



# *Encrinus aculeatus* von Meyer, 1849 (Crinoidea, Encrinidae) from the Middle Triassic of Val Brembana (Alpi Orobie, Bergamo, Italy)

Hans Hagdorn<sup>1</sup> · Fabrizio Berra<sup>2</sup> · Andrea Tintori<sup>3</sup>

Received: 27 June 2018 / Accepted: 12 October 2018 / Published online: 1 November 2018  
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## Abstract

The Triassic crinoid *Encrinus aculeatus* is described from a single bedding plane of uncertain Pelsonian or early Illyrian or (less probable) late Ladinian origin from Val Brembana (Alpi Orobie, Bergamo, Italy) based on 36 more or less complete crowns and columns. The specimens represent an obrutational echinoderm lagerstätte of the Muschelkalk type. The individuals are semi-adult and juvenile; adult individuals are lacking. Morphological description and comparison with the holotype and additional material from the Lower Muschelkalk and basal Middle Muschelkalk of Upper Silesia (Poland) prove the assignment to *Encrinus aculeatus*. However, the species concept of genus *Encrinus* is critical because several characters are inconsistent. *E. aculeatus* occurs in the Middle Triassic (Bithynian to early Illyrian, ? early Ladinian) of the western Tethys shelf and Peritethys basins (Southern Alps, Balaton Upland, Germanic Basin). *Encrinus aculeatus* is regarded ancestral to the Upper Muschelkalk (latest Illyrian) *E. liliiformis*. Until now, *E. liliiformis* has not yet been proven with certainty from outside the Germanic Basin; references are based on isolated and undiagnostic material.

**Keywords** Benthic crinoids · Encrinida · Middle Triassic · Tethys · Muschelkalk · Italy · Alpi Orobie

## Abbreviations

BGR	Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin
GIUS	Geological Institute Silesian University Sosnowiec
MHI	Muschelkalkmuseum Hagdorn Ingelfingen
MPUM	Paleontological Museum—Dipartimento di Scienze della Terra ‘A. Desio’, UNIMI
NLH	Niedersächsisches Landesmuseum Hannover
SBG	Collection Bielert Göttingen

## Introduction

During Middle Triassic times, the crinoid family Encrinidae inhabited shallow marine areas of the entire Western Tethys and Peritethys realm. However, only a few complete encrinid cups and crowns determinable at genus or species level have hitherto been described from outside the Germanic Basin (Benecke 1868; Hildebrand and Pia 1929). Unlike the Germanic Muschelkalk with its well-studied echinoderm conservation lagerstätten that yielded a plethora of perfectly preserved articulated and complete specimens, Middle Triassic crinoid remains from the Alps are mostly confined to crinoidal limestones (encrinites) with accumulations of disarticulated material of low diagnostic significance. Hence, all Middle Triassic encrinid species and genera were established based on Muschelkalk specimens. Moreover, encrinid-like columnals mentioned in the stratigraphical and palaeoecological literature dealing with the Alpine Middle Triassic were generally assigned to the small-sized *Dadocrinus gracilis* or to *Encrinus liliiformis*. However, the latter species has not been proven with certainty from the Alpine Triassic.

An encrinid cup and isolated cup elements from the Anisian Recoaro Formation (Calcare a Brachiopodi) of Recoaro (Vicentinian Prealps, Italy) figured by Benecke

Editorial Handling: C. Klug.

✉ Hans Hagdorn  
encrinus@hagdorn-ingelfingen.de

<sup>1</sup> Muschelkalkmuseum Ingelfingen, Schloss-Straße 11, 74653 Ingelfingen, Germany

<sup>2</sup> Dipartimento di Scienze, della Terra ‘A. Desio’, Via Mangiagalli 34, 20133 Milano, Italy

<sup>3</sup> Triassica-Institute for Triassic Lagerstätten, Perledo, LC, Italy

(1868: pl. 4) were assigned to *Encrinus* sp. and *Encrinus carnalli* (now *Carnallicrinus*, Family Dadocrinidae); the latter cup (Benecke 1868: pl. 4, Fig. 1a–c) could also belong to *Encrinus robustus* Assmann 1926. Hildebrand and Pia (1929) emphasized the importance of two findings of articulated encrinid crowns from the Southern Alps: (1) a fragmentary specimen from the Anisian Braies (Prags) Formation of the Dolomites (South Tyrol, Italy) showing four arms from the first primibrachial almost to the tips was assigned with reservation to *Encrinus robustus* by Hildebrand (in Hildebrand and Pia 1929), (2) an almost complete but strongly weathered crown was collected by von Arthaber (1896) in the debris of an abandoned quarry below Cappella Rotonda in Giudicarie (Lombardy, Italy) derived from the topmost part of the Angolo Formation or basal Prezzo Limestone (Cimago Limestone Autorum, but see Gaetani 1969) (Anisian). This specimen was assigned by Hildebrand (in Hildebrand and Pia 1929) and Gasche (1938) to *Encrinus aculeatus* von Meyer, 1849. Types and additional material of both species figured and described by Assmann (1926, 1937) come from the Anisian Lower Muschelkalk (Upper Gogolin, Górażdze, and Karchowice formations) of Upper Silesia (SW Poland, formerly Oberschlesien, Germany). *Encrinus aculeatus* and *robustus* also occur in the Lower Muschelkalk (Jena Formation) of Germany (Wagner 1886, 1891, Emmert et al. 1972, Bielert and Bielert 2000). For a full list of references see Biese (1934). To date, no further diagnostic encrinid material has emerged from outside the Germanic Basin.

