

Triassic Muschelkalk of Central Europe

HANS HAGDORN

WITCHES' MONEY AND CHICKEN LEGS: THE RESEARCH HISTORY OF *ENCRINUS LILIIFORMIS*

Long before the advent of scientific palaeontology, common fossils were connected with superstition and legends of popular belief (Abel 1939). In Lower Saxony the abundant columnals of the Muschelkalk sea lily *Encrinus liliiformis* were called *Sonnenräder* (sun wheels), and in Thuringia and Hessia they were called *Bonifatiuspfennige* (St. Boniface's pennies) because the saint who baptised the German tribes was said to have cursed all the pagan money, which turned into stone. In southwestern Germany, *Encrinus* columnals were called *Hexengeld* (witches' money). According to a legend from Beuthen in Upper Silesia, in 1276 St. Hyacinth's rosary broke when he was praying at a fountain, and the beads dropped into the water. The saint prayed for them to multiply, and since then the fountain has been producing rosary beads: columnals of a diverse Middle Muschelkalk crinoid association (Hagdorn *et al.* 1996).

Therefore, it is not astonishing that columnals of *Encrinus liliiformis* were among the first crinoid remains described in the scientific literature. In his monograph, *De natura fossilium* (1546), Georgius Agricola from Chemnitz in Saxony introduced the name '*Encrinus lilienstein*', which means stone lily. However, he used this name for *Chladocrinus* columnals from the Lias of Hildesheim. For the cylindrical columnals of *Encrinus liliiformis*, Agricola coined the names '*Trochites*' (wheel

stones, a translation of their trivial German name, *Rädersteine*) for single columnals and '*Entrochus*' for pluricolumnals. A hundred years later, Fridericus Lachmund, in *Oryctographia Hildesheimensis* (1669), illustrated columnals, cups and cup elements (*Pentagonus*) as well as a fragmentary crown, the arms of which he compared to chicken legs. Misinterpreting Agricola, he transferred the name '*Encrinus*' to these fossils. From that time onward, the name '*Encrinus*' became attached to this common and earliest recognized crinoid crown. In 1719 the Hamburg physician Michael Reinhold Rosinus figured complete crowns and elements of crown and stem that he regarded as fragments of some kind of starfish. Other 18th-century authors explained them as vertebrae of sea animals, marine plants, corals or parts of 'Jew stones' (sea urchins). Finally, the complete animal was correctly reconstructed by Johann Christophorus Harenberg in 1729. *Encrinus* specimens were found and described from many sites in Germany, such as the classic sites of Hildesheim, Erkerode, Göttingen (all in Lower Saxony), Crailsheim, Schwäbisch Hall and Neckarwestheim (in Württemberg).

Before the introduction of binominal scientific nomenclature, Harenberg's *Lilium lapideum* (stone lily) was the most common name for the fossil. Until 1840, *Encrinites fossilis* Blumenbach 1802, *Encrinites trochitiferus* Schlotheim 1813 and *Encrinites moniliferus* Miller 1821 were used in parallel, but eventually Lamarck's name, *Encrinus liliiformis* 1801, was formally established as the valid species name (comp. ICZN 1962; opinion 636).

Chronostratigraphy		Lithostratigraphy			Crinoid Biostratigraphy					
Stage	Substage	Germany		Upper Silesia (Poland)	Distribution of important taxa		Biozones			
Ladinian	Longobardian	Keuper	Lower	Lettenkeuper	Keuper	<i>Holocrinus doreckae</i>				
	Fassanian		Upper	<i>Holocrinus</i> -Bank				Boruszowice Beds	<i>Encrinurus liliiformis</i>	<i>E. sp.</i>
Anisian	Illyrian	Muschelkalk	Trochitenkalk	Neckarw. Mbr.	Wilkowice Beds	<i>Holocrinus meyeri</i>	<i>Silesiacrinus</i>	<i>Encrinurus liliiformis</i>		
				Crailsheim Mbr.					Tarnowice Beds	<i>Chelocrinurus schlottheimi</i>
				Hassmersh. Mbr.						
	Pelsonian		Lower	Schaumkalkbänke	Karchowice Beds	<i>Holocrinus acutangulus</i>	<i>Holocrinus dubius</i>	<i>Chelocrinurus aculeatus</i>	<i>Chelocrinurus carnalli</i>	
				<i>Freyburg + Gutendorf</i>	Terebratula Beds					<i>Silesiacrinus</i>
				Terebratelbänke	Gorazdze Beds					<i>Encrinurus aculeatus</i>
Aegean/Bithynian	Upper	Oolithbänke	Gogolin Beds	<i>Dadocrinus</i>	<i>Holocrinus acutangulus</i>	<i>Encrinurus aculeatus</i>				
		Konglomeratbänke								
Buntsandstein	Lower		<i>Gogolin</i>	<i>Dadocrinus</i>						
	Röt		<i>Myophoria</i> Beds							

Fig. 178. Stratigraphic table of the Muschelkalk with crinoid Lagerstätten. Biostratigraphy of Middle Triassic crinoids; distribution of some important crinoid species.

THE MUSCHELKALK SEA

The middle Triassic Muschelkalk (Fig. 178) forms the central group of the tripartite Germanic Triassic beginning with mostly continental red beds of the Buntsandstein, followed by the marine Muschelkalk carbonates

and evaporites, which in turn are overlain by the multi-coloured Keuper claystones, sandstones and evaporites deposited under changing terrestrial, playa lake or even marine conditions. The Muschelkalk deposits cover an area of Europe between the French Massif Central, Fennoscandia and the Russian Platform (Fig. 179). Towards

