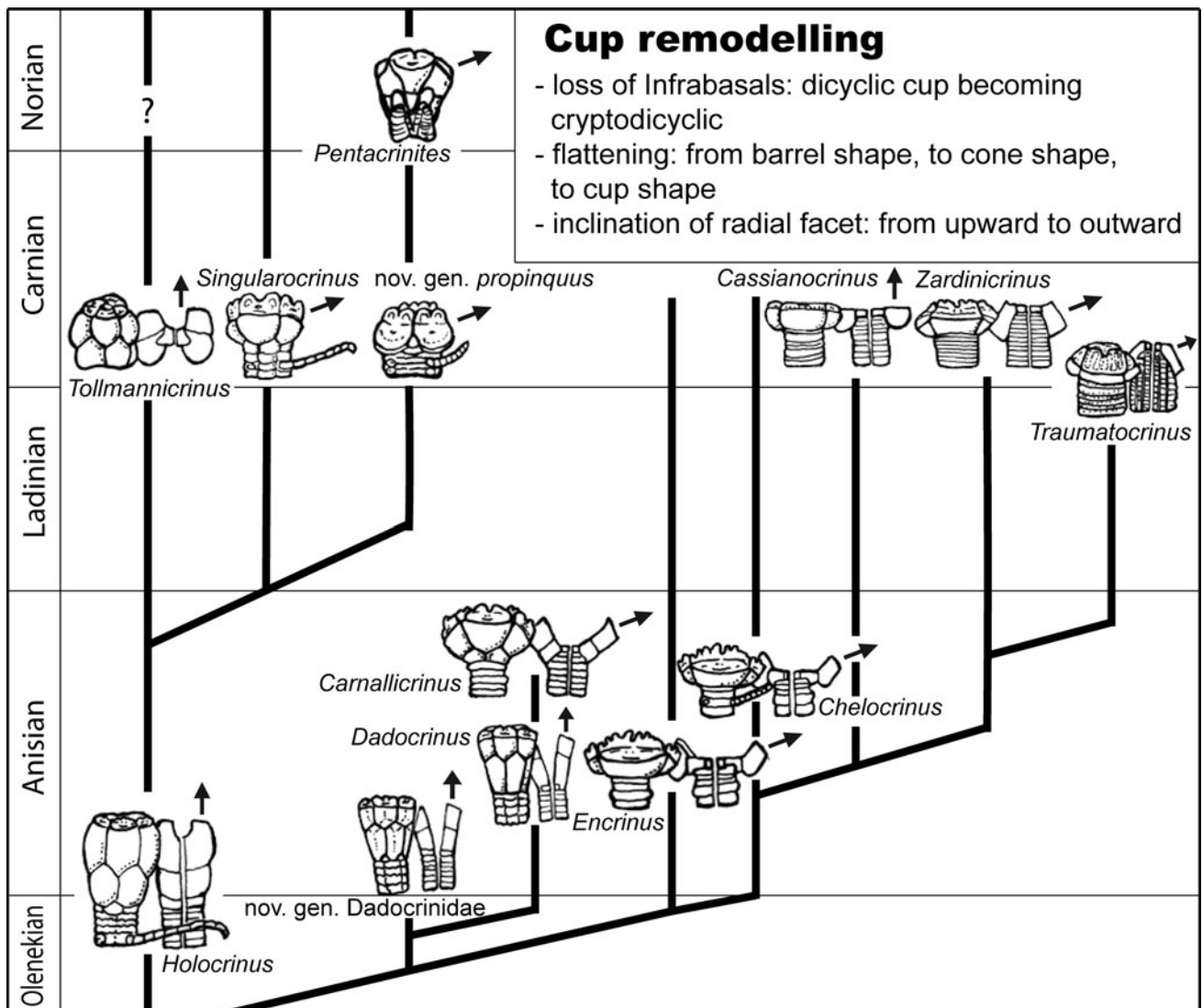


Fig. 3 Cup remodeling in Holocrinida/Isocrinida and Encrinida. Arrows indicate the orientation of the radial facets

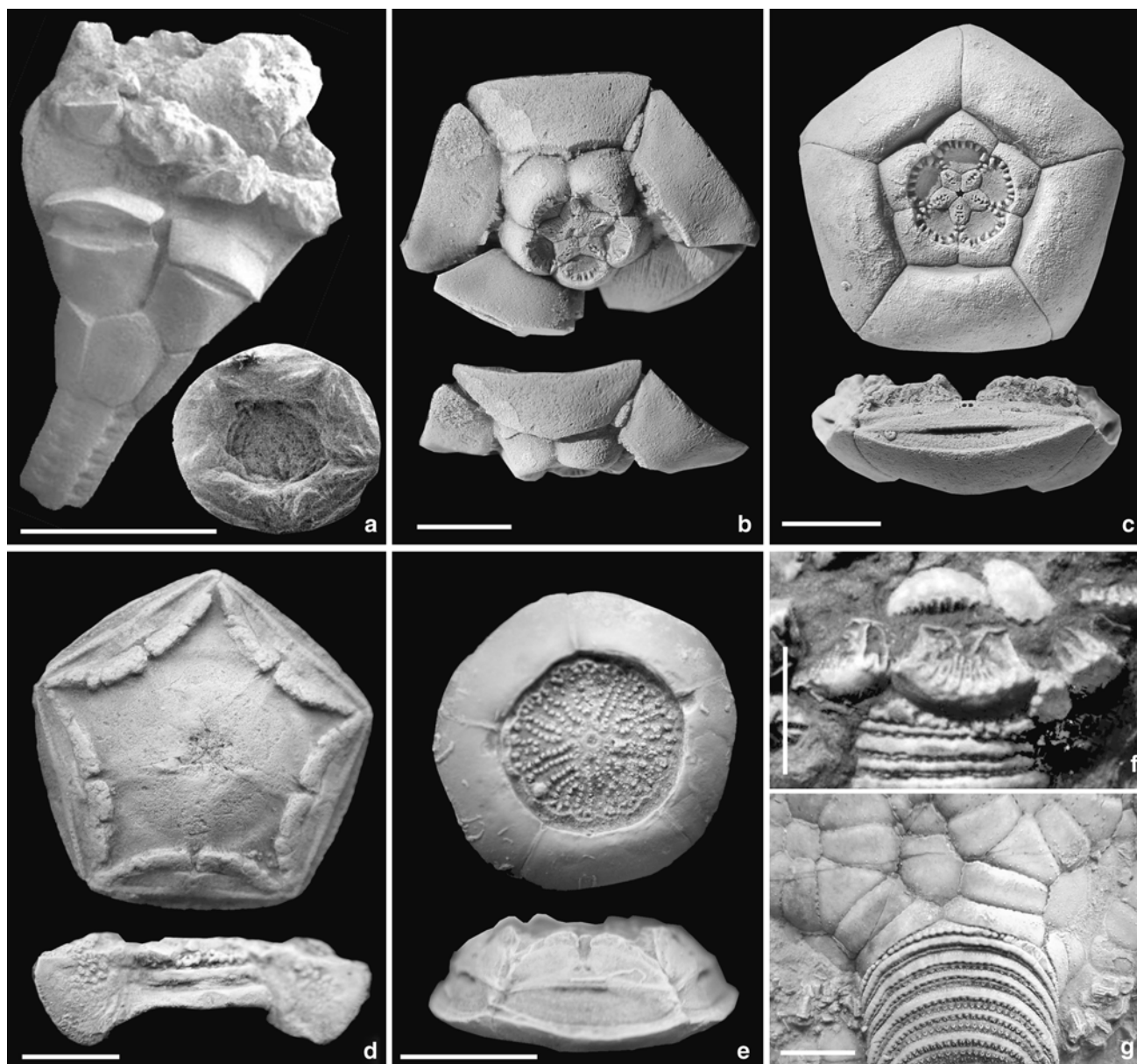


Fig. 4 Encrinida cups. **a** *Dadocrinus gracilis*, lateral view, Lower Gogolin Formation, Gogolin (Poland), MHI 1284/2; ventral view, Formazione à *gracilis*, Recoaro (Italy), MHI 1283/29. **b** *Carnallicrinus carnalli*, Lower Muschelkalk, Freyburg/Unstrut (Germany), MHI 1602. **c** *Encrinus liliiformis*, Upper Muschelkalk, Mistlau/Jagst (Germany), MHI 1214/1 (H. Hess ded.; same specimen as in Fig. 8c). **d** *Cassianocrinus varians*, ventral side with radial facets, Cassian Formation, St. Kassian, NHMW2006 z 0261/0001; synostosomal

interradial facets, basals, with two columnals in stem pit, NHMW 2006 z 0261/0004. **e** *Zardiniocrinus granulosis*, dorsal side with large columnal, lateral side with radial facets, Cassian Formation, St. Kassian, NHMW 2006 z 0265/0005. **f** *Traumatocrinus hsui*, radials with facets exposed, Xiaowa Formation, Guanling (China), MHI 1850. **g** *Traumatocrinus hsui*, dorsal side of radials, primibrachials, interbrachials, note fossulae openings along interbrachial sutures, Xiaowa Formation, Guanling (China), MHI 1882/5. Scales 5 mm

their distal parts remain visible in dorsal view. The latest encrinids, *Cassianocrinus* and *Zardiniocrinus*, have even smaller basals that remain almost completely or completely concealed by the first columnal, while the high and wide radial facets are directed outwards providing space for an immediately widening arm fan (Fig. 4d, e). By a trend towards of zygosynostosomal basal-radial and interradial

facets the cup became more solid by extremely short ligament fibers. In *Traumatocrinus*, the basals are even more strongly reduced and the cup is extremely small compared to the arms. Nevertheless, their radial facets are directed outward (Fig. 4f, g). All interplate facets of *Traumatocrinus* are ligamentary with a system of dorsally open grooves similar to the intercolumnar fossulae (Fig. 4f, g).

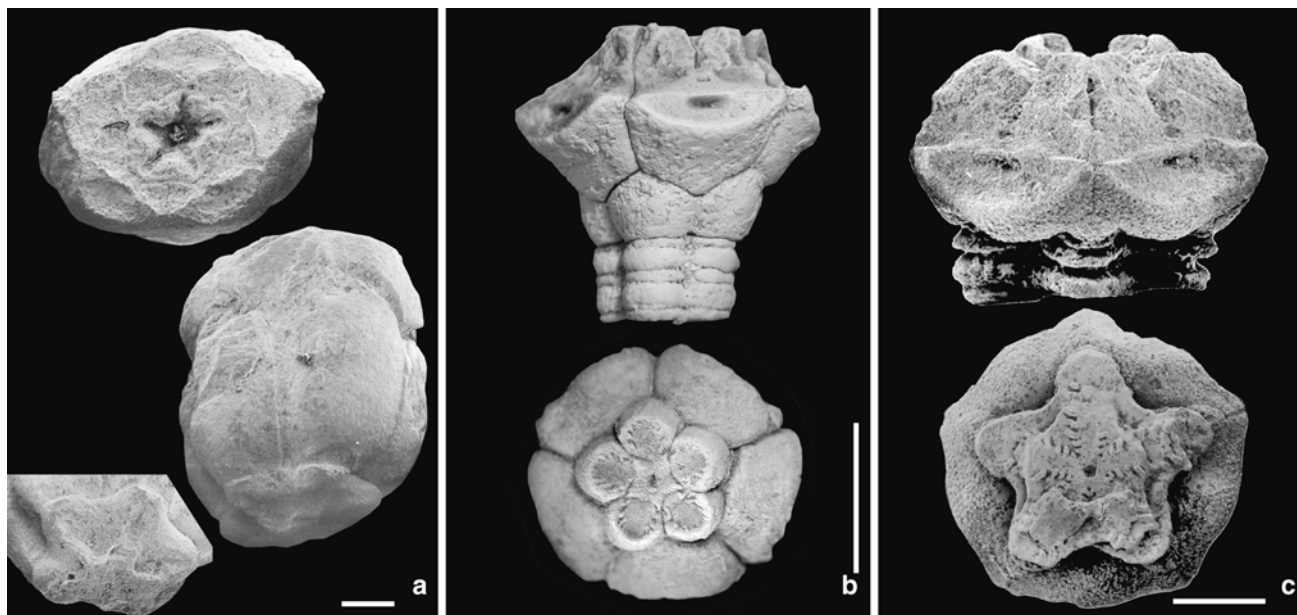


Fig. 5 Holocrinida and Isocrinida cups. **a** *Holocrinus dubius*, infra-basal circle, from lateral, radial circle with facets directed upward, Lower Muschelkalk, Jena Formation, Rittersdorf (Thuringia, Germany), scale 1 mm, MHI 1175/1. **b** *Singularocrinus* sp., large basals in lateral contact, radial facets directed outward, Hanwang Formation,

Hanwang (China), scale 5 mm, MHI 1603/1/1, 1603/1/7. **c** “*Isocrinus*” *propinquus*, small basals not in lateral contact, large radial facets directed outward, Cassian Formation, Forcella di Giau (Dolomites, Italy), scale 1 mm, MHI 2050/1

The same trend from a dicyclic to a cryptodicyclic cup by shortening of the basals and widening of the radials and turning their facets outwards has convergently taken place in the lineage from Holocrinida to Isocrinida. However, the isocrinids never attained the extreme degree of cup reduction seen in the *Zardincrinus*–*Traumatocrinus* clade.