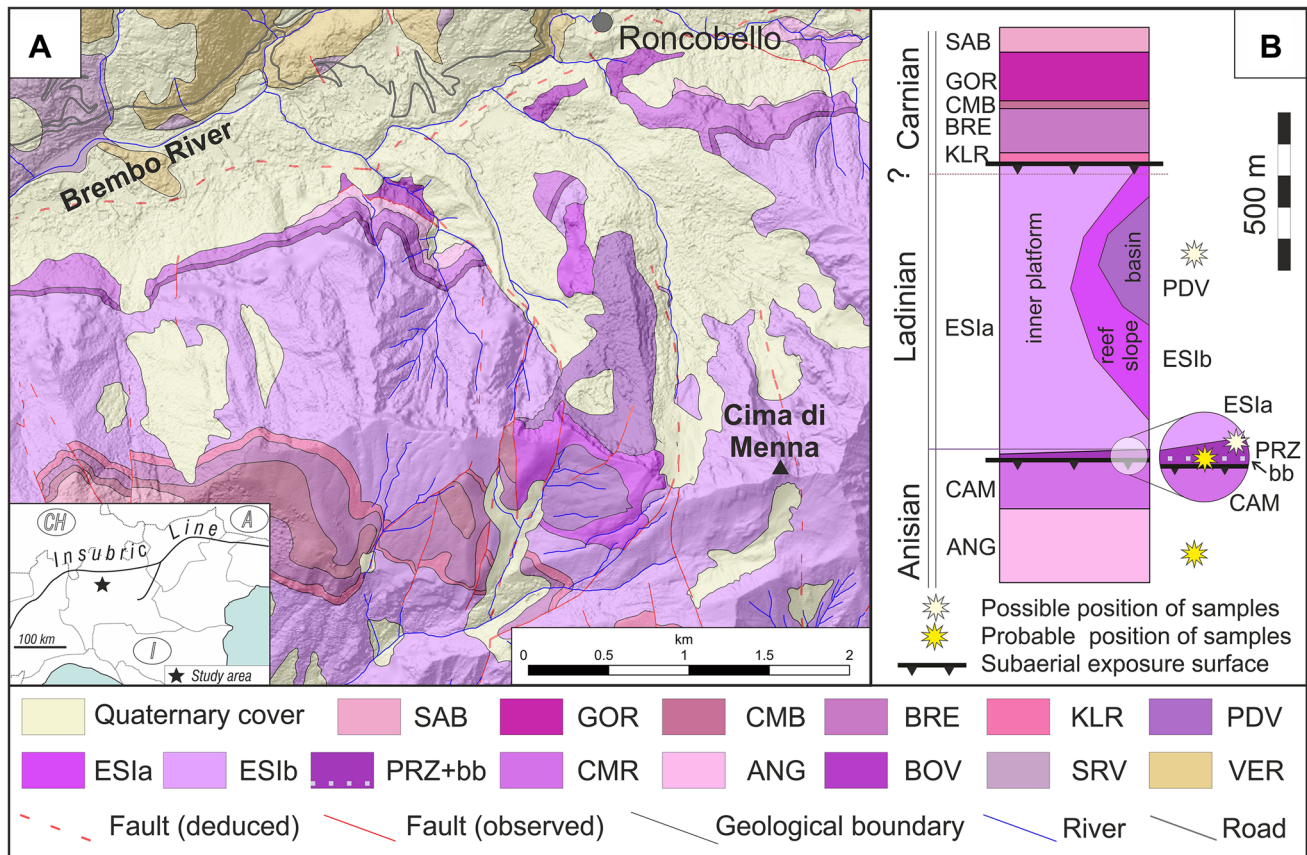
Hence, the encrinid material described below contributes to the knowledge of the Alpine Middle Triassic crinoid fauna. The specimens are compared to historical and new material from the type area in Poland and from Germany.

## Locality and stratigraphy

Two slabs with remains of altogether 36 crinoids were collected by unknown private collectors in Val Brembana (Alpi Orobie, Bergamo, Lombardy, Italy) at an elevation of approx. 2000 m from loose blocks. Formation and age are unidentified. In the study area, a succession spanning from the Anisian to late Ladinian crops out (Jadoul et al. 2012; Fig. 1). The succession records two successive carbonate platform systems. The lower one (early through middle Anisian in age) is characterized by peritidal dolostones of the Camorelli Limestone covering subtidal, burrowed bioclastic packstones and wackestones of the Angolo Limestone (Berra et al. 2005). The upper system is characterized by a high-relief, steep-sloped carbonate platform (Esino Limestone) prograding over basinal sediments consisting of ammonoid-bearing marly limestones

(Prezzo Limestone of Illyrian age), postdating the drowning of the underlying peritidal facies of the Camorelli Limestone after local subaerial exposure (Assereto and Casati 1965; Balini 1992). Dark fine-grained limestones are present in the upper part of the Esino Limestone, interpreted as deposits of intraplatform troughs (Wengen Formation and Perledo Varenna Limestone). The transition from the lower to the upper system is marked by a sharp surface (the top of the Camorelli Limestone) paraconformably covered by 5–10 m of bioclastic packstones within the Prezzo Limestone referred to as “Banco a Brachiopodi” (a brachiopod lumachelle, Gaetani et al. 1986). This unit consists of burrowed, poorly-bedded bioclastic packstones, floatstones, and wackestones characterized by the presence of abundant crinoid ossicles and locally brachiopods (Jadoul et al. 2012). This unit is characterized by the occurrence of the foraminifers *Pilammina densa* and *Palaeomiliolina judicariensis* (Gaetani et al. 1986). The age of the “Banco a Brachiopodi” is ascribed to the base of the Illyrian (*cimeganus* Zone, Monnet et al. 2008). The “Banco a Brachiopodi” can be traced all across the Lombardy Basin and represents an important marker bed that separates the two different carbonate systems of Anisian and Ladinian age, respectively. This unit is considered to register the drowning of the Anisian platform and reduced sedimentation (Berra et al. 2005, Jadoul et al. 2012) documented by abundant brachiopods and by intensive bioturbation in deposits rich in skeletal grains (mostly crinoid ossicles but also pelagic bivalves at the base; Jadoul et al. 2012).

Because the crinoid slabs have been collected from loose blocks in a poorly defined area, the attribution of the samples to a definite lithostratigraphic unit can rely only upon lithological comparison between the sample and the general characteristics of the units cropping out in this area. The studied sample consists of dark, fine-grained, bedded wackestone containing crinoid ossicles and rare thin-shelled bivalves. According to the facies association, the sample can be derived from four of the units described: (1) the Angolo Limestone, (2) “Banco a Brachiopodi”, (3) the Prezzo Limestone, (4) the Perledo Varenna Limestone. The Esino Limestone (massive light-coloured carbonates) and the Camorelli Limestone (grey peritidal stromatolitic dolostone with a typical fenestrate fabric) can be excluded because of major lithological differences. Considering the four units and the presence of crinoids in the sample, the Angolo Limestone or the “Banco a Brachiopodi” is the most probable source. Actually, the Prezzo Limestone can be excluded because of the presence of marls, the dominance of mudstone and the typical occurrence of white mica that is completely absent in the studied sample; furthermore, crinoids are rare in the Prezzo Limestone. The Perledo Varenna Limestone consists of well-bedded



**Fig. 1** Simplified geological map (from Jadoul et al. 2012) of the area of provenance of the samples (a) and schematic stratigraphic section of the Anisian–Carnian succession (b). VER Verrucano Lombardo, SRV Servino, BOV Carniola di Bovegno, ANG Angolo Limestone, CAM Camorelli Limestone, PRZ Prezzo Limestone (bb Banco a