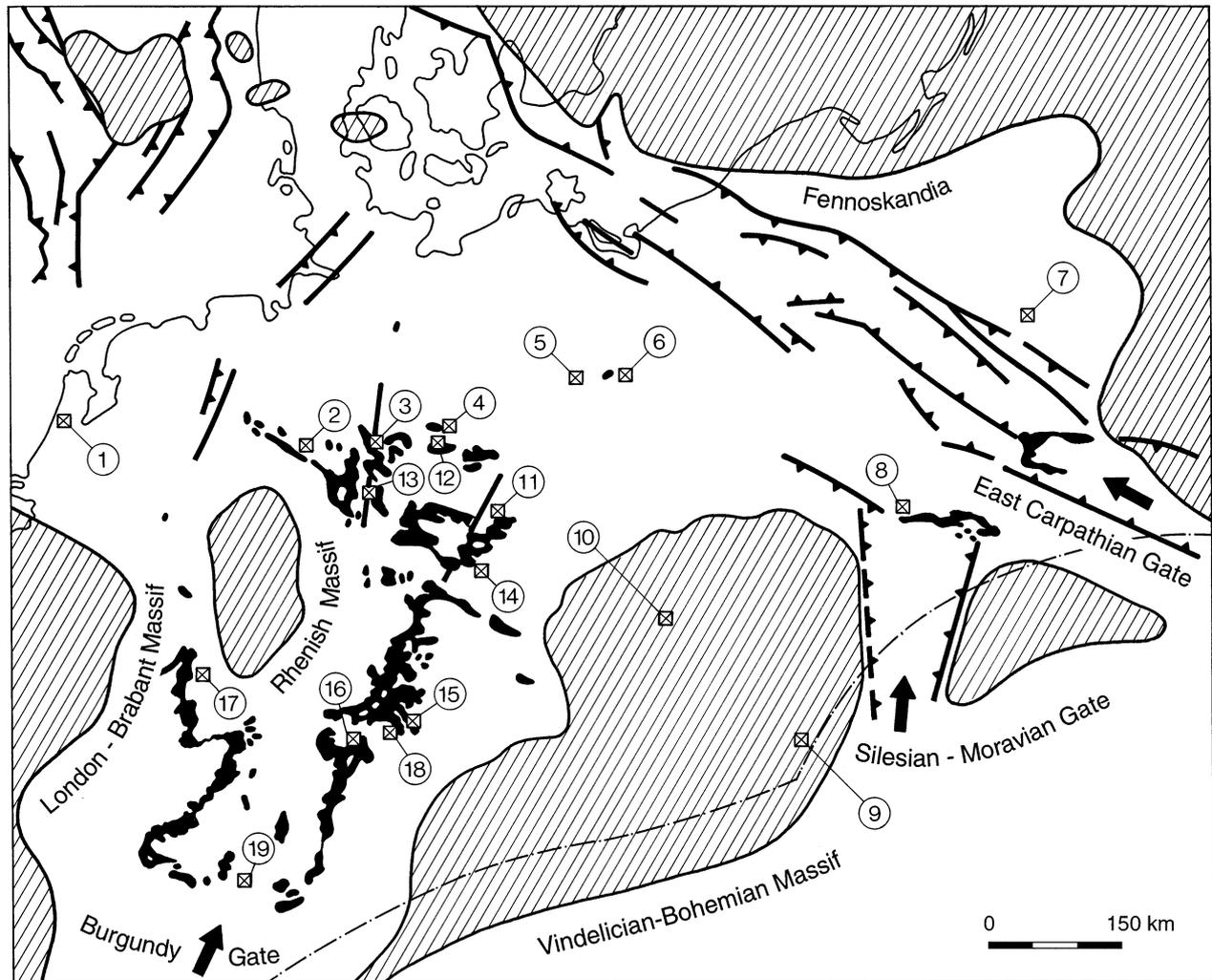


Fig. 179. Palaeogeographic map of the Germanic Basin during Middle Triassic with Muschelkalk outcrops (black) and position of crinoid *Lagerstätten*. Key: 1, Amsterdam; 2, Örlinghausen; 3, Hildesheim; 4, Erkerode; 5, Berlin; 6, Rüdersdorf; 7, Warsaw; 8, Gogolin; 9, Vienna; 10, Prague; 11, Freyburg/Unstrut; 12, Wittmar; 13, Göttingen; 14, Gutendorf near Weimar; 15, Crailsheim; 16, Neckar-westheim; 17, Ralingen-Kersch; 18, Schwäbisch Hall; 19, Basel. (Palaeogeography according to Ziegler 1982; from Hagdorn 1991.)

the North Sea Central Swell, the Muschelkalk sediments grade into terrestrial red beds. To the south, the basin was separated from the western branches of the Tethys Sea by the Vindelician-Bohemian Massif. During the Muschelkalk transgression, marine faunas immigrated into the Germanic Basin. The first transgression, in Early Anisian times, brought elements from the Asiatic faunal province via the northern Palaeotethys branch through the East Carpathian Gate into the eastern and central part of the Germanic Basin (Kozur 1974). During Pelsonian and Early Illyrian times (upper part of Lower Muschelkalk) the eastern part of the Germanic Basin was closely connected with the Alpine

realm via the Silesian-Moravian Gate. Therefore, the middle and upper parts of the Lower Muschelkalk in Upper Silesia belonged to the Austroalpine faunal province with abundant and diverse stenohaline benthos composed of crinoids, echinoids, brachiopods, corals and hexactinellid sponges. Towards the west, faunal diversity generally decreased due to elevated salinity. Later in the Early Illyrian, the Germanic Basin became isolated by the lowering of sea level, and only euryhaline faunas lacking crinoids survived this salinity crisis. Along the subsidence centres, conditions leading to evaporite development did not allow any benthic life. Towards the end of Anisian times, renewed transgression from the

Tethys induced faunal exchange documented in the Upper Muschelkalk by *Encrinus liliiformis*. This incursion connected the western part of the basin with the western Tethys via the Burgundy Strait. Lower and Upper Muschelkalk crinoid faunas are closely related, although they do not have any species in common. A detailed scenario of crinoid and echinoid immigration and spreading over the Muschelkalk Basin was reconstructed by Hagdorn (1985) and refined by Hagdorn and Gluchowski (1993).

During Anisian and Early Ladinian times, a first rapid speciation among the encrinids and holocrinids took place, and this is best documented in Muschelkalk sediments. The second radiation occurred during latest Ladinian and Early Carnian. Consequently, a parastratigraphic biozonal scheme based on distinct isolated crinoid and echinoid ossicles has been proposed by Hagdorn and Gluchowski (1993) for the eastern part of the Muschelkalk Basin (Fig. 178). This scheme can also be applied to the western Tethys and its marginal basins (southern and northern Alps, Bakony, Hungarian Muschelkalk in the Mecsek Mountains).

The Muschelkalk sediments were deposited in a warm and shallow carbonate-dominated sea with considerable terrestrial influx, indicated by a clastic marginal sand facies and by thinly bedded limestones, becoming intercalated with mudstones (marls) and shales in the central part of the basin. On the tops of regional or local elevations, thickly bedded skeletal and oolitic limestones give evidence of extremely shallow water. Excellent exposures in cliff-like escarpments along valleys and small gorges, as well as extensive quarrying, have allowed high-resolution bed-by-bed litho- and ecostratigraphy. During the past few years, this has been interpreted in terms of sea level fluctuations and sequence stratigraphy.

Unlike the contemporaneous rocks of the Alpine Triassic, the Muschelkalk is rich in *Lagerstätten* (Seilacher 1993) resulting from smothering of epibenthic organisms *in situ*, thus representing a snapshot of the sea floor. Some of these *Lagerstätten* have yielded articulated skeletons of crinoids, echinoids, ophiuroids, asteroids and even holothurians.

ENCRINUS LILIIFORMIS IN WÜRTTEMBERG'S CRINOID GARDENS

Since Quenstedt's collecting trips to the Gaismühle on the river Jagst northwest of Crailsheim during the 1850s,

the Crailsheim Trochitenkalk has become as famous for *Encrinus liliiformis* as the North German localities. Extensive quarrying for building stones has yielded hundreds of specimens. From the facies patterns, Vollrath (1958) reconstructed a regional shoal of thickly bedded crinoidal limestones situated several tens of kilometres offshore from the Vindelician Massif. Towards the basin centre, this 16-m-thick limestone sequence (Crailsheim Member) grades into single crinoidal beds interbedded with mudstones and micritic limestones (Hassmersheim and Neckarwestheim Members) (Fig. 184). Most of the crinoidal beds can be used as stratigraphic marker horizons.