Among the poorly documented cups of Triassic isocrinids (unpublished material MHI), two morphologies can be observed, (1) relatively large basals that form a continuous circle (Fig. 5b), and (2) very small basals that are not in contact on the dorsal side of the cup (Fig. 5c). The latter group might be regarded as ancestral to the family Pentacrinitidae.

Ontogenetic sequences of Encrinidae (Hagdorn and Schulz 1996) and of Traumatocrinidae (unpublished material MHI) clearly mirror this general phylogenetic trend. The relatively large cone-shaped cup of juveniles with large and laterally visible basals becomes progressively lower and wider during ontogeny and eventually is much smaller relative to the size of the arms (negative allometry).

The highly specialized *Ainigmocrinus* from the early Carnian has a cup, the dorsal side of which is hidden by an extremely enlarged last nodal, the calycinodal (Hagdorn 1988). It must have been modified for a protective function at a certain time in ontogeny. At the same time the formation of new nodals must have stopped; otherwise, the

calycinodal would later on have shifted away from the cup (developmental count down).

Larger and more outwardly directed radial facets presumably strengthened the muscular attachments, enlarged the tilting angle, and allowed the introduction of additional arm rays. Thus, this trend indirectly improved the filtration capacity (Fig. 3).

Increasing arm number

As a second convergent phylogenetic trend, arm numbers and arm lengths increased among Encrinida (Fig. 6) as well as Holocrinida/Isocrinida (Fig. 7). The most primitive state is represented by the small 5-armed dadocrinid genus. However, this character could also be interpreted as a secondary reduction from the primitive ten-armed state, probably arising through paedomorphosis (M. Simms, pers. comm.). Instead of being axillary, their primibrachial 2 has a muscular facet for a non-axillary third primibrachial on the outer side of the ray and a pinnular socket (with a pinnule attached) on the inner side (Fig. 8a). This character is regularly found in juveniles and adults of this dadocrinid from the early Anisian Muschelkalk (Lower Gogolin Formation). In the 10-armed genus *Dadocrinus*, regular arm branching occurs at the axillary primibrachial 2 (Fig. 8b). In *Carnallicrinus*, which here is included in the Dadocrinidae, this branching

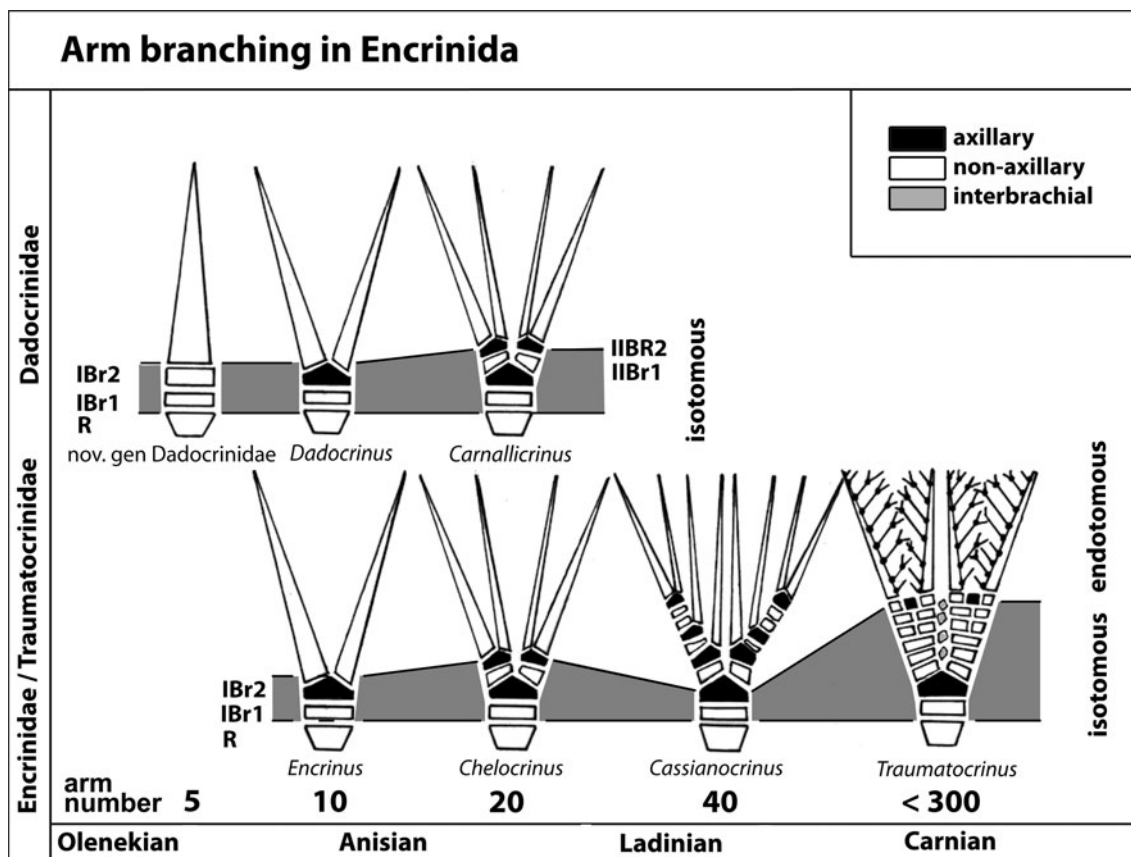


Fig. 6 Isotomous to endotomous arm branching in Encrinida

pattern is repeated once more, at axillary secundibrachials 2. As a rule, *Carnallicrinus* has 20 arms branching isotomously (Fig. 8c). The distal axillary facets are muscular, the proximal facets are ligamentary.

Encrinidae have 10 (*Encrinus*, Fig. 8d) or 20 arms (*Chelocrinus*, Fig. 8e) that branch isotomously, paralleling the situation found in *Dadocrinus* and *Carnallicrinus*. In *Chelocrinus*, an occasional third division of the arms may occur in arms regenerated after traumatic events. This was the case in the type specimen of *Ch. schlotheimi* (Hagdorn 1982). However, such additional branchings are only found in outer arm branches. In the early Carnian *Cassianocrinus* (Fig. 8f, g) and *Zardinicrinus*, the latest known encrinids, this branching pattern is found regularly; it was obviously genetically fixed. In other words, their arms are isotomous up to the second branching and then become endotomous (Hagdorn 2004).

The Traumatocrinidae carry this trend still further. They still have four major arm branches in each ray, but total arm number is greatly enlarged by successive endotomous armllets with each arising from the inner sides of arm pairs resulting from the last isotomous branching (Fig. 8i). Moreover, in the distal arms of adult *Traumatocrinus* an

additional isotomous branching of each armllet occurs at an axillary that bears a long dorsal spine (Fig. 9f). Before being compactionally flattened, the *Traumatocrinus* crown resembled a plicated coffee filter with the 20 major arms forming the exterior “ribs”. It was held together by a mechanism that Seilacher and Hauff (2004) compared to a velcro-like adhesion between neighboring major arms. Sharing the pore systems (tubuli) in the stem, *Traumatocrinus* and *Zardinicrinus*, respectively represent a pseudo-planktonic and a still benthic offshoot of a common Ladinian ancestor. The boreal *Vostocovacrinus* has the same endotomous branching pattern as *Traumatocrinus*, but its arms are uniserial and the brachials are low (Yel'tysheva and Polayrnaya 1986).

Among the Holocrinida, the transition from 10-armed isotomous branching to an initial endotomous pattern is already to be observed in the 15-armed *Moencrinus*, whose arms branch a second time, but only in the left arm of each ray. While their benthic descendants, the Isocrinidae, retained the isotomous pattern, the pseudoplanktonic Pentacrinitidae (*Pentacrinites* and *Seirocrinus*) switched to a highly advanced endotomous branching pattern before the end of Triassic times (Simms 1990a).

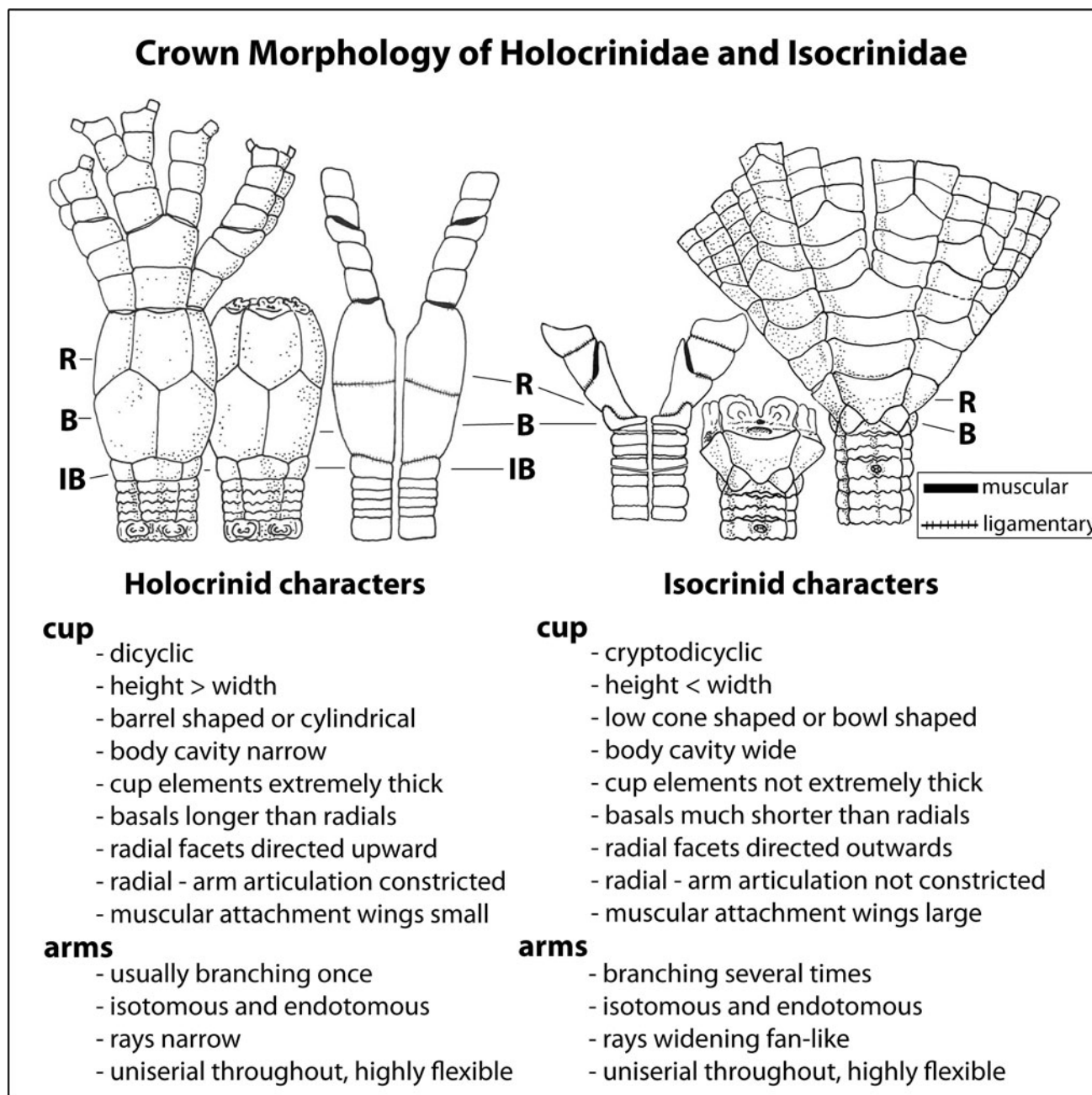


Fig. 7 Crown morphology of Holocrinidae and Isocrinidae

This morphological change to endotomous branching, seen in both the Pentacrinitidae and Traumatocrinidae, is interpreted as a convergent attempt to improve nutrition by enlarging the filter fan and the food gathering system. Compared to crinoids that are anchored on the sea bottom and are constantly provided with plankton and organic detritus by currents, pseudoplanktonic crinoids required more effective filters because their substrate drifted with the current (Seilacher and Hauff 2004; Seilacher, this

volume) and because there was a requirement for rapid growth (Simms 1986).