Brachiopodi at the base), BUC Buchenstein Formation, PDV Perledo-Varenna Limestone, ESla Esino Limestone, inner platform facies, ESib Esino Limestone, reef and slope facies, LOZ Lozio Shale, BRE Breno Formation, CMB Calcare Metallifero Bergamasco, GOR Gorno Formation, SAB Val Sabbia Sandstone

limestone, and thus should be a possible source for the samples; however, crinoids are not so abundant. Crinoids are abundant in the Angolo Limestone and especially in the “Banco a Brachiopodi”. The Angolo Limestone is in general characterized by bioturbated mudstones with dispersed crinoids and foraminifera and by dark, thin-bedded to massive bioturbated limestones with thin marly layers. Upsection, the Angolo Limestone grades into peritidal dolostone of the Camorelli Formation. In the “Banco a Brachiopodi”, instead, crinoids are abundant, even if they are usually disarticulated. In general, the “Banco a Brachiopodi” is characterized by intensive bioturbation that typically produces a pseudonodular aspect. Although bedding is poor, it is possible to observe locally bedded intervals. Such bedded, transgressive facies with crinoids and pelagic bivalves are reported at the base of the “Banco a Brachiopodi” in the study area (Jadoul et al. 2012).

According to these considerations, the best candidate for the provenance of the studied slabs is the early Illyrian “Banco a Brachiopodi”. However, the bedded facies of the Pelsonian Angolo Limestone cannot be excluded.

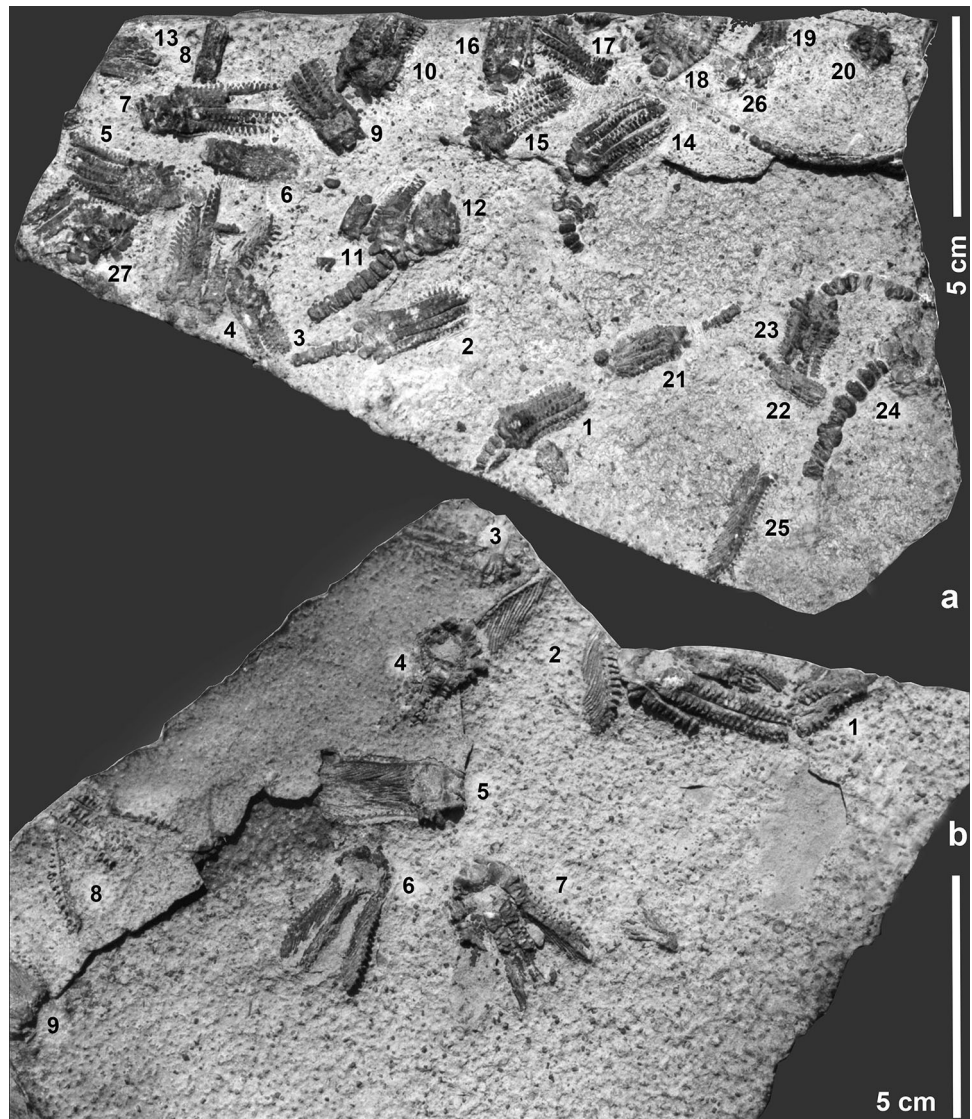
## Description

### Overview

The material comprises two slabs with altogether 36 more or less complete crowns, arms and column fragments. Slab 1 (MPUM 11758) measuring  $26 \times 16$  cm contains 27 specimens, some of them with remains of proximal columns (Fig. 2a). Slab 2 (collection M. Salmoiraghi, uncatalogued) measuring  $20 \times 17$  cm contains nine crowns and crown fragments (Fig. 2b); the original specimen was available for study; resin casts are kept in MPUM and MHI. Both slabs are derived from the same bed of a 5-cm-thick black micritic limestone which became dark grey after weathering. It was covered by a 2-mm-thick sheet of similar micritic limestone, which is still preserved along one margin of the slabs. The two layers are separated by an extremely thin joint. Due to pressure solution, the surface of the lower bedding plane is coarse and uneven. Pressure solution affected also the surface of the cover bed, however, at a minor extent. The crinoid crowns are in lateral