THE NECKARWESTHEIM SEA LILY BED

One of these marker beds is the Trochitenbank 6 (*pulcher* Biozone). At Neckarwestheim near Heilbronn, approximately 70 km west of Crailsheim, it has yielded well-preserved and complete *Encrinus* specimens. In several excavations, Linck (1954, 1965) recovered big slabs that consisted of three units:

- (a) a 5- to 10-cm-thick micritic limestone that was extensively burrowed (*Balanoglossites*) and had an eroded surface; this firmground was patchily cemented and subsequently bored (*Trypanites*);
- (b) a thick (up to 20 cm) graded skeletal and crinoidal limestone with large intraclasts eroded from unit a; the surface has megaripples;
- (c) an ochre-coloured marl (up to 10 cm) with silt and pellet-filled feeding traces that are also present between the closed crinoid arms of the unit below and may even penetrate the tegmen.

The crinoids – adult specimens with a length of up to 160 cm – are distributed irregularly on the upper surface of unit b and covered by unit c. The mudstones below and above Trochitenbank 6 contain thin shelly layers of soft-bottom infauna and are devoid of crinoids. Some of the crinoids have holdfasts still attached to an intraclast or to a valve of the big oyster-like terquemiid *Enantiostrongylo* or *Newaagia*. The stems of about half of the specimens end with ruptures in their distal or central parts (Fig. 180). Secondary callus growth on these 'regenerated terminal stems' (Linck 1954) indicates that the animals survived the traumatic event that broke their stem. Linck's (1954) reconstruction of uprooted, yet still upright and floating crinoids implies buoyancy

of the crown, which is most improbable. The presumed lifestyle of such 'terminally regenerated' animals is further described in the section titled '*Encrinurus liliformis*: A Gregarious Sea Lily with Intraspecific Tiering'. A certain number of the Neckarwestheim *Encrinurus* specimens are preserved without their arm tips. The reason for this is not known, because regenerated arms, which would indicate ecological stress or partial predation some time prior to final burial, have rarely been recovered. Further outcrops of this bed demonstrate that this *Encrinurus* habitat covered several hundreds of square kilometres.

From this sedimentological and preservational evidence, a habitat between wave base and storm wave base may be assumed. Currents provided the suspension-feeding community with nutrients. Occasional storms (which also caused megaripples) affected populations in a limited area. Such storms repeatedly caused the crinoid remains that had previously accumulated to disintegrate. The animals killed during a final event were uprooted, sank to the bottom and were covered by mud. Subsequently, crinoids and other epibionts from unaffected areas resettled suitable anchoring grounds. Such

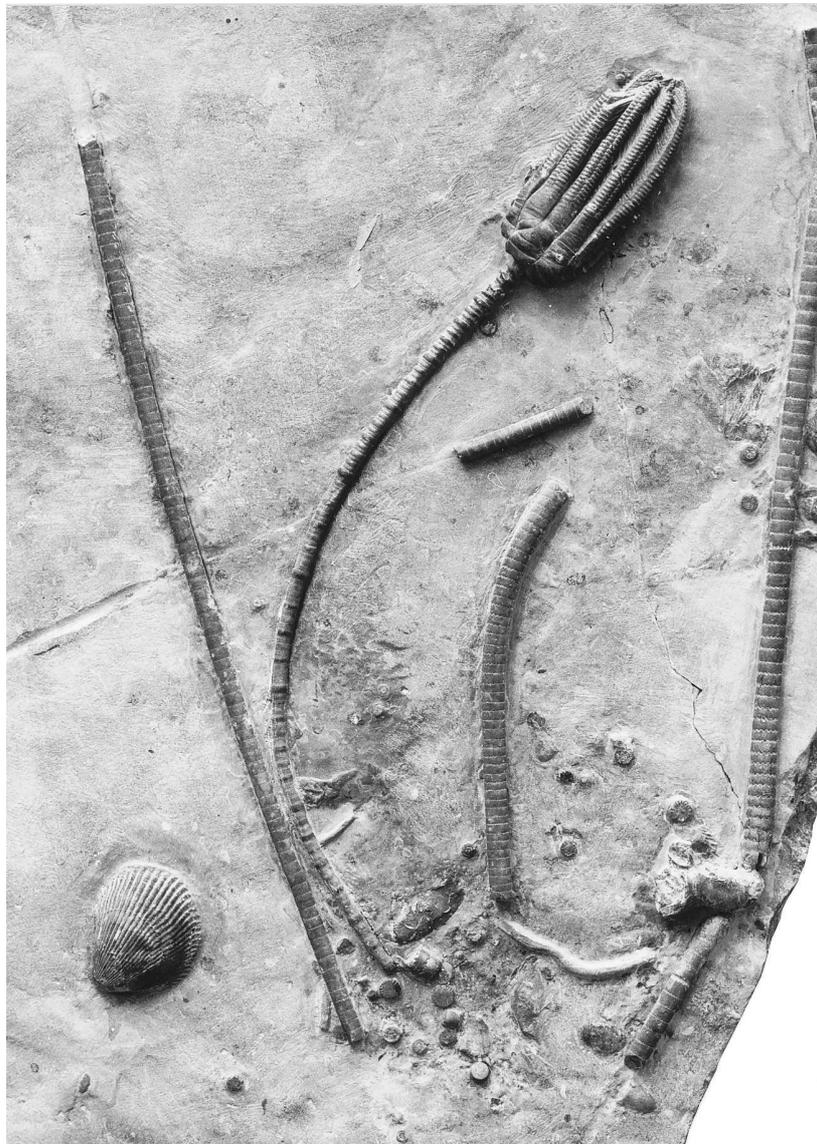


Fig. 180. Complete specimen of *Encrinurus liliformis* from Neckarwestheim, arms closed. Note regenerated stem, distally rounded. The length of these crinoids reached 160 cm. (Paläontologisches Museum, Zürich; courtesy H. Rieber.) $\times 0.4$.

a scenario explains the fairly uniform size in these crinoid populations. The final preservation of the Neckarwestheim crinoid bed is due to increased subsidence, a long period without a severe storm and an increasing background sedimentation, as documented by the succeeding mudstones (Hagdorn & Simon 1984).

THE CRAILSHEIM CRINOID BIOHERMS

From the Neckarwestheim occurrence, Linck (1965) concluded that the 16-m-thick crinoidal limestones around Crailsheim (Crailsheim Member) accumulated from complete animals floating onshore from deeper parts of the basin. He assumed that *Encrinurus* occupied vast areas, but was rather patchily distributed, similar to the Neckarwestheim occurrence. However, Linck did not take into account that only the very top of the Crailsheim Member can be time-correlated with Trochitenbank 6 of Neckarwestheim.

Unequivocal evidence for the autochthony of *Encrinurus liliiformis* in the Crailsheim Member came from the discovery of bioherms with encrinid roots preserved *in situ* (Hagdorn 1978) (Fig. 181). Such structures also occur in the Hassmersheim Member, which was deposited in the deeper parts of the southwestern German Trochitenkalk carbonate ramp (Aigner 1985; Hagdorn 1991). It is characterized by a cyclical change of four skeletal beds and intercalated mudstones devoid of crinoids. The skeletal beds with epifaunal suspension-feeding communities and bioherms are interpreted as parts of high-frequency sequences with flooding surfaces on their tops (Aigner & Bachmann 1992; Hagdorn & Ockert 1993). The calcareous mudstones with infaunal suspension and deposit-feeding communities, preserved in tempestite beds and gutters, represent the relative highstands. Towards the shallow ramp, the mudstones wedge out in the skeletal limestones of the Crailsheim Member (Fig. 182). Bed-by-bed lithostratigraphy has allowed the tracing of these marker beds from the Hassmersheim to the Crailsheim Member with their changing facies and communities. The offshore-onshore zonation of infaunal to epifaunal communities corresponds to the spectrum of community replacement in the high-frequency sequences (Hagdorn & Ockert 1993).