Associated with the overall size increase of the crown and the widely splaying arm rays, the areas between the primibrachials were closed by polygonal interbrachial plates, probably of tegminal origin (Figs. 4g, 8i). Thus, the functional calyx was enlarged by integration of the proximal arms, whereas the original cup was reduced to a minor, dorsal part of the calyx. This remodeling of the calyx

happened convergently in both the Encrinidae to Traumatocrinidae and the Holocrinidae to Pentacrinitidae transitions, and again in an analogous way, although without the development of endotomous branching, in the Cretaceous *Uintacrinus*.

Development of biserial arms

A second evolutionary strategy to improve the filtration can be observed in Dadocrinidae and Encrinidae. The early Anisian dadocrinids still have uniserial arms with relatively long brachials (Figs. 8a, b, 9a). In *Carnallicrinus*, the arms have low, wedge-shaped brachials with oblique articulation facets, representing lowly developed biseriality (Fig. 9c). The same is true in earlier (Pelsonian, early Illyrian) encrinids, whereas the late Illyrian *Encrinus liliiformis* and *Chelocrinus schlotheimi* have advanced biserial arms with a narrow zigzag-suture and wide horizontal articulations between brachials in one row (Figs. 8d, e, 9d). This advanced biseriality was maintained in Carnian encrinids and *Traumatocrinus* (Fig. 9e, f).

In the 1978 Treatise the Encrinidae were assigned to the subclass Inadunata because of their biserial arms, while the otherwise very similar Dadocrinidae with uniserial arms were included in the millericrinid Articulata. However, juvenile encrinids have uniserial arms with long brachials that become gradually lower and biserial during ontogeny (Hagdorn and Schulz 1996; Fig. 9b). As biseriality allows a greater number of pinnules than a uniserial arm (Simms 1990a) it should be considered as an advanced character and as an adaptation to improve the effectivity of the filtration fan.

However, biserially arranged brachials require ligamentary articulations that make the arms inflexible. Only in the proximal, uniserial arms of encrinids did the brachials have muscular articulations that allowed outward tilting to a certain degree. Therefore, the encrinid crown was relatively immobile (Jefferies 1989).

The Holocrinida/Isocrinida lineage maintained long and slender uniserial arms and increased the number of muscular articulations. This imparted a much greater degree of arm flexibility and even the ability to crawl away for defense against cidaroid predators (Baumiller and Messing 2007; Baumiller et al. 2009). This adaptation, however, required a non-permanent attachment, as provided by cirri. In contrast, all Encrinida were permanently fixed to their substrate by holdfasts or similar structures and were unable to re-fix themselves or to regain an upright feeding position after detachment. However, Linck (1965) demonstrated that such individuals of *Encrinus liliiformis* remained alive sufficiently long to close their open central canals by callus and to regenerate bulbous terminal columnals (Fig. 10b–d).

However, their inflexible arms did not allow the animal to re-assume a feeding position (Baumiller et al. 2008).

Remodeling of the stem and of attachment structures

Like the crown of the Triassic crinoids, their stem and its attachment to the substrate underwent substantial modification. The hypothetical “proto-Articulata” ancestor of the Triassic crinoids is inferred to have attached to hard substrates by a terminal discoid holdfast (Fig. 2). However, it must also have had cirriferous nodals as a plesiomorphic feature. These structures were prerequisite for the two Middle Triassic strategies of substrate attachment: (1) maintaining the holdfast for permanent attachment to hard substrates, (2) restructuring and strengthening the cirri as a flexible attachment tool that allowed re-attachment after stem rupture and even some degree of motility. During this transformation, the cirral articulation was modified from multiradiate to synarthrial with a strong transverse ridge. The Encrinida—and the less well known early Millericrinida—persisted with the first strategy, whereas the Holocrinida and their descendants developed the second.

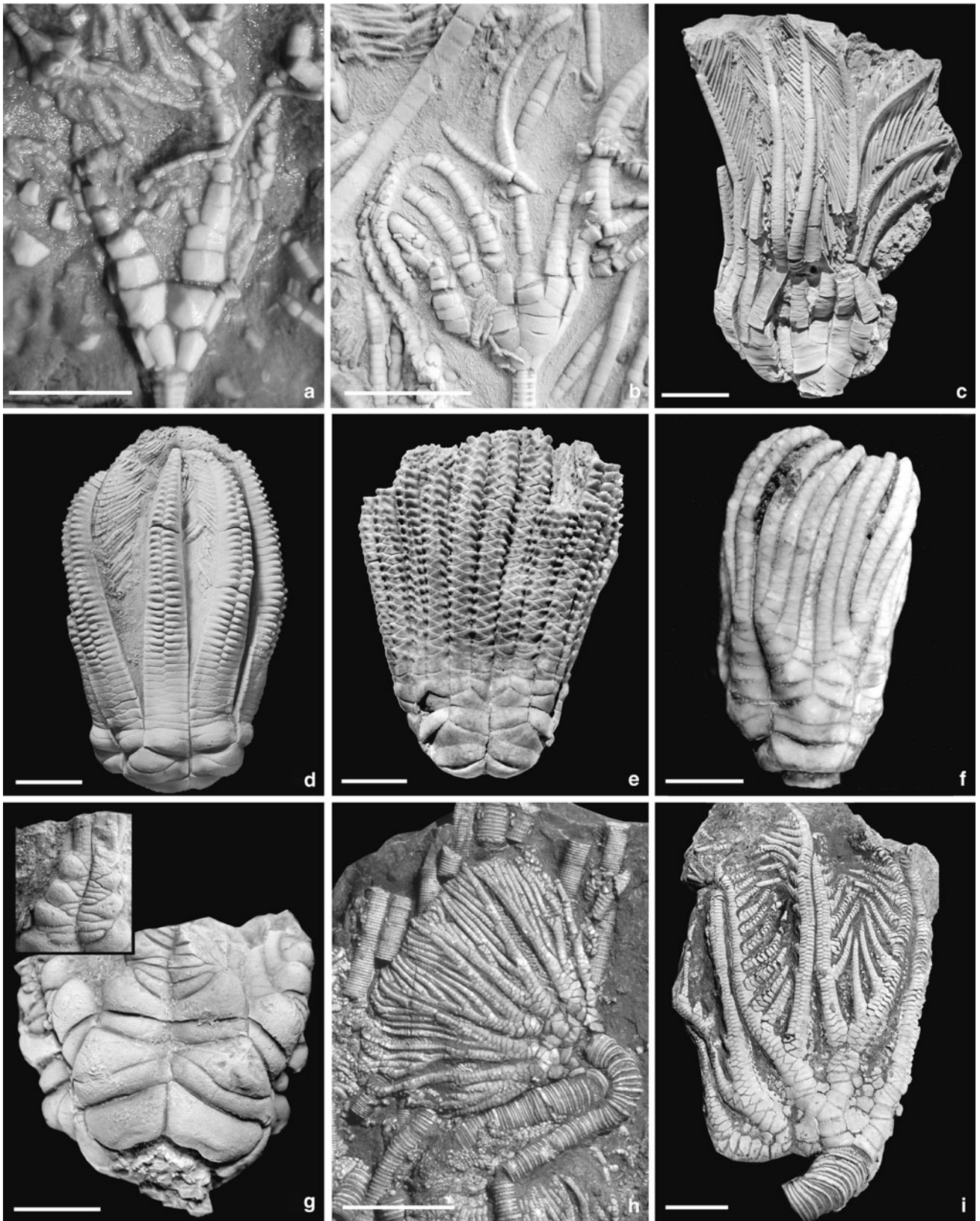
Permanent fixation by holdfast

Cirri at the proximal nodals were unnecessary in a long, upright stem attached by a holdfast. Therefore, the short encrinid cirri consisting of small barrel-shaped cirrals with multiradiate articulations lost any function and occur only as rudiments in some species, e.g. in *Encrinus* cf. *E. brahli* (Hagdorn and Schulz 1996), or in some populations of *Ch. schlotheimi* (Hagdorn 1982). However, multiradiate cirrus scars can still be observed in some nodals of the Carnian *Cassianocrinus varians*. Dadocrinids have no cirri at all; neither do Millericrinidae. The cirri at the nodals of juvenile encrinids must have been shed while these nodals moved distally through ontogeny.

Cylindrical cirri with multiradiate facets also occur in *Eckicrinus*, a poorly known Pelsonian/Illyrian crinoid with characters that are otherwise holocrinid in nature. Its irregularly arranged cirri may become extremely thick and directed towards one side. Such cirri probably acted as props for the stem as it lay horizontally on the sea floor (Hagdorn et al. 1996, Fig. 6; Seilacher and MacClintock 2005).

The stem of the reef-dwelling *Ainigmocrinus* remained probably rather short, because after the designation of a cirrinodal as a calycinodal, no additional nodals could be formed. Its laterally enlarged cirrals may have protected the arms (Hagdorn 1988).

In contrast, the Traumatocrinidae modified the encrinid stem by extreme columnal production to attain lengths of more than 10 m (Hagdorn et al. 2007). Systems of longi-



◀ **Fig. 8** Increase of arm number in Encrinida. **a** Dadocrinidae gen. nov., the IBr2 is not axillary, but has the first pinnule attached, Lower Muschelkalk, Lower Gogolin Formation, Wojkowice (Poland), scale 5 mm, MHI 1285/1. **b** *Dadocrinus kunischi*, branching at axillary IBr2, Lower Gogolin Formation, Gogolin (Poland), scale 1 cm, MHI 1284/1. **c** *Carnallicrinus carnalli*, Lower Muschelkalk, Jena Formation, Freyburg/Unstrut (Germany), scale 1 cm, MHI 1602 (H. Hess ded.; same specimen as in Fig. 4b). **d** *Encrinus liliiformis*, Upper Muschelkalk, Trochitenkalk Formation, Schwäbisch Hall (Germany), scale 1 cm, MHI 1043/1. **e** *Chelocrinus schlotheimi*, regular second branching at axillary IIBr2, Upper Muschelkalk, Trochitenkalk Formation, Örlinghausen (Germany), scale 1 cm, MHI 1093/14. **f** *Cassianocrinus varians*, juvenile individual with endotomous branching starting at axillary IIBr2, Cassian Formation, St. Kassian (Italy), scale 1 cm, NHMW 1865/IX/130. **g** *Cassianocrinus varians*, adult individual with endotomous branching starting at axillary IIBr2, axillaries dorsally inflated, Cassian Formation, St. Kassian (Italy), scale 1 cm, NHMW 20006 z 0262/0001. **h** *Traumatocrinus hsui*, juvenile individual with armllets slightly smaller than major arms, Xiaowa Formation, Guanling (China), scale 1 cm, MHI 2051. **i** *Traumatocrinus hsui*, semiadult individual with armllets smaller than major arms, distal armllets isotomously branching at axillaries with dorsal spines (better seen in Fig. 9f), Xiaowa Formation, Guanling (China), scale 1 cm, MHI 1882/4

tudinal canals (tubuli) run through the entire stem and horizontal intercolumnar fossulae connect with the tubuli, reducing the weight of these pseudoplanktonic crinoids and thereby prolonging the floating time of the driftwood. Bunches of tubuli filled with mutable collagen fibers may have prevented torsion and breaking of the long stems and made them flexible or even motile. The Pentacrinitid *Seirocrinus* whose stem was even longer (Haude 1981; Seilacher et al. 1968; Seilacher and Hauff 2004; Seilacher, this volume) achieved flexibility and lightweight construction by lensoid intercolumnar spaces and long intercolumnar collagen fibers. Both characters are alternative adaptations to a pseudoplanktonic life style.

Intermittent fixation by cirri and motility

A major feature of Holocrinidae and Isocrinidae was their ability to shed distal stem parts at a preformed rupture point on the distal side of the nodals. This innovation originated during Anisian times. In holocrinids, this facet remains an unmodified symplectical articulation (Hagdorn 1983; Fig. 10k, l). Nevertheless, the fossil record indicates the presence of this autotomy site also among holocrinids (Baumiller and Hagdorn 1995; Fig. 10j). In isocrinids, the distal nodal facets are modified as cryptosymplexes (Fig. 10o, p) or as smooth synostoses (Fig. 10m, n). After distal parts of the stem are shed, the remaining part was automatically equipped with a cirriferous nodal that could take over the attachment function. This innovation originated during the Anisian times. The pseudoplanktonic pentacrinitids, however, required lifelong solid attachment

structures and solid, flexible stems devoid of rupture points; otherwise, they would have sunk to the seafloor.