**Fig. 2** *Encrinurus aculeatus*, crowns, arms, column fragments, Val Brembana (Alpi Orobie, Italy). ? Angolo Limestone (Pelsonian), ? “Banco a Brachiopodi”, (early Illyrian). **a** MPIUM11758 (Slab 1). **b** Private collection M. Salmoiraghi (Slab 2)



position, most of them with their arms closed, and half embedded into the underlying lower limestone. Their upper sides are partly covered by the micritic sheet as far as it is still preserved. The most elevated parts of some of the crowns at the proximal arms remained in the cover sheet and were lost when the two layers were separated. However, by this splitting the pinnulation of some arms became visible. The crinoids are preserved in a dark blocky calcite. There was no attempt to additionally prepare them from the hard matrix. Assumably, the thin limestone sheet resulted from a smothering event lethal for the crinoids, which, however, preserved them as articulated skeletons. This is evidenced by two dominating directions of the long axes of the crinoid crowns following bottom currents. Some of the crowns are preserved with more or less long parts of their proximal columns attached. Presumably, more distal parts of the columns and possibly also the holdfasts were lost in

the cover sheet. Hence, the crinoids were embedded as complete articulated individuals, probably after being smothered by suspended mud which was subsequently deposited as cover sheet. Therefore, the two slabs represent a typical echinoderm obrutational conservation lagerstätte comparable to the well-known Muschelkalk echinoderm lagerstätten (Seilacher and Westphal 1971). The lack of adult specimens gives additional evidence for a sudden smothering event affecting a population of semi-adult and juvenile individuals. The lower sides of the limestone slabs were etched by hydrochloric acid and turned black and glossy. By this treatment, some weakly silicified crinoid sclerites appeared at the etched surface. However, the limestone is a mudstone with very sparsely distributed delicate crinoid remains.

Figure 2 shows slabs 1 and 2 in overview and the numbering of the individual specimens. Only complete

**Table 1** Measurements of specimens from Val Brembana

Slab/specimen	1/1	1/2	1/3	1/8	1/9	1/14	1/15	1/17	1/21	1/22	1/23	2/1	2/7
Overall length of crown	24.9	31.0	23.4	15.9	26.4	31.3	32.0	–	22.8	16.0	–	~ 41	~ 32
Diameter of cup	8.0	10.3	7.5	5.7	9.4	~ 11.3	10.6	–	8 (+)	~ 5.5	10.5	–	~ 11
Crown diameter at axillaries	12.4	14.5	~ 9	~ 7	–	~ 17.5	16.0	–	8 (+)	–	15.2	–	–
Arm length from mid of axillaries	21.4	24.7	–	–	19.9	~ 24.5	~ 24	~ 24	11.8	–	–	~ 30	~ 24.5
Arm width at mid arm length	1.8	2.0	2.0	~ 1.5	–	3.5	3.5	3.0	2.2	1.7	~ 3.5	4.0	~ 3.5
Maximum arm width	2.5	2.5	2.4	~ 1.5	3.4	4.7	4.0	3.7	–	1.7	4.2	4.0	–
Secundibrachial number in a row	17	20 (+)	14	–	~ 16	19 (+)	~ 19	17 (+)	–	–	–	23 (+)	15 (+)
Begin of biseriality at secundibrachial number	6	6	7	–	6	–	–	7	7	–	6	6	~ 6

crowns were measured (Table 1). These are specimens 1–3, 8, 9, 14, 15, 17, and 21–23 from slab 1, and specimens 1 and 2 from slab 2. Pluricolumnals 1/1 and 1/24 from slab 1 are analyzed in Table 2.

## Description of specimens

**General shape** The laterally embedded crowns are slightly constricted at the proximal part of the arms (Fig. 3). Juvenile crowns are almost cylindrical (specimens 1/8, 1/21; Fig. 4c). Generally, their articulated preservation does not allow observation of articular facets. In the proximal column, nodals and internodals are distinctly structured; some proximal nodals show cirrus scars. Distally, the columnals become indistinct barrel-shaped.

**Table 2** Analysis of two proximal columns of Val Brembana specimens

Column 1/1	Column 1/24
Base	Base
N1	?
1IN	N ? clrr (?)
N2 cirr	2IN (?)
2IN	1IN
1IN	N (?) cirr
2IN	1IN (?)
N3	2IN (?)
2IN	N
1IN	2IN
2IN	1IN
N4 cirr	N
1IN	?

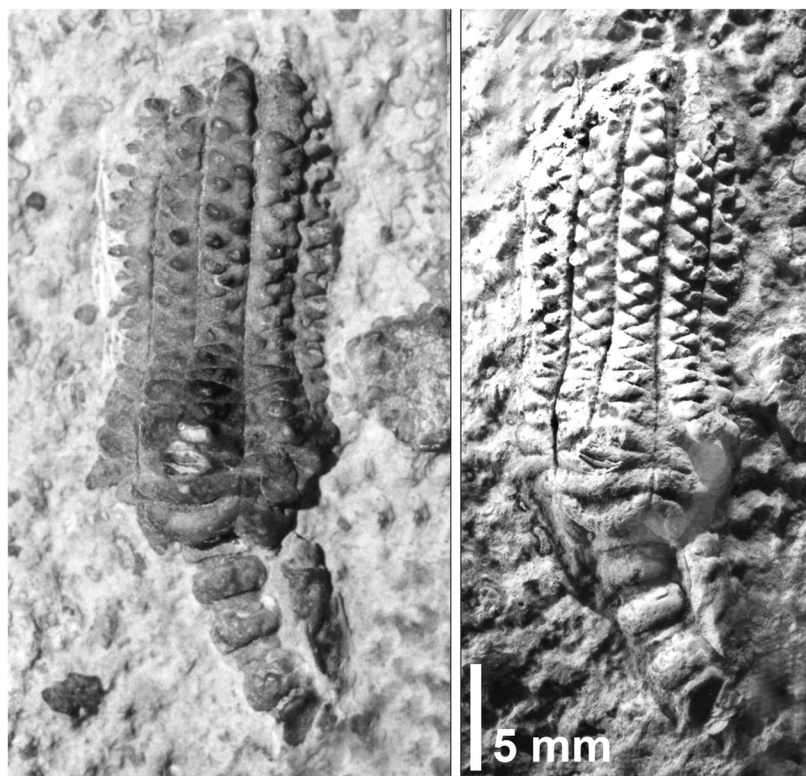
**Cup** Due to the preservation of all crowns in lateral position, no cup can be observed in dorsal view. The radials are dorsally extremely inflated; due to these sack-like dorsal extensions, the subhorizontal to horizontal basal circle remains invisible in side view. In specimen 1/2, the cup is dorsoventrally broken and shows the depressed position of the horizontal basal circle and the extent of the dorsal inflations of the radials (Fig. 4b).