Bioherms are most abundant (up to 1 per 100 m²) in a 2-m-thick sequence of crinoidal limestones interbedded with sheets of marl in the Crailsheim Member (*Encrinurus* Platten). Bioherms also occur in the thick, oolitic

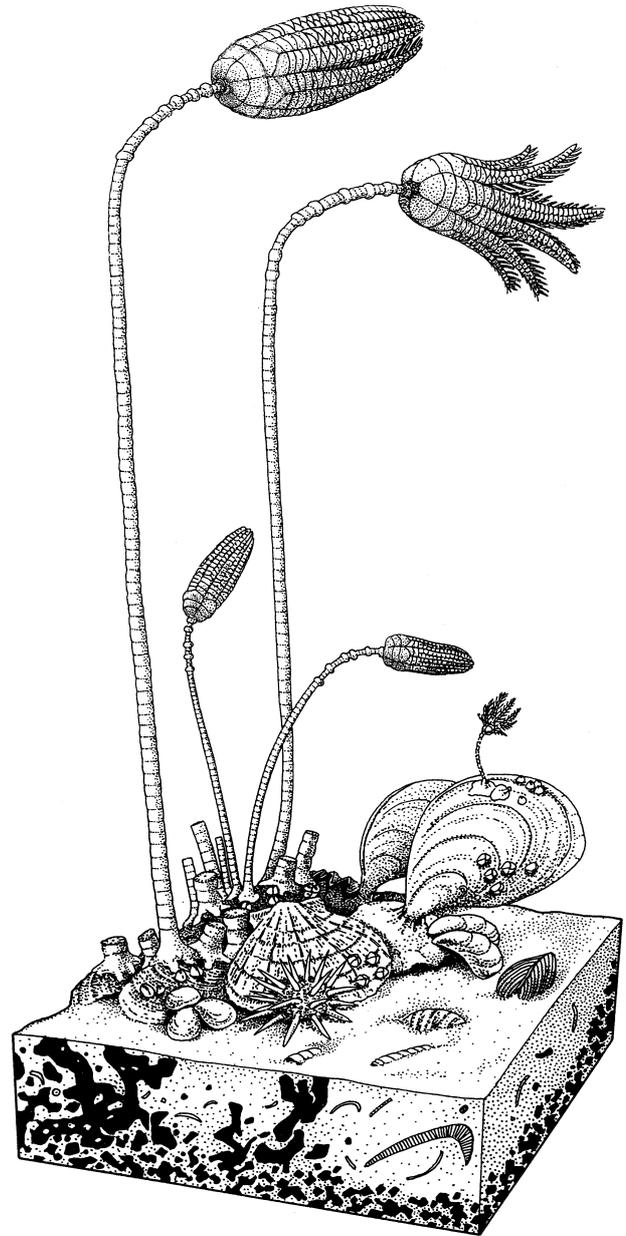


Fig. 181. Reconstruction of *Encrinurus liliiformis* on an encrinid-terquemiid bioherm. Crinoids of different age are attached to the oyster-like terquemiids *Enantiostrion* and *Newaagia* (left) with holdfasts; juvenile individuals are attached to the mussel *Myalina* (right, fixed by byssus threads to a *Newaagia* shell). Large stems of *Encrinurus* are broken near the base. (Redrawn from Hagdorn 1991.)

shallow-water limestones but are less common there. This may be due to frequent sediment reworking, diminishing their preservation potential. The bioherms have a diameter of 2–3 m and a thickness of up to 1.8 m.

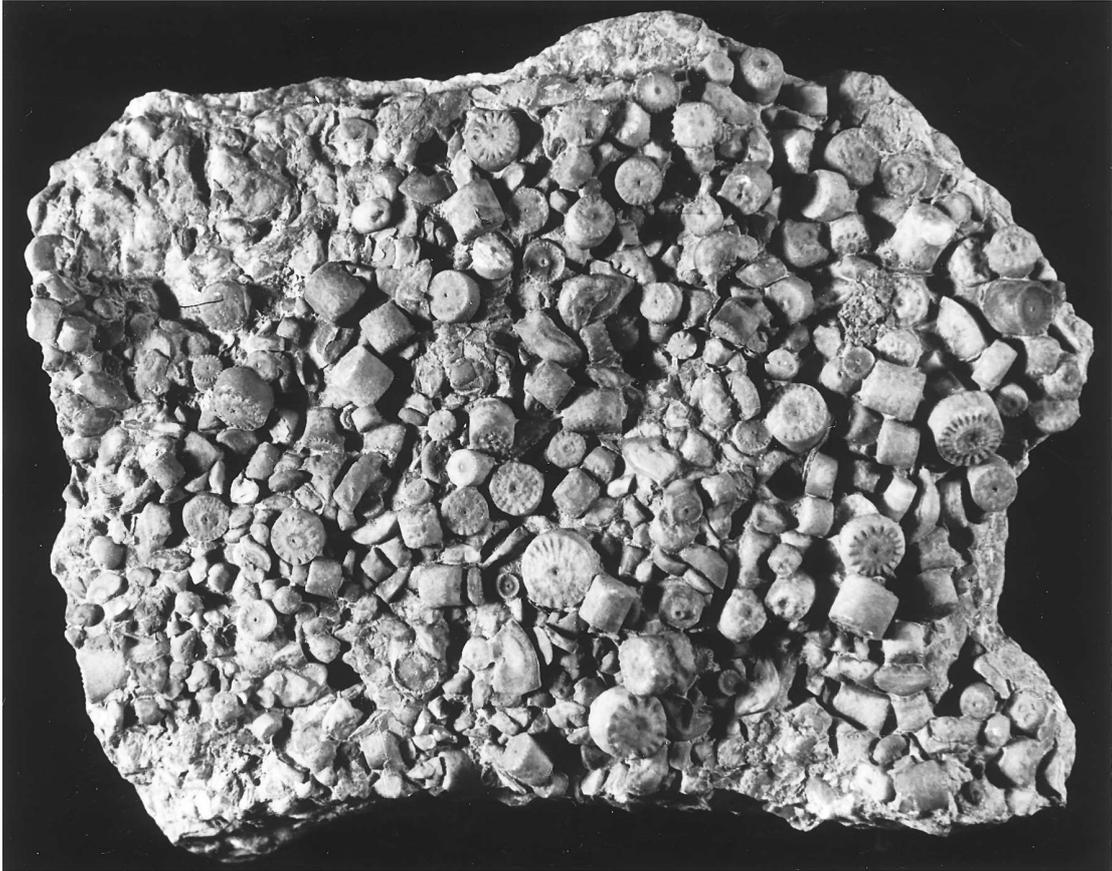


Fig. 182. Trochitenkalk with disarticulated *Encrinurus* ossicles (mainly columnals) from the flank of an encrinid–terquemiid bioherm. Upper Muschelkalk, Crailsheim Member, Mistlau near Crailsheim. (Muschelkalkmuseum, Ingelfingen; photograph H. Hagdorn.) $\times 1.2$.