Eleutherozoic lifestyle by stem reduction

In contrast to the extremely elongated stems of pseudo-planktonic crinoids, extreme shortening of the stem led to an eleutherozoic lifestyle. Stem reduction took place twice and independently during Triassic times: (1) before the Rhaetian within the lineage Holocrinida–Isocrinida in *Eocomatula* and *Paracomatula*, i.e. in short-stemmed offshoots of the Pentacrinitidae (Hagdorn and Campbell 1993; Hess 1950; Simms 1994). Their stems are reduced to a few cirriferous nodals plus internodals devoid of cirri. Fusion into a true centrodorsal did not appear before Early Jurassic times (Kristan-Tollmann 1988); (2) before the late Ladinian within a lineage that led to the planktonic somphocrinids. So far, there is no evidence when these highly specialized “Schwebcrinoiden” (German for planktonic crinoids) originated, or from which group. The miniaturization and lightweight construction that eventually enabled them to be dispersed by currents over the entire Tethys must have fundamentally changed their morphology. This may be the reason why it is so difficult to find the ancestors. In contrast, eocomatulids and paracomatulids retained their ability to attach and detach at will by means of their cirri and could change locations by either crawling or active swimming.

Habitat occupation

The dynamic changes in stem morphology and attachment structures happened in connection with active or passive habitat changes. During the Palaeozoic, crinoids occupied a broad range of ecological niches, to which they adapted in size and morphology. Following the Permian/Triassic crisis, crinoid diversity was reduced to small unspecialized benthic animals attached by holdfasts or cirri to solid substrates. However, during the ensuing 50 million years of Triassic times, many of these niches were re-colonized by descendants of the only surviving clade. In this ecological radiation crinoids diversified again by modifying and expanding the inherited morphospace in two realms, the seafloor and the open ocean (Fig. 11).

Benthic strategies

Most crinoids are sessile. A stalk elevates them above the seafloor into a zone of stronger currents and above other competing benthic filter feeders. In Palaeozoic crinoid communities different species occupied different tiers above the seafloor (Ausich and Bottjer 1985). Among the

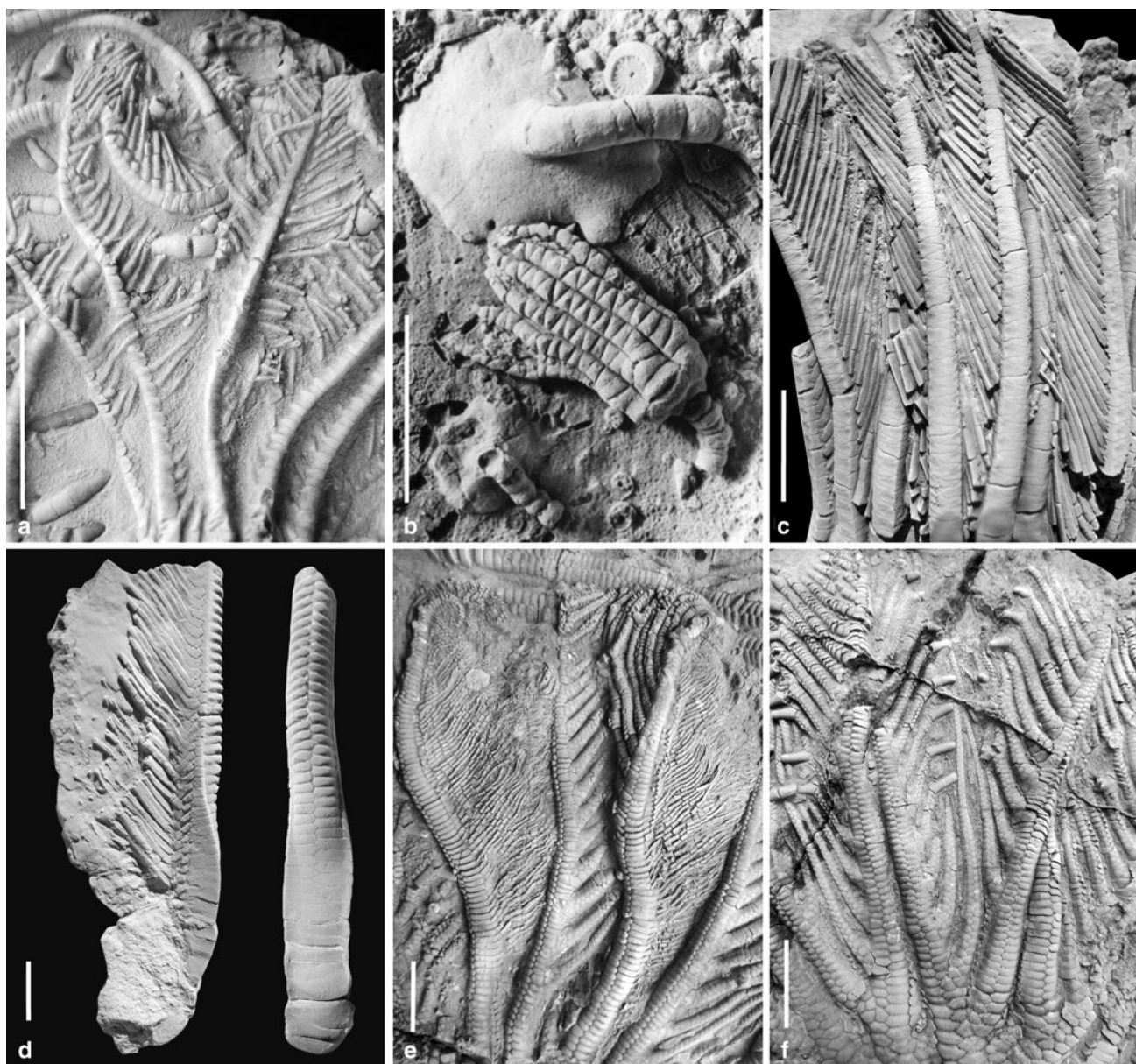


Fig. 9 Brachial arrangement and pinnulation in Encrinida: a trend from uniserial to biserial arms. **a** *Dadocrinus kunischi*, uniserial brachia, widely spaced pinnules, Lower Gogolin Formation, Gogolin (Poland), MHI 1284/1. **b** *Encrinus liliiformis*, juvenile individual with wedge-shaped uniserial brachials, Upper Muschelkalk, Trochitenkalk Formation, Mistlau/Jagst (Germany), IGPT 1525/6. **c** *Carnallicrinus carnalli*, immature biseriality of low wedge-shaped brachials, wide zigzag-suture, medium spaced pinnules, Lower Muschelkalk, Jena Formation, Freyburg/Unstrut (Germany), MHI 1602 (same specimen

as in Fig. 8c). **d** *Encrinus liliiformis*, mature biseriality, narrow zigzag-suture, densely spaced pinnules, Upper Muschelkalk, Trochitenkalk Formation, Neckarwestheim (Germany), MHI 1116/5. **e** *Traumatocrinus hsui*, adult individual, 4 mature biserial major arms and densely spaced pinnules (pinnules on armlets not to be seen), Xiaowa Formation, Guanling (China), MHI 1882/5. **f** *Traumatocrinus hsui*, same individual, major arms and biserial armlets branching distally at axillaries with dorsal spines, Xiaowa Formation, Guanling (China), MHI 1882/5. Scales 10 mm

Triassic crinoids, the following benthic strategies can be observed.

Settling on hardgrounds and in bioherms

Attachment by a discoid holdfast that was inherited from Palaeozoic ancestors and consists of a specialized terminal

columnal is the most common strategy (Fig. 10f). During the Triassic dadocrinids and encrinids, as well as the poorly known early Millericrinida, were attached by a holdfast (Fig. 10g–i; for *Silesiacrinus*, cf. Hagdorn et al. 1996, Pl. 6, Fig.t). In the late Anisian Upper Muschelkalk (Trochitenkalk Formation), encrinids encrusted patches of terquemiid “oysters” that were slightly elevated above the seafloor

and were thus less likely to be smothered by mud. In these biohermal bodies, which reached 2–3 m in diameter and 1.5 m thickness, the encrinids acted as frame builders, because their holdfasts formed irregular, solid crusts (Hagdorn 1978, Hagdorn and Ockert 1993; Fig. 10e). Within the bioherms, the stems of adult crinoids also provided solid anchoring grounds for subsequent generations. It has to be stressed that after the post-Palaeozoic reef crisis, crinoids were—together with bivalves—among the first animals to contribute to reef formation. In the slightly older bioherms in the Upper Silesian Muschelkalk (early Illyrian Karchowice Formation), the reef building role of crinoids is secondary only to hexactinellid sponges and the earliest post-Palaeozoic hermatypic corals (Fig. 12).

Secondary soft-bottom dwelling

Holdfast fixation always requires a solid substrate for anchorage. This prevents the larvae of holdfast-crinoids from settling on muddy seafloors unless they find cephalopod shells or other suitable starter substrates. The early Anisian *Dadocrinus* used mudsticking endobyssate bivalves, such as bakevelliids, for initial fixation. However, in turbulent water the bivalve byssus was insufficient to fix larger dadocrinid groups. The small size of *Dadocrinus* may be a major reason for its ecological success in the soft ground palaeocommunities of the early Anisian Lower Gogolin Formation of Poland and the contemporaneous *Formazione à gracilis* of the Vicentinian Alps in Italy (Hagdorn 1996).

Large holdfasts from the Norian and Rhaetian Hallstatt Limestones of the Austrian Alps and from Timor (Fig. 10g–i) showing millericrinid characters already resemble the large and heavy multilayered Jurassic millericrinid roots that anchored these crinoids on soft seafloors (Kleinert 1969; Seilacher and MacClintock 2005).

Pseudoplanktonic strategies

As has been demonstrated by Seilacher et al. (1968), Simms (1986), Wignall and Simms (1990) and Seilacher and Hauff (2004) in Liassic examples and by Hess (2010b) generally for any pseudoplanktonic crinoids, the adaptation to a pseudoplanktonic lifestyle on driftwood required fundamental morphological remodeling. Recent studies of complete *Traumatocrinus* driftwood-“colonies” from early Carnian black shales of South China have led to a better understanding of the same lifestyle and corresponding morphologies (Hagdorn et al. 2004, 2007). Among these are extremely enlarged, flexible stems and multiply branching endotomous arms that provide dense pinnulation and extremely long food groove systems arranged like the

roads in a banana plantation (Cowen 1981). With diameters reaching more than 40 cm, *Seirocrinus* and *Traumatocrinus* crowns by far exceed those of any known benthic crinoids.