**Basals** None of the specimens shows sutures or even clear outlines of the basals.

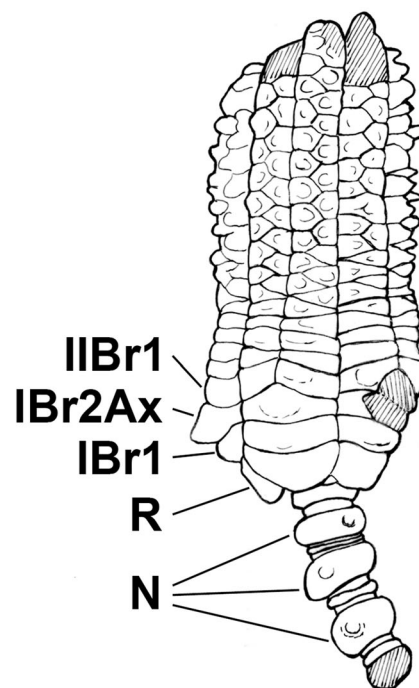
**Radials** In dorsal view, the radials are trapezoid with the sack-like extensions directed downwards. Interradial suture lines are deepened; interradian articulations are zygosynostial with a moderate depression and faint dorsal crenulation (specimen 1/9; Fig. 4b). The distal radial facets are directed upward, but not visible in any specimen. The suture line with the first primibrachial is medially slightly recessed.

**First primibrachial** In dorsal view, the first primibrachials are low rectangular with a medially extended proximal suture line (articulation with radial) and a recessed distal suture line. Articulation facets are not visible in any specimen. The sack-like dorsal extensions are directed outwards. A deep gap between the extensions of the radials and the first primibrachials allow outward tilting of the arms at the muscular radial facets (Fig. 5).

**Second primibrachial** At the axillary second primibrachials the arms are branching (Fig. 3). In dorsal view, axillaries are broad pentagonal with a medially extended proximal suture line, very short lateral and the two distal sutures meeting at an angle of 130°–140°. The articular facets are concealed. The dorsal side is strongly inflated



**Fig. 3** *Encrinurus aculeatus*, crown 1/1 with proximal column, Val Brembana (Alpi Orobie, Italy). Specimen in natural view, whitened with ammonium chloride, and in camera lucida sketch morphological



analysis; explanations: *R* radial, *IBr1* first primibrachial, *IBr2Ax* axillary second primibrachial, *IIBr1* first secundibrachial, *N* nodals with cirrus sockets

with extensions that may be elongated resembling a blunt spine.

**First secundibrachial** The dorsal side is rhombical with a central blade-shaped ornament along the transverse axis. A deep gap between the extensions of the axillaries allows outward tilting of the arm branches at the muscular axillary facets. Facets are concealed.

**Subsequent brachials** The subsequent proximal brachials are low and become distally increasingly wedge-shaped (Figs. 3, 4a). Their dorsal sides are ornamented with high blade-shaped extensions that run out towards the margins causing deep interbrachial indentations. Distally from secundibrachial 6 or 7, the brachials of either series do not reach the opposite margin of the arms anymore. From this point, the brachials are arranged in a manner with the interbrachial zigzag suture lines wide and forming angles of less than  $90^\circ$  (immature biseriality). Their dorsal ornaments are blade-like spines that may be directed obliquely outwards but do not reach the margins (Figs. 3, 4a, f, see also Fig. 7m). Thus, the straight dorsal sides of the arms have an angular marginal edge. Among juvenile crowns, arms remain uniserial with oblique interbrachial suture lines (Fig. 4b).

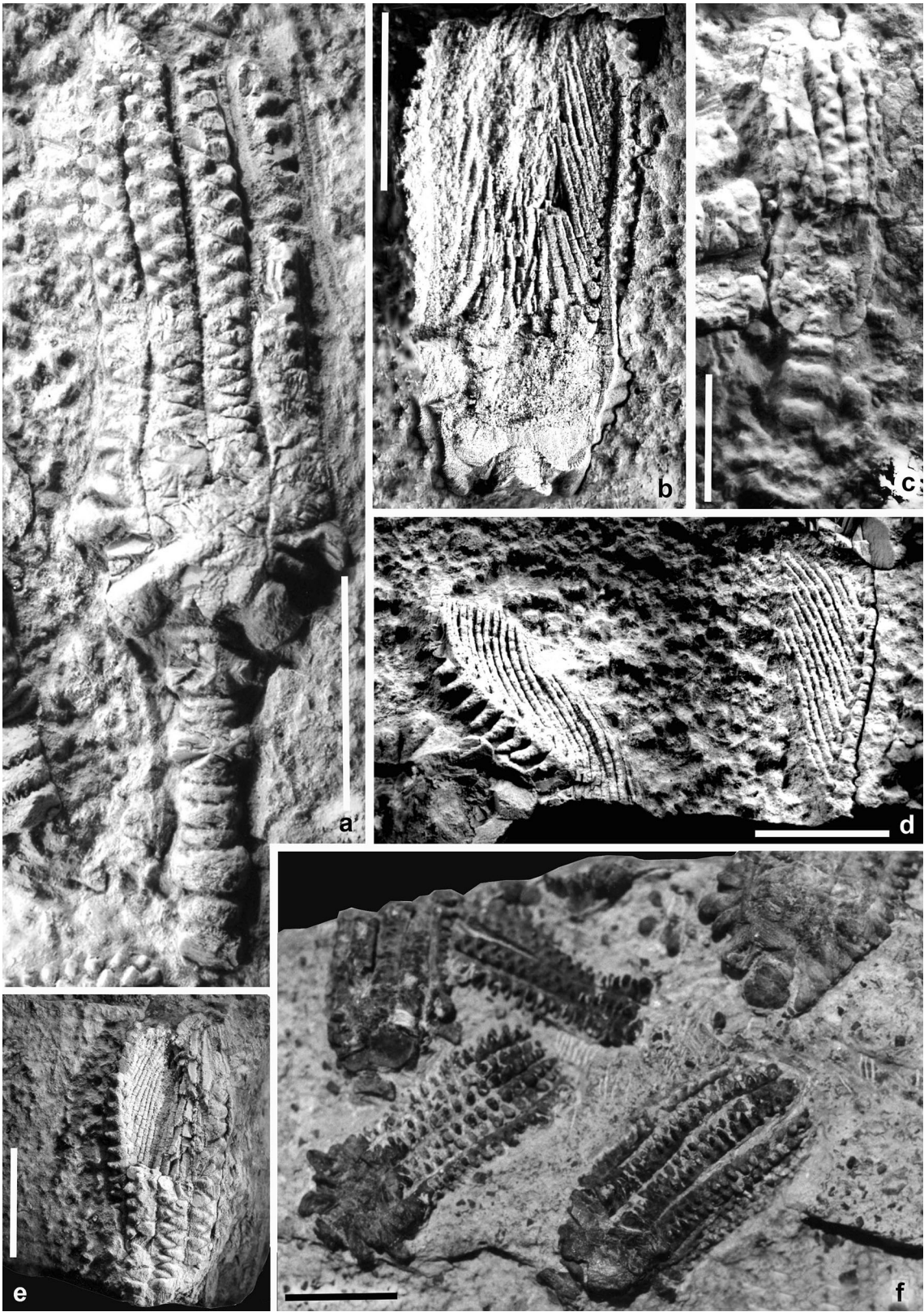
**Pinnules** The pinnules are directed upwards (Fig. 4b, d, e). They comprise ca. 14 pinnulars of which the first is