Their framework was built primarily by terquemiid false oysters and is commonly encrusted with small *Placunopsis*, spirorbid worm tubes and foraminifera (Fig. 181). *Encrinurus* roots encrust the framework most densely towards the bioherm tops and contribute to it. Bioherms are extensively bored by phoronids (*Talpina*, *Calciroda*), acrothoracican barnacles and algae. According to Schmidt (1992), the bioherms originated in the photic zone at a maximum depth of 50 m. Monaxon spicules indicate the presence of frame-binding sponges; algal or bacterial mats have not been recovered (Hüssner 1993). Articulate brachiopods and byssate bivalves were flexibly attached to the bioherm; the bivalves are commonly encrusted by a single or by small groups of *Encrinurus* holdfasts (Fig. 183). In bioherms situated towards the deeper water on the carbonate ramp (Hassmersheim Member), crinoids decrease in number and brachiopods (*Coenothyris*) become dominant (Fig. 184).

Near Schwäbisch Hall, approximately 30 km west of

Crailsheim, a large bioherm complex in an intermediate position on the carbonate ramp persisted through two sedimentary cycles, with periods of lateral expansion during transgression and restriction during regression, when terrigenous mud was prograding. It has yielded 120 *Encrinurus* specimens with a crown length ranging from 6 to 120 mm. The juvenile crinoids with their entirely flexible stem were still attached to the bioherm framework, whereas larger specimens were found uprooted in the bioherm flanks, either directly on top of a shell bed with *in situ* brachiopod and bivalve colonies or in the mudstones covering this bed.

As a rule, complete *Encrinurus* specimens are most abundant close to a bioherm on the muddy tops of shell beds. Low-tier brachiopod colonies in life position also occur there; these grew on a shelly bottom devoid of mud. Such communities appear to have been smothered by bottom backflows of mud avalanches originating from higher areas of the carbonate ramp (Aigner 1985).

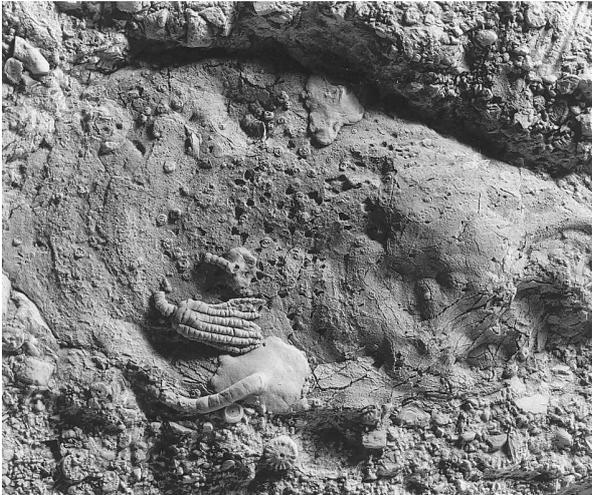


Fig. 183. Juvenile individual of *Encrinus liliiformis* attached to the mussel *Myalina*, discoid holdfast and distal stem of a slightly larger specimen. The bivalve covering the small specimen was deposited at the base of a thin bed of crinoidal limestone from a bioherm flank. Upper Muschelkalk, Crailsheim Member, Mistlau near Crailsheim. (Museum für Geologie und Paläontologie, Tübingen; photograph W. Wetzel.) $\times 1$.

Complete *Encrinus* specimens also occur inside metre-thick, oolitic, crinoidal limestones deposited in extremely shallow water. During lateral shift of the skeletal material, single crinoids were buried by the moving sediment. Due to early cementation, their crowns were not laterally compressed, but remained completely closed, resembling corn cobs.

In southwestern Germany, *Encrinus liliiformis* settlements persisted through two ceratite zones, or six high-frequency sequences on the shallow carbonate ramp of the Crailsheim shoal. Towards the deep ramp, the crinoids are restricted to the transgressive crinoidal marker beds and disappear in the interbedded mudstones that were dominated by soft-bottom communities during sea level lowstands. With rising sea level, the epifaunal communities with crinoids expanded laterally towards the deep ramp until they were covered again by mud deposited during low sea level of the next sequence.

ENCINUS LILIIFORMIS: A GREGARIOUS SEA LILY WITH INTRASPECIFIC TIERING

The Crailsheim and Neckarwestheim *Encrinus Lagerstätten* demonstrate that this crinoid was living between extremely shallow water above wave base and deeper

water below storm wave base (Fig. 184). Larvae settled in the bioherms close to the adults, preferentially on their basal stems. Thus, they succeeded in finding solid anchoring ground slightly above the muddy sea floor, where they were less endangered by smothering. From this, a short larval period and gregarious behaviour of *Encrinus* may be inferred. After a pioneer settlement on winnowed shell beds during omission periods, bioherm frame builders (terquemiids, encrinids) were able to compensate for increasing sedimentation rates by upward growth. In the *Lagerstätten* just discussed, *Encrinus liliiformis* is the only crinoid species. Its size distribution in the Crailsheim and Schwäbisch Hall bioherms indicates intraspecific gradual tiering between juveniles, occupying low-level tiers, and adults, occupying high-level tiers up to 160 cm above the sea floor. Unlike other crinoids, *Encrinus* did not reach its maximum size in a short time by accelerated juvenile growth.

The crown of larger individuals was elevated by a stem that was rigid in the distal and middle parts but flexible in the proximal growth zone (Seilacher *et al.* 1968); thus, current pressure could be compensated for by passive orientation. Nevertheless, in an environment with occasional storms, rupture of the distal stem uprooted many individuals (Fig. 180). Post-rupture secondary growth of the terminal stem by sealing the axial canal indicates that these animals were able to survive for some time, possibly with part of the stem along the sea floor. However, in such a position they were in increased danger of being buried. Unlike the cirriferous holocrinids, encrinids were unable to become reattached after their stem broke. For successful long-term settlement, they needed solid substrates as provided by the bioherm framework. Individuals settling on flexibly attached bivalves like *Myalina* (Fig. 183) lost their attachment when growing up because the bivalve byssus was not able to anchor such large passengers against stronger current pressure. *Myalina* shell fragments, marginally overcrusted by the crinoid holdfasts, indicate that such crinoids shared the fate of those with broken stems.