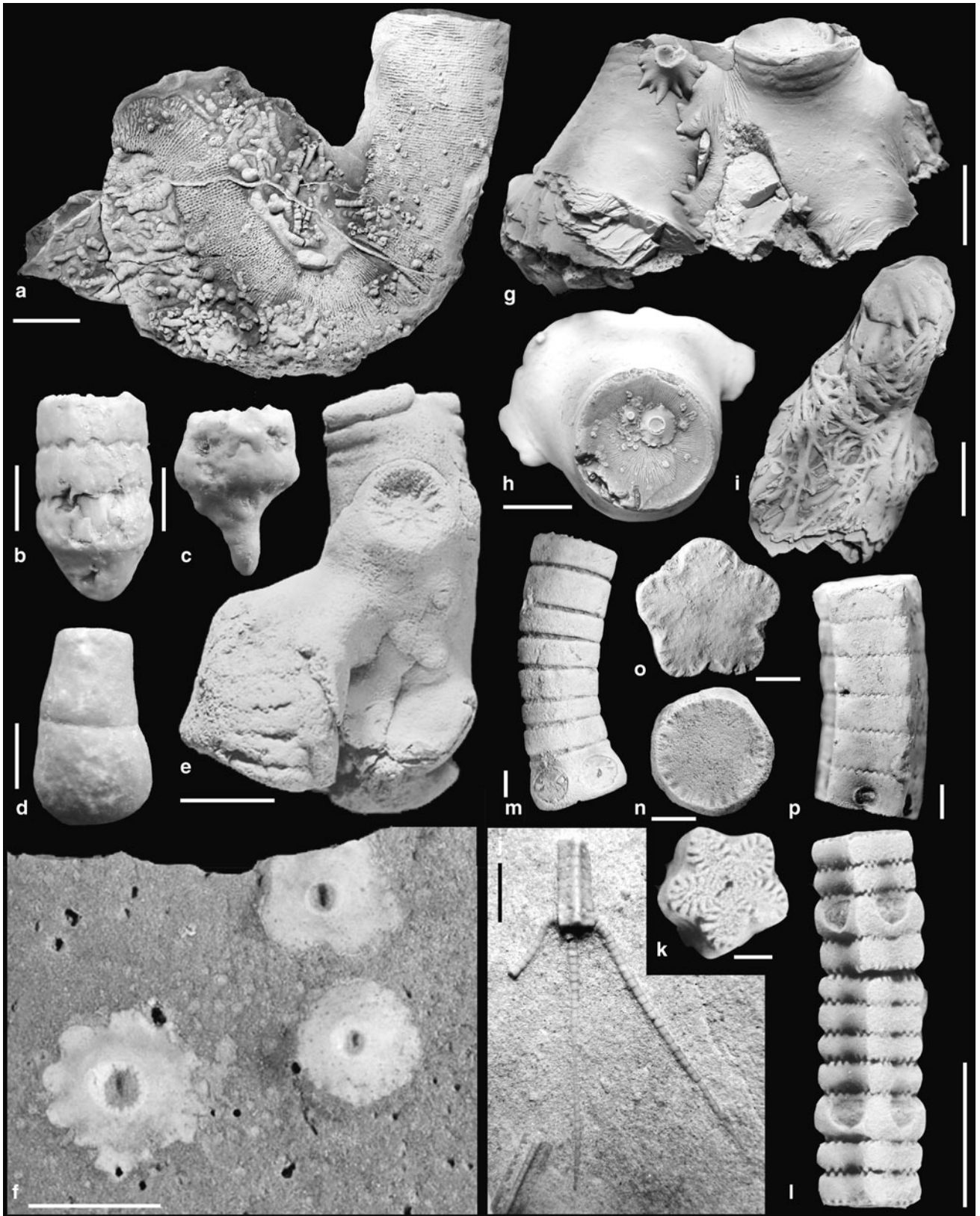
Another requirement is a solid and flexible attachment to the driftwood. The traumatocrinids transformed the terminal holdfast of their encrinid ancestors, which consisted of a single sclerite, into a complex multielement attachment structure comprising many columnals and assisted by rootlike, irregularly branching cirri with multiradiate articulations (Fig. 10a; Hagdorn et al. 2007, Fig. 6). Such an attachment structure could grow on with the animal by integrating more distal columnals and by covering the wooden substrate with thin sheets of callus. It also remained flexible enough to buffer current drag and wave action. In contrast to encrinid cirri in the proximal stem (see above), traumatocrinid cirri occur only in the most distal stem part and do not seem to be restricted to nodals. Therefore, it is an open question whether they are homologous with true cirri.

Adult pentacrinids were devoid of a holdfast and had to get attached by cirri. However, attachment structures of available specimens are difficult to study because they are hidden under bunches of cirrals and stem fragments. Presently, it is impossible to describe them in more detail. Seilacher (this volume) interprets the densely spaced long cirri with rhomboid cross sections of the Norian and Liassic *Pentacrinites* as motile enough to produce a filter current of their own. However, as no other attachment structure has been observed in this short-stemmed pentacrinid, their primary function was probably for attachment (Simms 1986). If one considers the second function (self ventilation or filter current; Seilacher, this volume) it was primary in an ontogenetic sense.

Another peculiarity of pseudoplanktonic crinoids has to be explained. Among hundreds of *Traumatocrinus* and *Pentacrinites* crowns no regenerating arms have been observed. While benthic crinoids commonly autotomized their arms when exposed to sediment suspended by storms, or when attacked by predators, no such disturbance occurred in pseudoplanktonic filter feeders. This allowed them to keep their arms splayed continuously.

Eleutherozoic life styles

In the present oceans, the most diverse crinoid group is the order Comatulidina, members of which reduced their stems to a fused, cirriferous centrodorsal. Their long and slender arms with muscular articulations enable them to change their locations for feeding and to escape slow predators by active swimming or hiding. This eleutherozoic mode of life became the most successful adaptation of crinoids after the Mesozoic trophic revolution (Vermeij 1977). Today,



◀ **Fig. 10** Attachment structures. **a** *Traumatocrinus hsui*, terminal stem with root cirri welded to driftwood, Xiaowa Formation, Guanling (China), scale 10 mm, MHI 1882/1. **b–e** *Encrinus liliiformis*, Upper Muschelkalk, Trochitenkalk Formation. **b–d** terminal stems with regenerated columnals, Wollmershausen (Germany), scales 5 mm, MHI 2052/1–2052/3. **e** Cluster of encrusting holdfasts from a bioherm, Warburg (Germany), scale 10 mm, MHI 1255/1. **f** *Carnallicrinus carnalli*, discoid holdfasts attached to a bored hardground, Lower Muschelkalk, Jena Formation, Gutendorf (Germany), scale 10 mm, MHI 1555/1. **g–i** Millericrinida gen. nov., discoid holdfasts with irregular lateral callus growth, Hallstatt Limestone, Timor, scales 10 mm, IPB Bather 1a–1c. **j–l** *Holocrinus dubius*, preformed rupture point below nodals. **j** Noditaxis with terminal nodal and cirri attached indicating stem rupture, Lower Muschelkalk, Udelfangen Formation, Ralingen-Kersch (Germany), scale 5 mm, MHI 1276/6. **k–l** proximal pluricolumnal with crenulated lower nodal sutures, symplectial lower nodal facet, Lower Muschelkalk, Jena Formation, Dietershausen (Germany), scales 5 mm (**l**), 1 mm (**k**), MHI 1182/3/1, 1182/3/2. **m–n** *Singularocrinus* sp. synostosial lower nodal facet, Hanwang Formation, Hanwang (China), scale 1 mm, MHI 1603/1/2, 1603/1/4. **o–p** *Tyrolecrinus tyrolensis*, cryptosymplectial lower nodal facet, Cassian Formation, St. Kassian, scale 1 mm, **o** (syntype) GBA 1865/3/83 × 7, **p** (holotype) GBA 1865/3/83 × 6

comatulids inhabit reefs and variable seafloor types. The earliest approach to this adaptive peak is represented by the Late Triassic (Norian/Rhaetian) *Eocomatula* and *Paracomatula*, which are holocrinid offshoots, probably derived from the early pentacrinid lineage (Simms 1994; Hagdorn and Campbell 1993). Both genera are better known from Jurassic representatives. The first true comatulids with a fully fused centrodorsal occur in the Early Jurassic (Kristan-Tollmann 1988).

Another eleutherozoic life style, that of the planktonic microcrinoids, occurred much earlier. Their immediate worldwide mass appearance in late Ladinian sediments (Kristan-Tollmann 1977) is poorly understood because the fossil record has provided so far no plausible ancestors. In any case, their stem became reduced to a fused centrodorsal that bears a radial circle, but no cirri. Their long uniserial arms have extremely long brachials with thickened, bonelike articulating ends (Wang et al. 2008, Fig. 11). Centrodorsals and radials are composed of a coarse meshwork that indicates a lightweight stereome modification. The Late Jurassic *Saccocoma* may represent still another life style within this clade or may represent an entirely separate clade derived independently from an unknown benthic ancestor (Hess 2002).

Tiering

In Palaeozoic crinoid communities recorded from the Mississippian of North America individual species occupied different tiers above the bottom. In the Upper Muschelkalk of South Germany, *Encrinus liliiformis* was the only crinoid and, within its palaeocommunity, was the dominant macrofossil. The lowest tier was dominated by

articulate brachiopods, also monospecific, and by various bivalves. Higher tiers up to 1.5 m above the seafloor were occupied by growth stages of *Encrinus liliiformis*. Such an intraspecific tiering did not require competitive growth rates. It is also unlikely that *E. liliiformis* was specialized on nannoplankton as suggested by Jefferies (1989) because there were no other filter feeders in the higher tiers that could have competed for food.

Stem lengths show a similar intraspecific tiering on a large driftwood with many adult *Traumatocrinus* attached, even though, being suspended beneath the driftwood, the tiering is inverted (Hagdorn et al. 2004). The crowns of almost identical size were positioned at different depths between 1 and more than 9 m. How this intraspecific, inverse tiering was “organized” within the group is an open question. In any case, filtering at different levels reduced the competition for food.

Conclusions

After the end-Permian near-extinction of the Crinoidea, this echinoderm class recovered during the Triassic and adapted to most of the niches that had been occupied by crinoids during the Palaeozoic. However, the full diversity was not reached before the mid Anisian, followed by an even more distinct diversity peak in early Carnian times. After that, the “Mid Carnian Wet Intermezzo” (Simms and Ruffell 1990; Kozur and Bachmann 2010) caused a global decrease of marine faunas. Due to a rise of surface temperature to 30°C in the Palaeotethys (Hornung et al. 2007), the pseudoplanktonic traumatocrinids became extinct, together with the entire order Encrinida. The open driftwood niche was re-occupied in Norian times by the pentacrinids and finally disappeared in Mid Jurassic times, when shipworms started their destructive activity on wood in marine environments (Hagdorn et al. 2007). Hence, the late Carnian through Rhaetian crinoid faunas were dominated by Isocrinida, who persisted without fundamental changes beyond the Triassic/Jurassic boundary. The niche of the holdfast-attached benthic encrinids was re-occupied by early millericrinids. As all Triassic crinoids probably derived from an unknown advanced cladid that survived the end-Permian crisis, all extant crinoids are descendants of this “proto-Articulata”. However, phylogenetic analyses are hampered by the convergent morphological trends that different clades underwent during their adaptation to similar habitats.

Encrinids are the most typical Triassic crinoids. During late Anisian times, they flourished in the Western Peritethys realm and contributed by their attachment structures to the buildup of small bioherms. In regional palaeo-highs, immense amounts of encrinid biodetritus resulted in

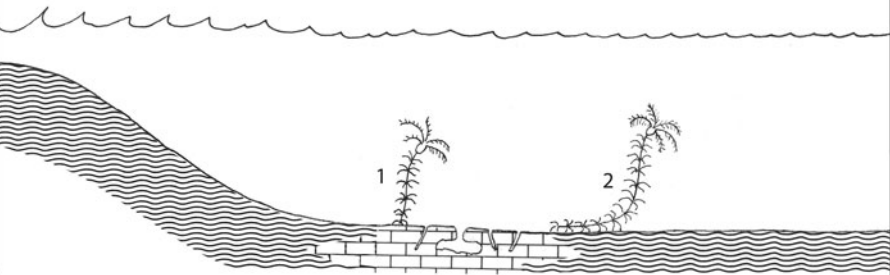
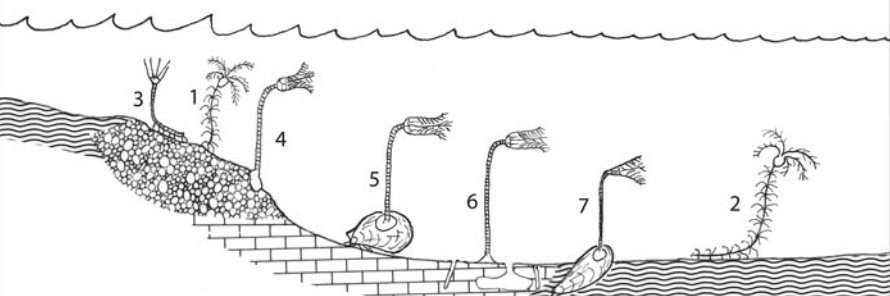
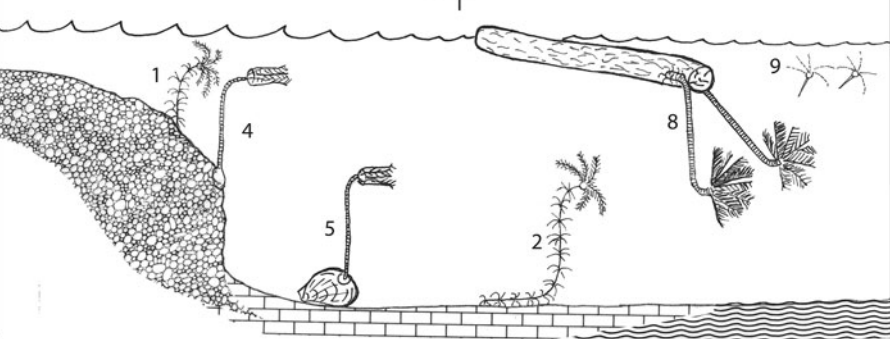
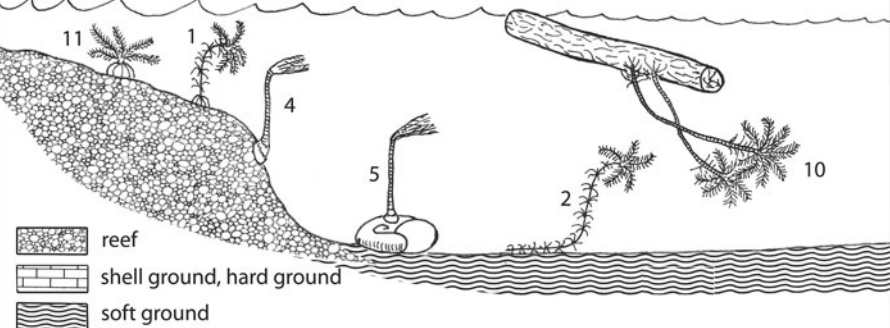
Age	dominance	Habitat adaptation of Triassic crinoids	mode of life
Olenekian/Indusian	1 holocrinid		benthic intermittently cirrus-attached
Anisian	2 holocrinid/encrinid		benthic intermittently cirrus-attached permanently holdfast-attached
late Ladinian/early Carnian	3 isocrinid/encrinid		benthic/pelagic intermittently cirrus-attached permanently holdfast-attached planktonic/pseudoplanktonic
Norian/Rhaetian	4 isocrinid/millericrinid		benthic/pelagic/eleutherozoic intermittently cirrus-attached permanently holdfast-attached pseudoplanktonic free swimming