**Fig. 4** *Encrinurus aculeatus*, details from slabs 1 and 2, Val Brembana (Alpi Orobie, Italy). **a** Crown 1/2 with proximal column. **b** Crown 2/5 with lost upper half, showing depressed base, sharp edges of arms, and pinnulation. **c** Juvenile crown 1/8 of cylindrical shape, with proximal column, arms uniserial: Scale 5 mm. **d** Distal arms 2/2 showing brachial ornamentation in side view and pinnulation. **e** Medial and distal arms 2/9 showing pinnulation and faint pectinate ornamentation of pinnulars. **f** Details from slab 1 with crowns 14–18, in natural, unwhitened view. **a–e** Whitened with ammonium chloride. Scales 10 mm, unless otherwise indicated

shorter and thicker than the subsequent ones. Their sides are straight, and the interpinnular sutures are indistinct. Faint lateral pectinate ornamentation was observed in specimen 2/5.

**Column** As in the typical encrinid column, nodals and internodals are distinct in the proximal part; however, in column 1/24 the proximal internodals are as wide as the nodals which makes the differentiation arbitrary (Table 2). Usually, the nodals are much longer and wider than the internodals, and have a thickened rim with a rounded epifacet. In some proximal nodals, small and indistinct cirrus facets are observed. Cirri are not present in any specimen. Up to four series of internodals occur (Fig. 5a). A column fragment from the middle part, which may belong to crown 1/17, comprises 16 barrel-shaped





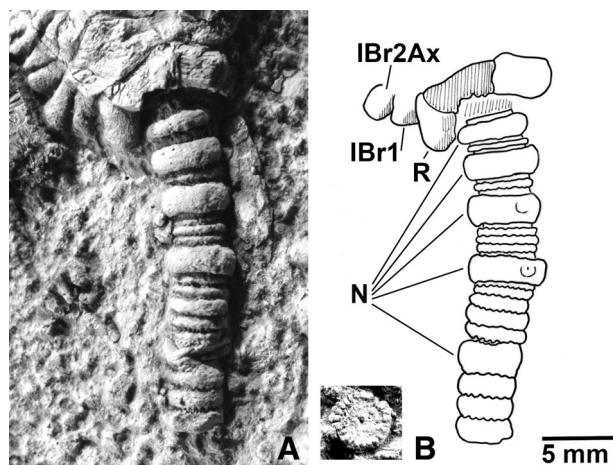


Fig. 5 *Encrinus aculeatus*, crown 1/11 with proximal column, Val Brembana (Alpi Orobie, Italy). **a** Specimen whitened with ammonium chloride, and in camera lucida sketch morphological analysis; explanations: *R* radial, *IBr1* first primibrachial, *IBr2Ax* axillary second primibrachial, *N* nodals, some with cirrus sockets. **b** Columnal showing multiradial articulation facet

columnals with slightly deepened, indistinctly crenulated suture lines (Fig. 2a). A proximal isolated columnal of 3.4 mm in diameter on slab 2 shows an articulate facet with ca. 20 very short multiradial crenellae (Fig. 5b). A 3.7-mm-wide distal columnal close to crown 1/21 has ca. eight short and coarse radial crenellae.

**Holdfast** There are no holdfasts preserved on either slab.

## Relations

With its ten arms, the Val Brembana crinoids clearly belong to the genus *Encrinus*. However, they differ in several characters from *Encrinus liliiformis*, the common and well-known Upper Muschelkalk (latest Illyrian) species. Additional species based on complete articulated and disarticulated specimens have been described from the Central European Muschelkalk of Germany and Poland, most of them from the late early Anisian through early late Anisian (Bithynian through early Illyrian) Lower Muschelkalk. Among these, the Val Brembana material shares most characters with *Encrinus aculeatus* von Meyer, 1849, a taxon established on an incomplete juvenile specimen from the “Sohlenstein” of the Friedrichsgrube (Fig. 6), a historical lead and zinc mine at Tarnowitz (Upper Silesia, now Tarnowskie Góry, Poland). Well-preserved crown and columnal specimens of juvenile and adult individuals from slightly younger sediments of the type region were assigned to *Encrinus aculeatus* by Assmann (1926); Figs. 7a–c, 8a). Specimens assigned to *Encrinus aculeatus* have also been described from the Lower



Fig. 6 *Encrinus aculeatus*. Original von Meyer, 1849 (holotype); BGR  $\times 6165$ . **a** After the lithography in von Meyer, 1849: pl. 32, Fig. 1. **b** Photography; total length 29 mm. **c** Original label in old hand (Hütteninspektor Mentzel ?): Kelchfragment von *Encrinites liliiformis* aus Muschelkalk Sohlenstein der Friedrichsgrube bei Tarnowitz in Oberschlesien. In later hand: *Encrinites aculeatus* Myr. **d** Later label: Geol. Landesmuseum Berlin [now BGR] *Encrinus aculeatus* H. v. Meyer. Orig. zu H. v. Meyer, Palaeont. Bd. 1. Taf. 32 Fig. 1. mul; 3. Wellenkalkhorizont. Friedrichsgrube bei Tarnowitz. leg. H. v. Meyer. Gr. A. 78 Nr. 34 Bl. Tarnowitz.  $\times 6165$ . The latter data refer to the Sheet Number of the Geological Map of Prussia. The collector of the specimen was Hütteninspektor Mentzel who provided most of the early 19th century fossils from the Upper Silesian Muschelkalk to the Geological Survey of Prussia



Muschelkalk Jena-Formation of Germany (see below, synonymy list; Fig. 8b–d).