The taphonomic record of isolated cups proves that *Encrinus liliiformis* had tightly sutured plate circlets forming a robust cup. Bending of the arms by active muscular movement was restricted to the radial and axillary facets and to the uniserial proximal part of the arms with straight muscular articulations. The oblique muscular articulation between the first pinnular and brachial allowed the pinnule to bend away from the arm. *Encrinus* was able to unfold a filtration fan with the arms at an angle of about 45° to the long axis. Between the arms

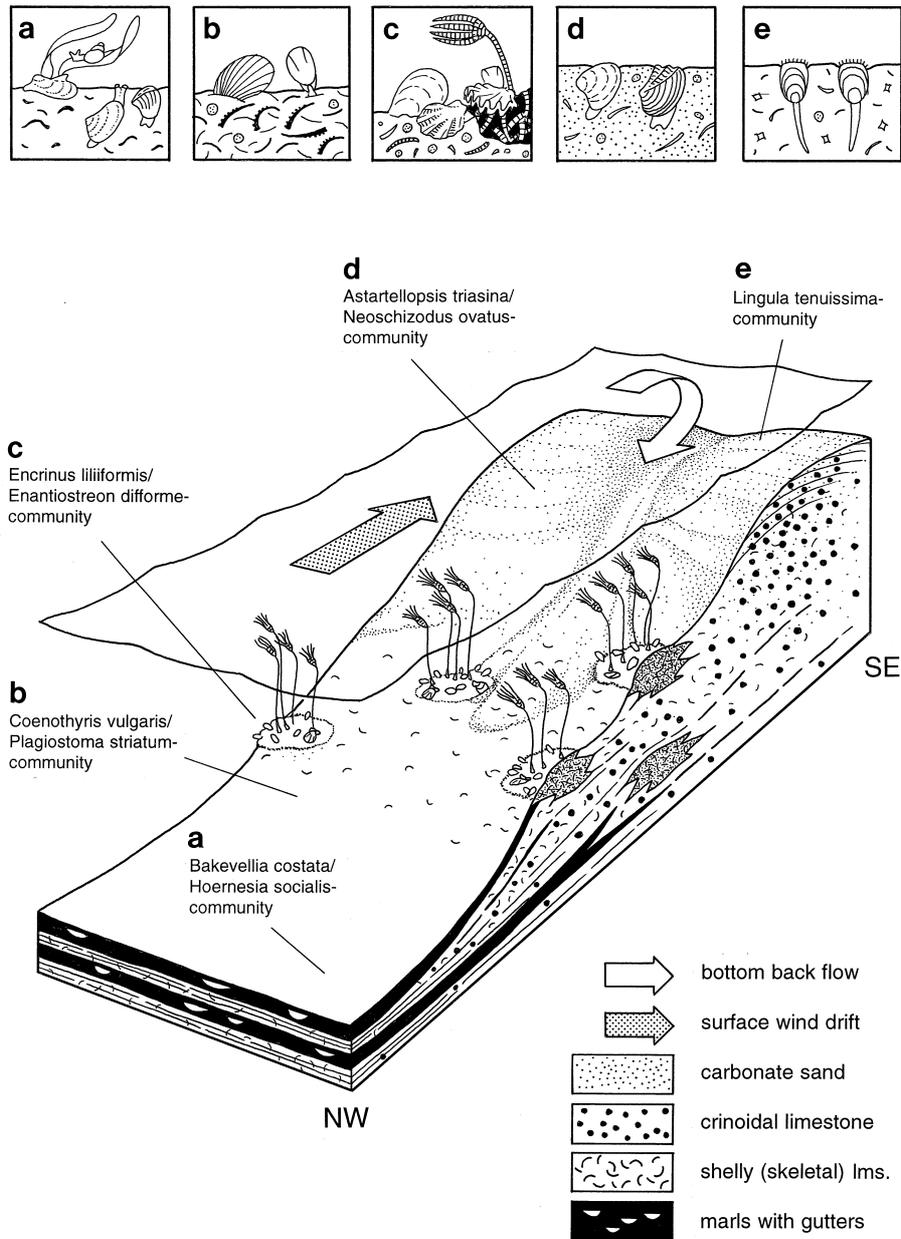


Fig. 184. Facies model and fossil community zonation on the southwestern German Trochitenkalk carbonate ramp during the *atavus* Biozone with crinoid bioherms. The profile covers an area extending approximately 90 km from northwest to southeast along the river Jagst, northeast of Stuttgart. Hassmersheim Member on the deep ramp (left), Crailsheim Member on the shallow ramp (right). According to Aigner's (1985) hydrodynamic model, fair-weather alongshore currents (SW-NE) provided nutrients. Storm-induced onshore wind-drift currents of surface water piled up skeletal debris that was continuously reworked in shallow water. Bottom backflows were responsible for the smothering of habitats in deeper water. (Redrawn from Hagdorn 1991.)

were dense pinnular combs, but the arms could not recurve into a parabolic fan (Fig. 48). Pectinate ornaments on the outer side of the pinnular food grooves were interpreted by Jefferies (1989) to be evidence of food specialization. He argued that this crinoid was not

able to form a real filtration fan, but rather used its dense pinnule system as a microfilter for extremely small plankton, creating its own currents. However, this hypothesis does not explain the lack of other crinoids that filtered normal-sized plankton in the southwest German

Trochitenkalk Sea. The extraordinary ecological success of *Encrinus liliiformis* may be due to its intraspecific tiering.

Encrinus liliiformis Lagerstätten in central and northern Germany and in France have not been studied in such detail. Bioherms of the Crailsheim type, occurring in most *Encrinus* localities, indicate similar habitats. In northwestern Germany another encrinid, the 20-armed *Chelocrinus schlotheimi*, occurs together with *Encrinus liliiformis* at the base of the Trochitenkalk (Gelbe Basis-schichten Member). In an assemblage from Wittmar (Lower Saxony), many specimens had their stems broken a few millimetres below the cup (Hagdorn 1982). Sealing of the axial canal or rounding of the stump indicates that the stemless crowns survived for some time on the sea floor, presumably with their oral side facing upward, as with the stemless *Agassizocrinus* or *Ailsacrinus* (Fig. 206).

CHELOCRINUS CARNALLI: VIOLET FLOWER NESTS

The Schaumkalk ('foamy limestone') derives its name from dissolved oolites. This makes it a soft, porous and easily worked building stone that has been quarried since the Middle Ages. Buildings as famous as the romanesque Naumburg Cathedral with its great statues have been constructed from local Schaumkalk. These marker beds belong to the basin-wide expansions of a shallow-water oolitic and skeletal sequence characterizing the upper part of the Lower Muschelkalk in central and eastern Germany. In deeper parts of the basin, oolitic beds are interbedded with thinly bedded, marly Wellenkalk ('wavy limestone'). Again, this interplay was governed by regional tectonics and sea level fluctuations. The quarries of Zscheiplitz and Schleberoda (near Freyburg an der Unstrut, Saxony-Anhalt) and Gutendorf (near Weimar, Thuringia) became famous for complete specimens of *Chelocrinus carnalli* found on top of the Lower Schaumkalkbank. As described by Jaekel (1894) and Biese (1927), the Freyburg quarries yielded large slabs with bundles of up to 25 complete specimens (Fig. 185) that were current-oriented in one or two