Fig. 11 Habitat adaptation. From Early to Late Triassic times, four subsequent crinoid associations can be identified (see also Fig. 1), which are characterized by an increasing diversity of niches. Niche adaptation caused a strong morphological change of overall size, cup, filtration fan, stem, and attachment structures. Convergent development occurred among different clades depending on the niches. The basic type was the holocrinid attachment by cirri to either hard or soft bottoms; this type remained most successful among isocrinids until today (1, 2). Stems with stout prop-like cirri are to be found in the poorly known *Eckicrinus* (3). The holdfast-attached encrinids settled on shells (5), on hardgrounds (6) and acted as frame builders in small bioherms (4). Their small size

allowed *Dadocrinus* to incrust mudsticking bivalves and thus to settle on softgrounds (7). In late Ladinian/early Carnian times two lineages led to a pelagic life: the traumatocrinids by settling on driftwood (8), and the somphocrinids by planktonic drifting (9). Due to the “Mid Carnian Wet Intermezzo”, the entire order Encrinida became extinct, and their niches were re-occupied by millericrinids (4, 5) and by the pseudoplanktonic pentacrinitids (10), respectively. As a new niche, the eleutherozoic lifestyle of the actively swimming feather stars was added by the paracomatulids and the eocomatulids (11). The Norian/Rhaetian crinoid association (4) persisted until Middle Jurassic times, in its fundamental parts until today

Fig. 12 Reconstruction of a typical Anisian Encrinid/Holocrinid habitat in the late Anisian (early Illyrian) sponge-coral reefs of the Karchowice Formation (Lower Muschelkalk, Upper Silesia, Poland).

Encrinus aculeatus was permanently attached by a holdfast, e.g. to hexactinellid sponges. The cirrus-attached *Holocrinus meyeri* was able to change its location



crinoidal limestones that reached up to 16 m thickness in the German Upper Muschelkalk (Hagdorn and Ockert 1993), comparable to the Mississippian Burlington Limestone (Ausich 1999) of Missouri and Illinois. With the mid Carnian decline of the encrinids, this Palaeozoic sediment type disappeared forever. The only comeback happened in the Early Jurassic Hierlatz Limestone of the Alps, derived from millerocrinid detritus, though, on a much smaller scale.

Compared to other echinoderm classes (such as the Echinoidea and Asteroidea) whose major post-Palaeozoic radiation did not take place until Jurassic times, the Triassic can be regarded as the crucial period of post-Palaeozoic crinoid phylogeny. This statement also includes the cyrtocrinids the earliest representatives of which have been recovered in the Carnian Hanwang Formation of Central China and await publication. Except for the Jurassic *Cotylederma* and the Cretaceous *Uintacrinus*, no basic

innovation appeared after the Triassic, and no new crinoid habitat has been invaded since that time.

Repository of specimens—GBA Geologische Bundesanstalt Wien; IPB Institut für Paläontologie Bonn; IFGT Institut für Geowissenschaften Tübingen; MHI Muschelkalkmuseum Ingelfingen; NHMW Naturhistorisches Museum Wien.

Acknowledgments I would like to thank Adolf Seilacher, Yale and Tübingen, for carefully reading an earlier draft of the manuscript. He and Hans Hess have always been constructive partners in my effort to understand the Triassic crinoids. Access to specimens under curation of A. Kroh, Naturhistorisches Museum Wien and Geologische Bundesanstalt Wien; J. Nebelsick, Institut für Geowissenschaften Tübingen; and M. Sander, Institut für Paläontologie Bonn, is gratefully acknowledged. The manuscript benefited much from the reviews by Michael J. Simms, Belfast, and Adolf Seilacher. The German Science Foundation provided travel grants for the Project Ha 2469/1-1 “Evolutionsbiologie der Crinoiden in der Trias”.

Appendix: Triassic crinoid taxa considered in Fig. 1

For additional detailed stratigraphic and geographic data see Biese (1934), Simms (1990a, b), and Klikushin (1987). The authors of taxa are not referenced.

Order Holocrinida Jaekel, 1918

Family Holocrinidae Jaekel, 1918

Holocrinus Wachsmuth & Springer, 1887—Olenekian–Ladinian; Europe, Asia, N-America.

Holocrinus n. sp.—Olenekian (Smithian); Hiraiso Formation, North Japan (Kashiyama and Oji 2004); Zhitkov Formation, South Primorye, Russia (Oji 2009); columnals, cirrals.

Holocrinus smithi Clark, 1908—Olenekian (Spathian); Virgin Limestone, Thaynes Formation, Western N-America (Schubert et al. 1992); columnals, cirrals.

Holocrinus n. sp. (Leonardi 1968, Fig. 60)—Olenekian (Spathian); Werfen Formation, Southern Alps; Czopak Marl Formation, Hungary; columnals, cirrals.

Holocrinus acutangulus (v. Meyer, 1847)—early Anisian; Lower Muschelkalk, Central Europe; columnals, cirrals, cup, brachials.

Holocrinus wagneri (Benecke, 1887)—early Anisian; Lower Muschelkalk, Germany; complete articulated specimens.

Holocrinus beyrichi (Picard, 1883)—middle Anisian; Lower Muschelkalk, Germany; complete articulated specimens.

Holocrinus dubius (Goldfuss, 1831)—middle–late Anisian; Lower Muschelkalk, Central Europe; complete articulated specimens.

Holocrinus meyeri Hagdorn & Gluchowski, 1993—late Anisian; Lower and Middle Muschelkalk, Poland; columnals, cirrals, cup, brachials.

Holocrinus doreckae, Hagdorn 1983—latest Anisian; Upper Muschelkalk, Germany; columnals, cirrals.

Holocrinus cisnerosi Schmidt, 1935—Ladinian; Muschelkalk, Spain; columnals, cirrals.

Moencrinus Hildebrand, 1926—early Anisian; Germany
Moencrinus deecke Hildebrand, 1926—early Anisian; Lower Muschelkalk, Germany; complete articulated specimens.

Eckicrinus Hagdorn & Gluchowski, 1993—middle – late Anisian; Central Europe, Southwest China

Eckicrinus radiatus (v. Schauroth, 1859)—middle–late Anisian; Recoaro Formation, Southern Alps, Hungary; Lower and Middle Muschelkalk, Poland; Quinyang Formation, Guizhou; columnals, cirrals.

Tollmannicrinus Klikushin, 1992—late Anisian–Rhaetian; Europe, Asia, Timor, New Zealand

Tollmannicrinus quinqueradiatus (Bather, 1909)—late Anisian–Rhaetian; Hungary, Turkey, Timor, New Zealand; columnals, cup, brachials.

Tollmannicrinus saklibelensis (Kristan-Tollmann, 1975)—late Anisian–early Carnian; Hallstatt Limestones Turkey; Quinyang Formation, Guizhou; columnals, cup, brachials.

Tollmannicrinus n. sp. (unpublished material MHI)—middle Carnian; Hanwang Formation, Central China; columnals, cup, brachials.

Order Encrinida Matsumoto, 1929

Family Dadocrinidae Lowenstam, 1942

Dadocrinus v. Meyer, 1847—early Anisian; Europe

Dadocrinus gracilis (v. Buch, 1845)—early Anisian; Formazione à *gracilis*, Southern Alps; Lower Muschelkalk, Poland, Germany, Hungary; complete articulated specimens.

Dadocrinus kunischi Wachsmuth & Springer, 1887—early Anisian; Lower Muschelkalk, Poland; complete articulated specimens.

Dadocrinus grundeyi Langenhan, 1903—early Anisian; Tatra Mountains, Lower Muschelkalk, Poland; complete articulated specimens.

Dadocrinidae gen. nov. (five-armed dadocrinid cf. Hagdorn 1996, Pl. 2, Fig. c)—early Anisian; Lower Muschelkalk, Poland; complete articulated specimens.

Carnallicrinus Hagdorn, 2004—middle Anisian; Central Europe

Carnallicrinus carnalli (Beyrich, 1856)—middle Anisian; Lower Muschelkalk, Germany, Poland; complete articulated specimens.

Family Encrinidae Dujardin & Hupé, 1862

Encrinus Lamarck, 1801—Anisian–Ladinian; Europe, Asia

Encrinus aculeatus v. Meyer, 1847—Anisian; Lower Muschelkalk, Central Europe; Prezzo Limestone, Southern Alps; complete articulated specimens.

Encrinus robustus Assmann, 1925—Anisian; Lower Muschelkalk, Central Europe; Prezzo Limestone, Southern Alps; complete articulated specimens.

Encrinus brahli Overweg, 1850—middle to late Anisian; Lower Muschelkalk, Central Europe; complete articulated specimens.

Encrinus spinosus Michael, 1893—late Anisian; Lower Muschelkalk, Poland; crown.

Encrinus liliiformis Lamarck, 1801—late Anisian; Upper Muschelkalk, Central Europe; complete articulated specimens.

Encrinus greppini Loriol, 1877—late Anisian; Upper Muschelkalk, Switzerland; complete articulated specimens.

Encrinus n. sp. (undescribed specimen SMNS)—early Ladinian; Upper Muschelkalk (Rottweil Formation), Germany; crown.

Encrinus n. sp. (undescribed material)—Ladinian; Muschelkalk, Spain, Israel; complete articulated specimens.

Encrinus n. sp. (cf. Quenstedt 1852, Pl. 54, Fig. 11)—late Ladinian—early Carnian; Cassian Formation, Southern Alps; crown, column.

Chelocrinus v. Meyer, 1837—middle Anisian—early Carnian; Europe

Chelocrinus n. sp. (Ernst and Löffler 1993, Fig. 2)—middle Anisian; Lower Muschelkalk, Central Europe; complete articulated specimens.

Chelocrinus schlotheimi (Quenstedt, 1835)—late Anisian, Upper Muschelkalk, Germany; complete articulated specimens.

Chelocrinus cassianus (Laube, 1864)—late Ladinian—early Carnian; Cassian Formation, Southern Alps; crown, column, holdfast.

Cassianocrinus Laube, 1865—late Ladinian—early Carnian; Southern Alps.

Cassianocrinus varians (v. Münster, 1841)—late Ladinian—early Carnian; Cassian Formation, Southern Alps; crown, column, holdfast.

Zardinicrinus Hagdorn, 2004—late Ladinian—early Carnian; Southern Europe

Zardinicrinus granulosis (v. Münster, 1834)—late Ladinian—early Carnian; Cassian Formation, Southern Alps; crown, column, holdfast.

Zardinicrinus coronensis (Jekelius, 1936)—late Ladinian—early Carnian, Romania, Southern Alps; column, cup.

Ainigmacrinidae Hagdorn, 1988

Ainigmacrinus Hagdorn, 1988—late Ladinian—early Carnian; Southern Alps

Ainigmacrinus calyconodalis Hagdorn, 1988—late Ladinian—early Carnian; Cassian Formation, Southern Alps; column, cirrals, cup.

Traumatocrinidae Mu, 1949

Traumatocrinus Wöhrmann, 1889—late Ladinian—early Carnian; Europe, Asia, N-America

Traumatocrinus caudex Dittmar, 1886—early Carnian; Hallstatt Limestone, Raibl Formation, Europe; North America; column.