However, it has to be emphasized that the species concept of *Encrinus* is critical because some characters are inconsistent. In the first line, this applies to shape and size of the dorsal ornamentations of cup and arm sclerites, but also to the erection angle of basals and to the presence or lack of cirri. Dynowski and Nebelsick (2011) demonstrated that arm length and brachial ornamentation of *Encrinus liliiformis* reflects ecophenotypic differences depending on water depth, water flow energy and predatory pressure, comparably to the Extant West Atlantic *Endoxocrinus parrae* (Oji 1996). Moreover, proximal nodals may or may not bear cirri. This has also been observed among populations of *Encrinus* sp. cf. *E. brahli* (Hagdorn and Schulz 1996) and *Chelocrinus schlotheimi* (Hagdorn (1982).

Anyway, the Val Brembana *Encrinus* shares most characters with *Encrinus aculeatus*. These are the subhorizontal to horizontal base, the long lasting uniserial brachial pattern, the immature biserial arrangement of brachials with wide low-angle interbrachial zigzag sutures, the extremely strong dorsal ornamentation of radials and brachials, and the presence of cirrus sockets in the proximal nodals. *Encrinus robustus* Assmann, 1926, which occurs together with *E. aculeatus*, has a higher bowl-shaped cup with long basals and long, less upright basals, unornamented radials and brachials, and proximal nodals devoid of cirri and indistinct epifacets (Bielert and Bielert 1995, 2000). Typical *Encrinus brahli* Overweg, 1850 have long, slender and poorly ornamented arms. However, the specimens described as *E. sp. cf. E. brahli* by Hagdorn and Schulz (1996) share characters with both typical *E. brahli* and *E. aculeatus*. Deeper water populations of *Encrinus liliiformis* from the Hassmersheim Member of the Upper Muschelkalk Trochitenkalk Formation may have strongly ornamented distal brachials; however, the arms of adult individuals are always advanced biserial with biseriality beginning no later than with secundibrachial 6 and the proximal brachials always devoid of ornaments. *Encrinus spinosus* Michael, 1883 that occurs with *E. aculeatus* in Upper Silesia has distal brachials with extremely elongated, hook-like spines (Fig. 7d). This character is regarded as ecophenotypic, comparable to the wide range of brachial ornamentations among the better-known *Encrinus liliiformis* (see above). For this reason, *E. spinosus* is here synonymized with *E. aculeatus*.

The proximal nodals of *Encrinus aculeatus* may have up to five cirrus scars or sockets (Fig. 8c–d). Because this character also occurs among *E. sp. cf. E. brahli* and *Chelocrinus schlotheimi*, isolated cirrinodals are not diagnostic of *E. aculeatus* with certainty. Only the strongly ornamented

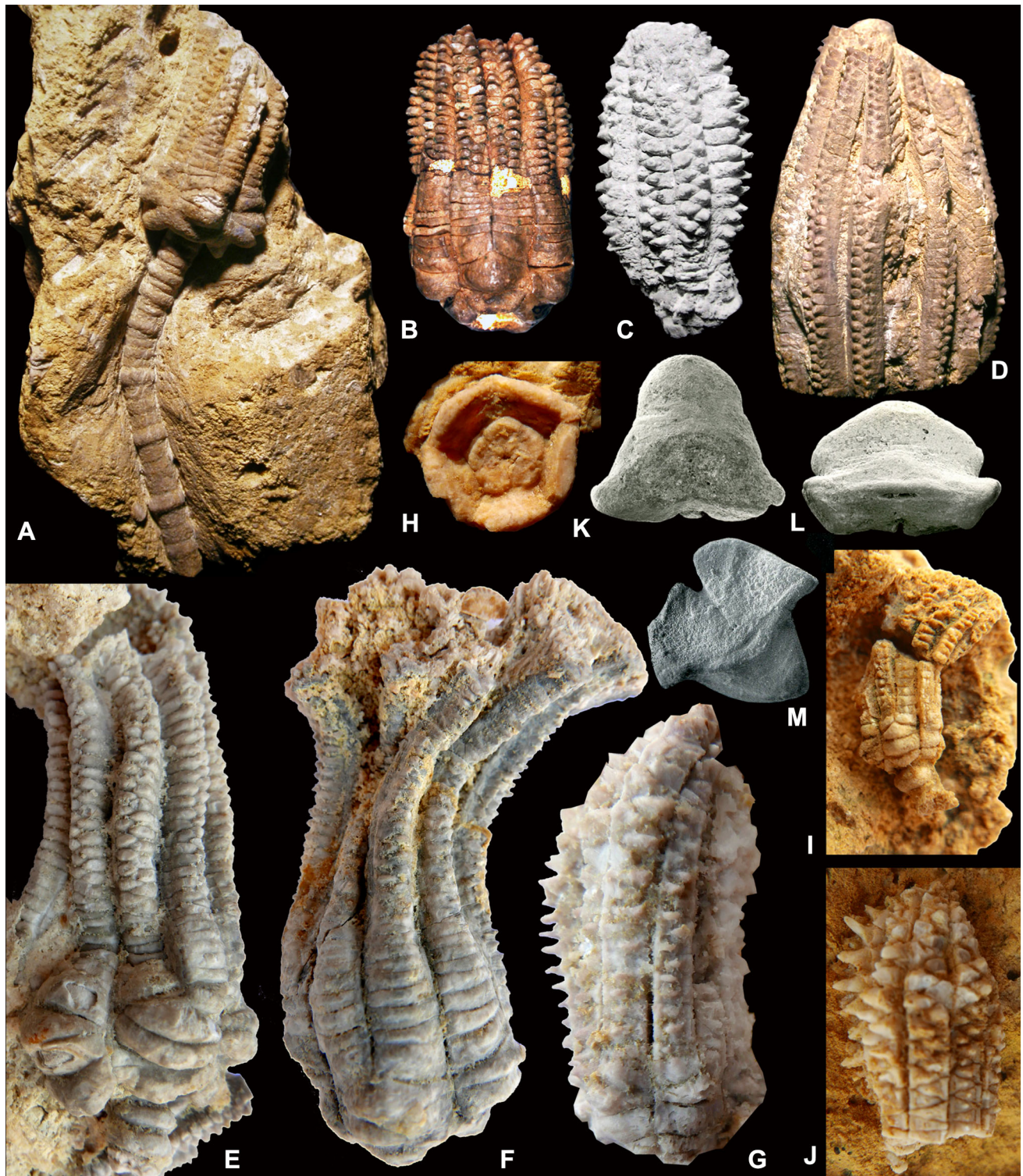
radials and primibrachials are likely to be assigned to *E. aculeatus* with more certainty. Under favourable circumstances, *Encrinus aculeatus* specimens have their original purplish pigmentation preserved (Fig. 8). The pigments have been analyzed by Wolkenstein et al. (2005) and were identified as hypericine and its diagenetically derived phenanthroperylenequinone pigments.