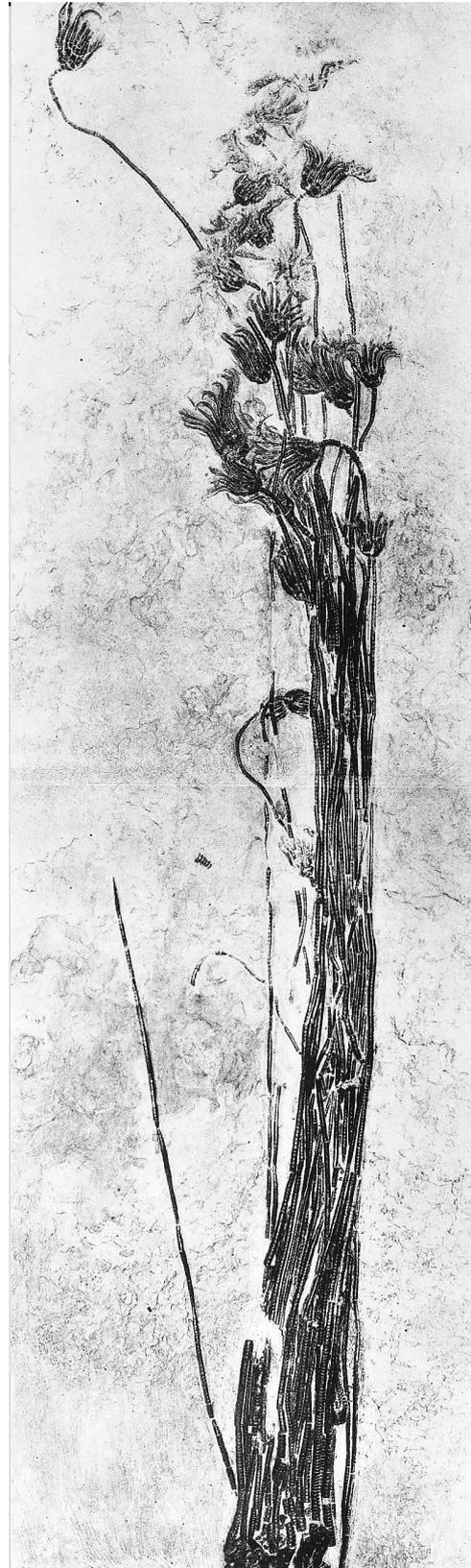


Fig. 185. A bundle of *Chelocrinus carnalli* with a cluster of holdfasts probably encrusting larger shells (not preserved). Lower Muschelkalk, Schaumkalk; Freyburg/Unstrut. (Museum für Naturkunde, Berlin; from Biese 1927.) $\times 0.22$.

directions (called *Blumennester*, flower nests, by the quarrymen). Many stems are preserved with their holdfasts, typically showing an attachment area perpendicular to the stem axis. This indicates anchorage on an unstable substrate because the stem would have broken above a tightly attached holdfast. The crinoids are on top of the oolitic Schaumkalk in an ochre-colored micritic limestone and were covered by greenish marl. The population, comprising individuals of different size, appears to have been rapidly killed and subsequently buried by mud. Very rarely, single specimens were found in skeletal layers inside the cross-stratified Schaumkalk Bed. In Gutendorf, the top of the Lower Schaumkalkbank is a hardground covered by a marly layer and by Wellenkalk. The hardground is extensively bored (*Trypanites*); it is encrusted by serpulids and individual *Chelocrinus* holdfasts (Fig. 186). These either are penetrated by *Trypanites* or fill up hollow *Trypanites* tubes with their stereom (Müller 1956b). Boreholes that are surrounded, but not covered, by stereom of holdfasts demonstrate that the boring organism was still alive. The stems of the Gutendorf specimens are broken either near the base or just below the cup. The crowns of the latter specimens are embedded with their 20 arms splayed out (Müller 1956a). The dominance of such individuals on the Gutendorf hardground indicates large areas favourable for settling. In Freyburg, on the other hand, groups of larvae had to anchor closely together on small solid



Fig. 186. Discoidal holdfasts of *Chelocrinus carnalli* on a hardground with *Trypanites* borings. Lower Muschelkalk, Schaumkalk; Gutendorf near Weimar. (Muschelkalkmuseum, Ingelfingen; photograph H. Hagdorn.) $\times 1.7$.

patches on which they grew up in clusters. Such gregarious behaviour appears to have been the result of a lack of proper anchoring ground. With their purple to violet colour, the Freyburg *Chelocrinus carnalli* contrasts beautifully with the sediment.

DADOCRINUS: THE SMALL COUSIN OF ENCRINUS

At first glance, *Dadocrinus* looks like a juvenile *Encrinus*. Indeed, cladistic analyses indicate that *Dadocrinus* is more closely related to the encrinids than to the millerocrinids, to which it had been assigned during previous decades. This Lower Anisian genus, with several species from the South Alpine and Germanic Muschelkalk, has uniserial arms. In the Germanic Basin, it is restricted to the eastern part, where dissociated ossicles built crinoidal limestones in the Lower Gogolin Beds. Their dispersal towards the west was prevented by a salinity barrier (Hagdorn & Gluchowski 1993). A hundred years ago, the classic site at Sakrau near Gogolin in Upper Silesia (now Poland) yielded beautiful slabs of a light yellowish grey limestone crowded with *Dadocrinus kunischi* (Fig. 187). Sedimentological and palaeoecological data indicate a muddy bottom with burrowing and mud-sticking bivalves (Hagdorn 1996). The crinoids grew in clusters, attached with their discoid holdfasts to the rear ends of the infaunal *Gervillella mytiloides* or to similar bivalves but also to the basal stem of other individuals. Holdfasts attached to hardgrounds have been observed at one locality. The size limitation of this species, with a maximum height of 20 cm, may be attributed to its preference for soft substrates; the bivalve byssus would not have been able to anchor larger crinoids on a muddy sea floor. In flat lenses, *Dadocrinus* specimens are concentrated on the upper and – less commonly – on the lower bedding plane with closely united holdfast clusters. In other localities, single specimens, stem fragments, cups and single, aborally recurved arms indicate stress-caused autotomy prior to burial. The *Dadocrinus* beds of Recoaro in the Vicentinian Alps (Italy) are very similar to those from Upper Silesia.

Its holdfast characterizes *Dadocrinus* as a primary hardground dweller. Living as an epibiont on mud-sticking mussels opened the possibility of secondary soft-ground colonization. This, however, limited the size of the crinoids and also prevented them from contributing to bioherm structures comparable to those of their larger encrinid relatives.