Traumatocrinus hsui Mu, 1949—late Ladinian—early Carnian; Xiaowa Formation, SW-China (Guizhou, Sichuan); complete articulated specimens.

Vostocovacrinus Yeltysheva & Polyarnaya, 1986—late Ladinian; Siberia, Spitsbergen

Vostocovacrinus boreus Yeltysheva & Polyarnaya, 1986—late Ladinian; Siberia, Spitsbergen; crown, column, holdfast.

Order Isocrinida Sieverts-Doreck, 1952

Pentacrinidae Gray, 1842

Pentacrinites Blumenbach, 1804—late Norian—Oxfordian; Europe, Russia

Pentacrinites n. sp. (Moosleitner 2004, Pl. 46, Fig. 14)—late Norian/Rhaetian; Zlambach Formation, Austria; columnals, brachials.

Pentacrinites n. sp. (unpublished specimen MHI)—late Norian; Siberia, Kotelny Island; crown, column.

Seiurocrinus Gislén, 1924—late Norian—Middle Jurassic; Europe, Russia, Asia, North America

Seiurocrinus klikushini Simms, 1989—late Norian; Siberia, Kotelny Island; crown, column.

Family Eocomatulidae Simms, 1988

Eocomatula Simms, 1988—Rhaetian—Pliensbachian; Europe, South America

Eocomatula decagonalis Simms, 1988—Rhaetian; Pucará Group, Peru; column.

Isocrinidae Gislén, 1924

Tyrolocrinus Klikushin, 1982—Anisian—Rhaetian; Europe, Asia

Tyrolocrinus tyrolensis Laube, 1865—late Anisian—early Carnian; Quingyan Formation, Southwest China; Cassian Formation, Southern Alps; column.

Tyrolocrinus scipio Bather, 1909 (incl. *T. sceptrum* and *T. candelabrum*)—Carnian; Hungary; column.

Tyrolocrinus hercuniae Bather, 1909—Carnian; Hungary; column.

Tyrolocrinus pecae Jurkovšek & Kolar-Jurkovšek, 1997—early Carnian; Slovenia; column.

Tyrolocrinus bavaricus Winkler, 1859—Rhaetian; Kössen Formation, Northern Alps; column.

Balanocrinus Agassiz in Desor, 1845—late Anisian—Early Cretaceous; Europe, Russia, China, Africa

Balanocrinus sp. indet. (Stiller 2001, p. 315)—late Anisian; Quingyan Formation, Guizhou; column.

Balanocrinus subcrenatus Münster, 1841—late Ladinian—early Carnian; Cassian Formation; Southern Alps; column.

Balanocrinus sp. indet. (Kristan-Tollmann & Tollmann, 1983, Figs. 7, 8; Moosleitner 2004, pl. 46, Figs. 19–20)—late Norian—Rhaetian; Austria, Timor; column.

- Singularocrinus* Klikushin, 1982—late Carnian–Norian; China, Russia
- Singularocrinus singularis* Klikushin, 1982—Norian; Russia; column.
- Singularocrinus* n. sp. (undescribed material MHI)—late Carnian; Hanwang Formation, Sichuan; cup, brachials, column.
- Laevigatocrinus* Klikushin, 1979—late Ladinian–early Carnian; Europe, Russia.
- Laevigatocrinus laevigatus* (v. Münster, 1841)—late Ladinian–early Carnian; Cassian Formation, Southern Alps; column.
- Isocrinidae gen. nov. *Pentacrinus propinquus* v. Münster, 1841 (? incl. “*Pentacrinites*” *carolinensis* Eagle, 2003, and “*Laevigatocrinus*” *balmacaanensis* Eagle, 2003)—late Ladinian–early Carnian; Cassian Formation, Southern Alps; Late Triassic, New Zealand; cup, column.
- Order Comatulida A. H. Clark, 1908
- Family Paracomatulidae Hess, 1951
- Paracomatula* Hess, 1951—late Norian–Middle Jurassic; New Caledonia, Europe.
- Paracomatula triadica* Hagdorn and Campbell, 1993—late Norian/Rhaetian; Bouraké Formation, New Caledonia; complete articulated specimens.
- Order Millericrinida Sieverts-Doreck, 1952
- Bangtoupocrinidae Stiller, 2000
- Bangtoupocrinus* Stiller, 2000—late Anisian; China.
- Bangtoupocrinus kokeni* Stiller, 2000—late Anisian; Quingyan Formation, Guizhou; column.
- Silesiacrinus* Hagdorn and Gluchowski, 1993—late Anisian; Europe, China.
- Silesiacrinus silesiacus* (Beyrich, 1857)—late Anisian; Lower to Middle Muschelkalk, Central Europe; column, holdfast.
- Silesiacrinus parvus* Stiller, 2000—late Anisian; Quingyan Formation, Southwest China; column.
- Millericrinida gen. nov. (*Entrochus* sp. Bather 1929, pl. 1, Fig. 1–3; Zapfe 1967 *Millericrinus* sp. pl. 1, Fig. 9)—late Norian/Rhaetian; Hallstatt Limestone, Timor, Northern Alps; column, holdfast.
- Order Roveacrinida Peck, 1943
- Axicrinidae Hess (2010a)
- Axicrinus* Kristan-Tollmann, 1977—early Carnian; Cassian Formation, Southern Alps
- Axicrinus alexandri* Kristan-Tollmann, 1977—early Carnian; Cassian Formation, Southern Alps; cup, brachials.
- Somphocrinidae Rasmussen, 1978
- Somphocrinus* Peck, 1948—Carnian; Central America, Europe, Timor
- Somphocrinus mexicanus* Peck, 1948—Carnian; Mexico; centrodorsal, cup, brachials.
- Ossicrinus* Kristan-Tollmann, 1970—late Ladinian; Europe
- Ossicrinus reticulatus* Kristan-Tollmann, 1970—late Ladinian; Cassian Formation, Southern Alps; cup, centrodorsal.
- Osteocrinus* Kristan-Tollmann, 1970—late Ladinian, Carnian; Europe, Asia, Timor
- Osteocrinus rectus* Kristan-Tollmann, 1970—late Ladinian–Carnian; Europe, Turkey, China, Timor; cup, brachials, centrodorsal.
- Osteocrinus acus* Kristan-Tollmann, 1970—late Ladinian–middle Carnian; Europe, Turkey; cup, brachials, centrodorsal.
- Osteocrinus spinosus* Kristan-Tollmann, 1970—late Ladinian–Carnian; Europe, Asia, China, Timor; cup, brachials, centrodorsal.
- Osteocrinus reticulatus* Kristan-Tollmann, 1970—middle Carnian; Europe, Asia, Turkey, Iran; cup, brachials, centrodorsal.
- Osteocrinus virgatus* Kristan-Tollmann, 1970—middle Carnian; Europe, Asia, Turkey, Iran; cup, brachials, centrodorsal.
- Order indet.
- Lanternocrinidae Kristan-Tollmann, 1990
- Lanternocrinus* Kristan-Tollmann, 1988—late Norian/Rhaetian; Austria, Timor
- Lanternocrinus lanterna* Kristan-Tollmann, 1988—late Norian/Rhaetian; Hallstatt Limestone, Austria, Timor; cup, arms.
- Nasutocrinus* Kristan-Tollmann, 1990—early Carnian–early Norian; Turkey, Timor
- Nasutocrinus leios* Kristan-Tollmann, 1990—early Carnian; Hallstatt Limestone, Turkey; isolated sclerites.
- Nasutocrinus dentatus* Kristan-Tollmann, 1990—early Norian; Hallstatt Limestone, Turkey, Timor; isolated sclerites.
- Leocrinidae Kristan-Tollmann, 1990
- Leocrinus* Kristan-Tollmann, 1990—Norian–Rhaetian; Europe, Asia
- Leocrinus krystini* Kristan-Tollmann, 1990—late Norian; Austria, Turkey, Timor; isolated sclerites.
- Leocrinus undulatus* Kristan-Tollmann, 1990—late Norian; Austria; isolated sclerites.
- Leocrinus diffissus* Kristan-Tollmann, 1990—late Norian–Rhaetian; Zlambach Formation, Austria; isolated sclerites.
- Leocrinus gracilis* Kristan-Tollmann, 1990—Norian; Austria, Turkey, Timor; isolated sclerites.
- Leocrinus armatus* Kristan-Tollmann, 1990—late Norian; Austria, Timor; isolated sclerites.
- Quingyanocrinidae Stiller, 2000
- Quingyanocrinus* Stiller, 2000—late Anisian; China
- Quingyanocrinus kueichouensis* (Dubatolova and Shao 1959)—late Anisian; Quingyan Formation, Guizhou; column.

- Tulipacrinidae Kristan-Tollmann, 1980
Tulipacrinus Kristan-Tollmann, 1980—early Carnian–Rhaetian; Europe
Tulipacrinus tulipa Kristan-Tollmann, 1980—early Carnian; Cassian Formation, Rhaetian, Zlambach Formation; Alps; isolated sclerites.
Tulipacrinus latus Kristan-Tollmann, 1990—early Carnian; Cassian Formation, Southern Alps; isolated sclerites. Family indet.
Bihaticrinus Kristan-Tollmann, 1990—Norian; Timor
Bihaticrinus manipulus Kristan-Tollmann, 1990—Norian; Hallstatt Limestone, Timor; isolated sclerites.

References

- Agricola, G. (1546). *De natura fossilium*. Übersetzt von G. Fraustadt. Durchgesehen und ergänzt sowie mit Registern und einer Einleitung versehen von F. Krafft 2006. (pp. 434) Wiesbaden: Marix.
- Ausich, W. I. (1999). Lower Mississippian Burlington limestone along the Mississippi River Valley in Iowa, Illinois, and Missouri. In H. Hess, W. I. Ausich, C. E. Brett & M. J. Simms (Eds.), *Fossil crinoids*. (pp. 139–145) Cambridge: Cambridge University Press.
- Ausich, W. I., & Bottjer, D. J. (1985). Phanerozoic tiering in suspension feeding communities on soft substrata: implications for diversity. In J. W. Valentine (Ed.), *Phanerozoic diversity patterns. Profiles in macroevolution* (pp. 255–274) San Francisco: Princeton University Press.
- Bather, F. A. (1929). *Triassic echinoderms of Timor*. *Paläontologie von Timor* 16 (pp. 215–251). Schweizerbart: Stuttgart.
- Baumiller, T. K., & Messing, Ch. G. (2007). Stalked crinoid locomotion, and its ecological and evolutionary implications. *Palaeontologia Electronica* 10(1):2A:1–10.
- Baumiller, T. K., Gahn, F. J., Hess, H., & Messing, Ch. G. (2008). Taphonomy as an indicator of behavior among fossil crinoids. In W. I. Ausich, & G. D. Webster (Eds.) *Echinoderm paleobiology* (pp. 7–20) Indiana University Press.
- Baumiller, T. K., & Hagdorn, H. (1995). Taphonomy as a guide to functional morphology of *Holocrinus*, the first post-Paleozoic crinoid. *Lethaia*, 28, 221–228.
- Baumiller, T. K., Salamon, M. A., Gorzelak, G., Mooi, R., & Messing, Ch. G. (2009). Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution. PNAS Early edition 1–4, <http://www.pnas.org/cgi/doi/10.1073/pnas.0914199107>.
- Biese, W. (1934). Crinoidea triadica. Fossilium Catalogus I: Animalia, Pars 66. (pp. 255) Berlin: Junk.
- Cowen, R. (1981). Crinoid arms and banana plantations: An economic harvesting analogy. *Palaeobiology*, 7, 332–343.
- Ernst, R., & Löffler, Th. (1993). Crinoiden aus dem Unteren Muschelkalk (Anis) Südniedersachsens. In H. Hagdorn, & A. Seilacher (Eds.), *Muschelkalk. Schöntaler Symposium 1991* (pp. 223–233). Korb: Goldschneck.
- Hagdorn, H. (1978). Muschel/Krinoiden-Bioherme im Oberen Muschelkalk (mo1, Anis) von Crailsheim und Schwäbisch Hall (Südwestdeutschland). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 156, 31–86.
- Hagdorn, H. (1982). *Chelocrinus schlotheimi* (Quenstedt) 1835 aus dem Oberen Muschelkalk (mo1, Anisium) von Nordwestdeutschland. *Veröffentlichungen des Naturkundemuseums de Bielefeld*, 4, 5–33.
- Hagdorn, H. (1983). *Holocrinus doreckae* n. sp. aus dem Oberen Muschelkalk und die Entwicklung von Sollbruchstellen im Stiel der Isocrinida. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1983 (pp. 345–368).
- Hagdorn, H. (1988). *Ainigmacrinus calyconodalis* n. g. n. sp., eine ungewöhnliche Seelilie aus der Obertrias der Dolomiten. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1988, 71–96.
- Hagdorn, H. (1995). Literaturbericht—Triassic crinoids. *Zentralblatt für Geologie und Paläontologie Teil II* 1995 (pp. 1–22).
- Hagdorn, H. (1996). Palökologie der Trias-Seelilie *Dadocrinus*. *Geologisch-paläontologische Mitteilungen Innsbruck*, 21, 18–38.
- Hagdorn, H. (2000). The Triassic—Crucial period of post-Paleozoic echinoderm phylogeny and its treasure trove in the Germanic Muschelkalk. *Zentralblatt für Geologie und Paläontologie Teil I* 1998 (pp. 983–987).
- Hagdorn, H. (2004). *Cassianocrinus varians* (Münster, 1841) aus der Cassian-Formation (Trias, Oberladin/Unterkarn) der Dolomiten—ein Bindeglied zwischen Encrinidae und Traumatocrinidae (Crinoidea, Articulata). *Annalen des Naturhistorischen Museums Wien*, 105 A, 231–255.
- Hagdorn, H., & Baumiller, T. K. (1998). Distribution, morphology and taphonomy of *Holocrinus*, the earliest-Paleozoic crinoid. In R. Mooi, & M. Telford (Eds.), *Echinoderms* (pp. 163–168). San Francisco: Balkema.
- Hagdorn, H., & Campbell, H. J. (1993). *Paracomatula triadica* sp. nov.—an early comatulid crinoid from the Otapirian (Late Triassic) of New Caledonia. *Alcheringa*, 17, 1–17.
- Hagdorn, H., & Gluchowski, E. (1993). Palaeobiogeography and Stratigraphy of Muschelkalk Echinoderms (Crinoidea, Echinoidea) in Upper Silesia. In H. Hagdorn, & A. Seilacher (Eds.), *Muschelkalk. Schöntaler Symposium 1991* (pp. 165–176). Korb: Goldschneck.
- Hagdorn, H., Gluchowski, E., & Boczarowski, A. (1996). The crinoid Fauna of the Diplopora-Dolomite (Middle Muschelkalk, Triassic, Upper Anisian) at Piekary Slaskie in Upper Silesia. *Geologisch-paläontologische Mitteilungen Innsbruck*, 21, 47–87.
- Hagdorn, H., & Ockert, W. (1993). *Encrinus liliiformis* im Trochitenkalk Süddeutschlands. In H. Hagdorn, & A. Seilacher (Eds.), *Muschelkalk. Schöntaler Symposium 1991* (pp. 245–260). Korb: Goldschneck.
- Hagdorn, H., & Schulz, M. (1996). Echinodermen-Konservatlagerstätten im Unteren Muschelkalk Ost Hessens. 1. Die Bimbacher Seelilienbank von Großenlüder-Bimbach. *Geologisches Jahrbuch Hessen*, 124, 97–122.
- Hagdorn, H., Wang, X., Bachmann, G. H., Cuny, G., Sander, M., & Wang, C. (2004). Kolonien der pelagischen Seelilie *Traumatocrinus* aus der obertriassischen Xiaowa-Formation von Guanling (Süd-China, Provinz Guizhou). In M. Reich, H. Hagdorn, & J. Reitner (Eds.), *Stachelhäuter 2004. 3. Arbeitstreffen deutschsprachiger Echinodermenforscher* (pp. 17–30). Ingelfingen: Universitätsdrucke Göttingen.
- Hagdorn, H., Wang, X., & Wang, Ch. (2007). Palaeoecology of the pseudoplanktonic Triassic crinoid *Traumatocrinus* from Southwest China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 247, 181–196.
- Haude, R. (1981). Mechanik, Morphogenese und palökologische Bedeutung der “Pelmatozoen”-Stiele. In W.-E. Reif (Ed.), *Funktionsmorphologie. Paläontologische Kursbücher 1* (pp. 187–202). München: Paläontologische Gesellschaft.
- Hess, H. (1950). Ein neuer Crinoide aus dem Mittleren Dogger der Nordschweiz (*Paracomatula helvetica* n. gen. n. sp. *Eclogae Geologicae Helveticae*, 43, 208–216).
- Hess, H. (2002). Remains of Saccocomids (Crinoidea: Echinodermata) from the Upper Jurassic of southern Germany. *Stuttgarter*

- Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)*, 329, 1–57.
- Hess, H. (2010a). Subclass Articulata. In W. I. Ausich (Ed.), *Treatise on invertebrate paleontology. Parts T Echinodermata 2.* (revised) (in press).
- Hess, H. (2010b). Paleocology of pelagic crinoids. In W. I. Ausich (Ed.), *Treatise on invertebrate paleontology. Parts T Echinodermata 2.* (revised) (in press).
- Hornung, T., Brandner, R., Krystin, L., Joachimski, M. M., & Keim, L. (2007). Multistratigraphy constraints on the NW Tethyan “Carnian Crisis”. In S. G. Lucas, & J. A. Spielmann (Eds.), *The Global Triassic. New Mexico Museum of Natural History and Science Bulletin* 41:59–67.
- Jefferies, R. P. S. (1989). The arm structure and mode of life of the Triassic crinoid *Encrinus liliiformis*. *Palaeontology*, 32, 483–497.
- Kashiyama, Y., & Oji, T. (2004). Low diversity shallow marine benthic fauna from the Smithian of Northeast Japan: paleoecologic and paleobiogeographic implications. *Paleontological Research*, 8, 199–218.
- Kleinert, K. (1969). Zum Wachstum von *Apiocrinus*-Wurzeln. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1969, 281–288.
- Klikushin, V. G. (1987). Distribution of Crinoidal remains in Triassic of the U.S.S.R. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 173, 321–338.
- Klikushin, V. G. (1992). Fossil pentacrinid crinoids and their occurrence in the USSR (pp. 358). Sankt Petersburg (in Russian).
- Kozur, H., & Bachmann, G. H. (2010). The Middle Carnian Wet Intermazzo of the Stuttgart Formation (Schilfsandstein), Germanic Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 290, 207–219.
- Kristan-Tollmann, E. (1977). Zur Gattungsunterscheidung und Rekonstruktion der triadischen Schwebcrinoiden. *Paläontologische Zeitschrift*, 51, 185–198.
- Kristan-Tollmann, E. (1988). *Palaeocomaster styriacus* n sp., eine Schwebcrinoide aus dem alpinen Lias des Salzkammergutes, Österreich. *Geologica et Palaeontologica*, 22, 81–87.
- Kristan-Tollmann, E. (1990). Mikrocrinoiden aus der Obertrias der Tethys. *Geologisch-paläontologische Mitteilungen Innsbruck*, 17, 51–100.
- Kristan-Tollmann, E., & Tollmann, A. (1983). Überregionale Züge der Tethys in Schichtenfolge und Fauna am Beispiel der Trias zwischen Europa und Fernost, speziell China. In H. Zapfe (Ed.), *Neue Beiträge zur Biostratigraphie der Tethys-Trias* (pp. 177–229). Wien: Springer.
- Leonardi, P. (1968). Werfeniano. In P. Leonardi (Ed.), *Le Dolomiti. R. Manfrini, Rovereto*, (pp. 107–128).
- Linck, O. (1965). Stratigraphische, stratinomische und ökologische Betrachtungen zu *Encrinus liliiformis* Lamarck. *Jahreshefte des geologischen Landesamts Baden-Württemberg*, 7, 123–148.
- Moore, R. C., & Teichert, C. (Eds.) (1978). *Treatise on invertebrate paleontology, Part T Echinodermata 2 (Crinoidea)* (Vols. 1–3, pp. 1026). Boulder: Lawrence.
- Moosleitner, G. (2004). Fossilien sammeln im Salzburger Land. Ein Führer zu klassischen und neuen Fundstellen (pp. 223). Wiebelsheim: Quelle und Meyer.
- Oji, T. (2009). Crinoids. In Y. Shigeta, Y. D. Zakharov, H. Maeda, & A. M. Popov (Eds.), *The fauna of the Abrek Bay (Far East Russia): A new window to the aftermath of the end-Permian mass extinction event. National Museum of Nature and Science Monographs* 38. Tokyo (pp. 180–181).
- Quenstedt, F. A. (1852). *Handbuch der Petrefaktenkunde* (pp. 792). Tübingen: Laupp.
- Rosinus, M. R. (1719). Tentaminis de lithozois ac lithophytis olim marinis jam vero subterraneis, prodromus sive, de stellis marinis quondam nunc fossilibus disquisitio (pp. 88). Hamburg: Nicolai Sauer.
- Schlotheim, E. F. v. (1820). *Die Petrefaktenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert* (p. 438). Gotha: Becker.
- Schubert, J. K., Bottjer, D. J., & Simms, M. J. (1992). Paleobiology of the oldest known articulate crinoid. *Lethaia*, 25, 97–110.
- Seilacher, A., Drozdowski, G., & Haude, R. (1968). Form and function of the stem in a pseudoplanktonic crinoid (*Seirocrinus*). *Palaeontology*, 11, 275–282.
- Seilacher, A., & Hauff, R. B. (2004). Constructional morphology of pelagic crinoids. *Palaios*, 19, 3–16.
- Seilacher, A., & MacClintock, C. (2005). Crinoid holdfasts: Key to secondary soft-bottom dwelling. *Palaios*, 20, 224–240.
- Simms, M. J. (1986). Contrasting lifestyles in Lower Jurassic crinoids: a comparison of benthic and pseudopelagic Isocrinida. *Palaeontology*, 29, 475–493.
- Simms, M. J. (1990a). The radiation of the post-Palaeozoic echinoderms. In P. D. Taylor & G. P. Larwood (Eds.), *Major evolutionary radiations* (pp. 287–304). Oxford: Clarendon Press.
- Simms, M. J. (1990b). Crinoid diversity and the Triassic/Jurassic boundary. *Cahiers Université Catholique Lyon, Séries Scientifiques*, 3, 67–77.
- Simms, M. J. (1994). Crinoids from the Chambara Formation, Pucará Group, Central Peru. *Palaeontographica A*, 233, 169–175.
- Simms, M. J. (1999). Systematics, phylogeny and evolutionary history. In H. Hess, W. I. Ausich, C. E. Brett, & M. J. Simms (Eds.), *Fossil Crinoids* (pp. 31–40). Cambridge: Cambridge University Press.
- Simms, M., & Ruffell, A. (1990). Climatic and biotic change in the late Triassic. *Journal of the Geological Society London* 147:321–327.
- Simms, M., & Sevastopulo, G. (1993). The origin of articulate crinoids. *Palaeontology* 36:91–109.
- Stiller, F. (2000). Two early millericrinids and an unusual crinoid of uncertain systematic position from the lower Upper Anisian (Middle Triassic) of Qingyan, southwestern China. *Journal of Paleontology*, 74, 32–51.
- Stiller, F. (2001). Fossilvergesellschaftungen, Paläoökologie und paläosynökologische Entwicklung im Oberen Anisium (Mittlere Trias) von Qingyan, insbesondere Bangtoupou, Provinz Guizhou, Südwestchina. *Münstersche Forschungen zur Geologie und Paläontologie* 92:523.
- Twitchett, R. J., & Oji, T. (2005). Early Triassic recovery of echinoderms. *Comptes Rendus Palevol*, 4, 463–474.
- Vermeij, G. (1977). The Mesozoic marine revolution: evidence from snails, predators and grazers. *Palaeobiology*, 3, 245–258.
- Wang, X., Bachmann, G. H., Hagdorn, H., Sander, M. P., Cuny, G., Chen, X., et al. (2008). The Late Triassic black shales of the Guanling Area (Guizhou Province, Southwestern China)—A unique marine reptile and pelagic crinoid fossil Lagerstätte. *Palaeontology*, 51, 27–61.
- Wignall, P. B., & Simms, M. J. (1990). Pseudoplankton. *Palaeontology*, 5, 359–378.
- Yeltyshewa, R. S., & Polyarnaya, Zh. A. (1986). Nachodki traumatokrindid w triasowych otloshenijach Nowosibirskich ostrowow. In A. N. Oleinikov, & A. I. Zhamoida (Eds.), *Parastratigraphic groups of Triassic fauna and flora* (pp. 112–116). Trudy VSEGEI 334, Leningrad.
- Zapfe, H. (1967). Beiträge zur Paläontologie der nordalpinen Riffe Die Fauna der Zlambach-Mergel der Fischerwiese bei Aussee, Steiermark. *Annalen des Naturhistorischen Museums Wien*, 71, 413–480.