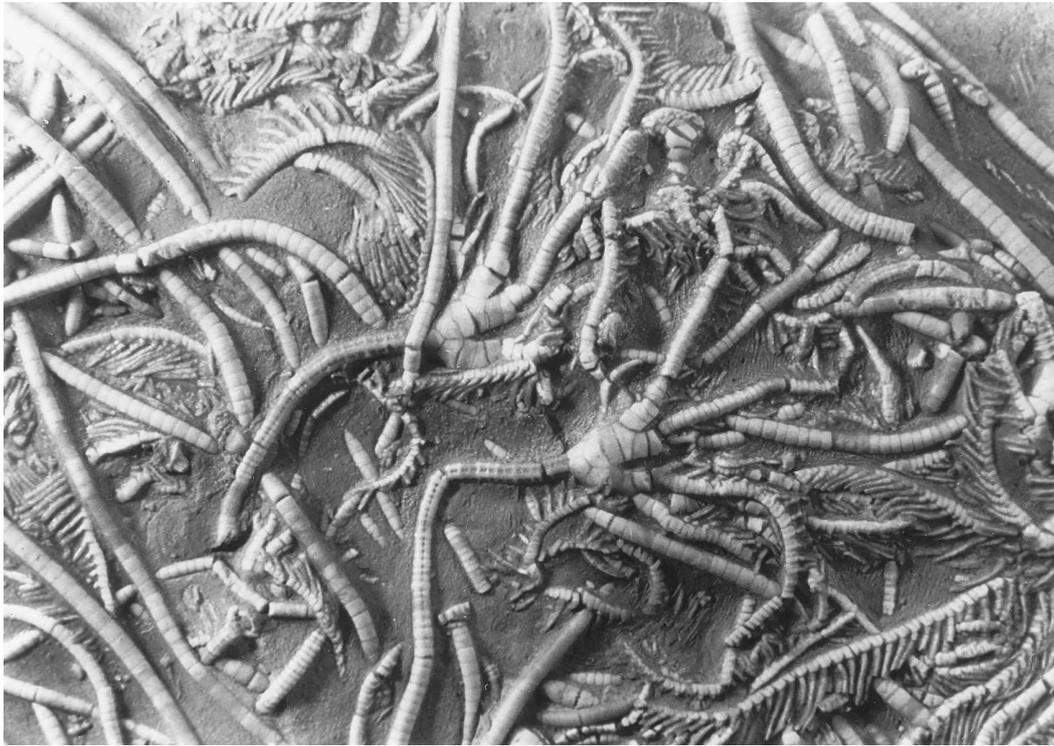


Fig. 187. *Dadocrinus kunischi* on top of a bedding plane. Lower Muschelkalk, Gogolin Beds; Sakrau near Gogolin, Upper Silesia. (Muschelkalkmuseum, Ingelfingen; photograph H. Hagdorn.) $\times 1.6$.

HOLOCRINUS: PRECURSOR OF ISOCRINIDS

Unlike encrinids and dadocrinids, holocrinids were not permanently fixed to the sea floor by a holdfast, but attached themselves actively with their cirri. Like their descendants, the isocrinids, they had stems with a preformed rupture point below the nodals so that after stress-induced autotomy the stem automatically ended with a cirrinodal. More or less smooth cryptosymplectial lower nodal facets, so typical of isocrinids, had not yet developed in holocrinids (Hagdorn 1983). However, taphonomic evidence from stem fragmentation patterns suggests that short ligament fibres connected nodals to infranodals. These were responsible for autotomy in holocrinids, and they must have been developed prior to the cryptosymplecties that are documented from Upper Ladinian onward (Baumiller & Hagdorn 1995). Complete *Holocrinus* skeletons remained extremely rare for a century, but recently several new sites have been discovered, yielding additional specimens. In the Upper Muschelkalk, isolated holocrinid ossicles occur in one sin-

gle marker bed in southwestern Germany (Hagdorn 1983), whereas they are more diverse and more common in the Lower Muschelkalk. Their remains are found, commonly together with encrinids, on the tops of hardgrounds where the animals were living closely together. In the clastic marginal facies of the Lower Muschelkalk of Ralingen-Kersch near Trier (Rhineland-Palatine, Germany), isolated and worn ossicles of *Holocrinus cf. dubius* are concentrated in shelly tempestite beds, whereas the articulated specimens are embedded at the base of, and inside, gutters. The stems of these specimens may be intact or may have disintegrated into single noditaxes and cirri (Fig. 188), and the arms are shed at the radial facet. As judged by the fossil record, regeneration of the arms must have been very common among holocrinids. The typical accumulations of distal columnals can be explained by life-long stem autotomy. Obviously, holocrinids were well adapted to shallow, storm-dominated habitats where traumatic events caused arm-shedding and stem autotomy. The animals reattached themselves with their new terminal cirri and regenerated their arms.

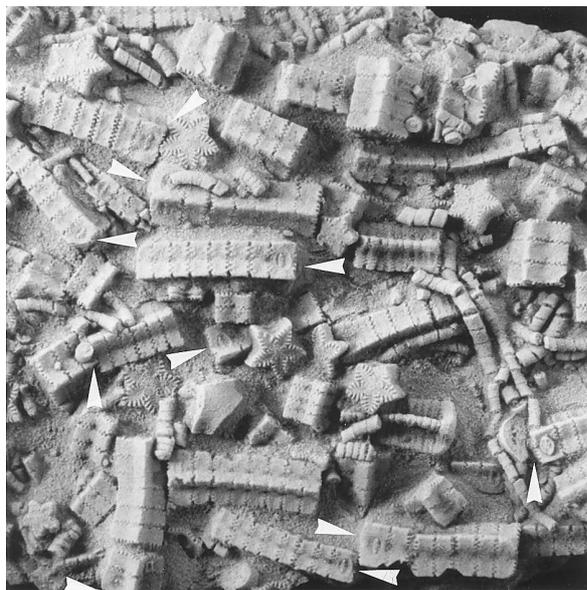


Fig. 188. Stem fragments of *Holocrinus* cf. *dubius* demonstrating that breakage and disintegration of the stem preferentially occurred between nodals and infranodals (arrows), although this articulation was symplectial. Lower Muschelkalk, Muschelkalksandstein; Ralingen-Kersch near Trier. (Muschelkalkmuseum, Ingelfingen; photograph H. Hagdorn.) $\times 2.7$.

THE MUSCHELKALK: A TRIASSIC CRINOID TREASURE-TROVE

The Germanic Muschelkalk provides the richest Triassic crinoid *Lagerstätten* with an excellent picture of crinoid diversification during Middle Triassic times after the end-Palaeozoic crisis. Unfortunately, such assemblages have still to be recovered from Lower and Upper Triassic strata. The famous Ladinian to Carnian St. Cassian Formation of the Dolomites (Italy) has yielded very diverse crinoid faunas. However, they consist mostly of disarticulated material that is far from being fully understood (Zardini 1976). One would hope that the Siberian or Chinese deposits will fill the Upper Triassic gaps of

the fossil record in the future. The literature on Triassic crinoids has been reviewed by Hagdorn (1995).

IMPORTANT COLLECTIONS IN GERMANY

Muschelkalk crinoids, especially crowns of *Encrinus liliiformis*, are kept in most natural history museums. The less common species and large slabs with *Encrinus liliiformis*, giving an impression of its taphonomy and palaeoecology, are concentrated in the following museums in Germany:

Museum für Naturkunde an der Humboldt-Universität zu Berlin. With the types and originals of many classic crinoid papers, for example, those of von Schlottheim, von Buch, Quenstedt 1835, Beyrich, Biese and Picard. Large *Chelocrinus carnalli* slab on exhibit.

Bundesanstalt für Geowissenschaften und Rohstoffe, Aussenstelle Berlin (formerly Preussisches Geologisches Landesmuseum and Zentrales Geologisches Institut der DDR). Largest collection of Upper Silesian crinoids, with originals and types of von Meyer, Wagner and Assmann. At present no exhibits.

Geologisch-Paläontologisches Institut und Museum der Universität Göttingen. Excellent collection of North German Lower and Upper Muschelkalk crinoids, containing originals of von Koenen. Large slab with *Encrinus liliiformis* on display.

Institut und Museum für Geologie und Paläontologie der Universität Tübingen. Excellent collection of Crailsheim *Encrinus liliiformis* specimens, including Quenstedt's figured specimens and a few types.

Werksmuseum Lauffen der Heidelberger Zementwerke AG, Lauffen am Neckar. Large slabs from Linck's Neckarwestheim excavations.

Muschelkalkmuseum Hagdorn Ingelfingen. Representative collection of crinoids from the whole Muschelkalk with many figured specimens. Exhibits of most taxa.