## Geographical and stratigraphical occurrence

Encrinid sclerites with strongly ornamented dorsal sides and cirrinodals occur also in Middle Triassic sediments of the western Tethys shelf: (1) primibrachials with sack-like dorsal ornaments from the Anisian (Pelsonian through early Illyrian) Dont to Perez formations of Pra della Vacca/Kühwiesenkopf (Braies/Prags Dolomites, South Tyrol, Italy), (2) proximal cirrinodals and strongly ornamented arm fragments from the early Ladinian (Fassanian, *Avisianum* Subzone) Väsölyi Formation, from Öskü (Veszprém Plateau, Hungary); uncatalogued material in MHI.

During middle to late Anisian times, Upper Silesia was closely connected to the western Tethys shelf via the open Silesian-Moravian Gate (Kozur 1974; Szulc 2000; Hagdorn 2018a). This is evidenced by a highly diverse flora and fauna including dasycladacean algae, hexactinellid sponges, hermatypic corals, echinoderms, brachiopods, and mollusks of Tethyan character that do not occur in the central parts of the Germanic Basin (Assmann 1937; Hagdorn 1985; Hagdorn and Głuchowski 1993). The Upper Silesian Lower Muschelkalk of the Opole Region is, therefore, regarded as a palaeobiogeographic extension of the Tethyan Realm.

The occurrence of *Encrinus aculeatus* within the Germanic Basin (Germany, Poland) is confined to the Anisian (Bithynian to early Illyrian) Lower Muschelkalk and the basal Middle Muschelkalk (Diplopora Dolomite) of Poland. If the isolated material from Öskü belongs to *E. aculeatus* and if the Val Brembana *Encrinus* would be of Ladinian age, its range would have to be expanded. As pointed out above, it clearly differs from *E. liliiformis*, but this taxon is more likely to be derived from *E. aculeatus* than from *E. robustus*. This is evidenced by *Encrinus aculeatus* individuals with characters close to *Encrinus liliiformis* (Fig. 7b). The salinar Middle Muschelkalk interval of approx. 1.1 Ma devoid of stenohaline faunal elements within the Germanic Basin obscures a continuous phylogenetic transition of *E. aculeatus* to *E. liliiformis*. However, *E. liliiformis* must have originated from an Illyrian *Encrinus* that survived in shallow water of the western Tethys Realm and immigrated into the Germanic





◀**Fig. 7** *Encrinus aculeatus* from Upper Silesia. **a–c** Originals Assmann (1926: pl. 8, Figs. 1–4), Karchowice Formation, Groß Stein (now Kamień Śląski, Polen); **a** semi-adult crown with proximal column, length of crown fragment 38 mm, BGR × 03270; **b** semi-adult crown, resembling *E. liliiformis*, length 43 mm, BGR × 03269; **c** distal fragment of adult crown with strongly ornamented brachials, length 47 mm, BGR × 03271. **d** Original of Michael (1893, fig. p. 500; holotype of *Encrinus spinosus*), Góraźdze Formation, Chorulla, length 61 mm, BGR × 6120. **e–g** Crowns from one limestone block, Karchowice Formation, Tarnów Opolski; **e** adult crown with proximal column, crown length 70 mm, MHI 1270/1a; **f** adult crown with beginning of biseriality at secundibrachial 9, crown length 72 mm, MHI 1270/2; **g** juvenile crown with spiny brachial ornamentation, crown length 24 mm, MHI 1270/1b. **h–j** Crown fragments, Karchowice Formation, Strzelce Opolskie; **h** cup with deeply impressed basal circle, infrabasals in column pit visible, radials with sack-like, dorsal extensions, width 7 mm, MHI 1268/2; **i** juvenile crown with proximal column, arms uniserial throughout, Crown length 15 mm, MHI 1268/1; **j** fragment of distal crown, arms immature biserial with long blade-like spines on distal brachials, length 23 mm, MHI 1268/3. **k–m** isolated sclerites from Middle Muschelkalk Diplopora Dolomite, Piekary Śląskie; **k** axillary primibrachial 2, proximal view with synostosomal facet and blade-like dorsal extension, width 5.4 mm., GIUS-7-21d; **l** primibrachial 1, proximal view, showing muscular facet with radial and extreme blade-like dorsal extension, width 5.3 mm, GIUS-7-21c; **m** proximal secundibrachial with muscular facet, blade-like extension on dorsal side, not reaching the margins, width 3.5 mm, GIUS-7-59/21b

Basin through the Western (Alemannic) Gate via the Swiss Alps (Hagdorn 1985; Hagdorn and Głuchowski 1993; Klug et al. 2005; Hagdorn 2018a). For an up to date correlation of Alpine Tethyan and Germanic Muschelkalk ammonoid biostratigraphy and lithostratigraphy see Hagdorn (Hagdorn 2018b).

## Systematic Palaeontology

Class Crinoidea Miller, 1821

Subclass Articulata Zittel, 1879

Order Encrinida Matsumoto, 1929.

Family Encrinidae Dujardin & Hupé, 1862.

Genus *Encrinus* Lamarck, 1801.

*Type species*: *E. liliiformis*, by subsequent designation ICZN, 1962 (plenary powers, Op. 636). = *Encrina* Bronn, 1848 (nom. nullum), = *Jenaicrinus* Jaekel, 1918: 67 (type *Encrinus* cf. *aculeatus* von Meyer, 1847 in Wagner 1886: 28, pl. 2, Fig. 15).

*Diagnosis* Cup low bowl-shaped, pentagonal to subcircular, base flat; basals partly concealed in columnar pit; interrachial articulations zygosynostosomal or synostosomal. Second primibrachial axillary; ten arms, proximally uniserial, biserial after secundibrachials four to ten; pinnular pectinate. Column moderate to very long, proximally weakly subpentagonal to cylindrical; proximal nodals

thickened, with or without cirri; distal columnar facets multiradiate. Holdfast discoid or irregularly encrusting.

*Encrinus aculeatus* von Meyer, 1849.

1847 *Encrinus aculeatus*; von Meyer, p. 576–577 [nomen nudum].

v 1849 *Encrinus aculeatus*; von Meyer, p. 262–265, pl. 32, Fig. 1.

1857 *Encrinus aculeatus*; Beyrich, p. 30, 38–39, pl. 1, Fig. 16.

1886 *Encrinus aculeatus*; Wagner, p. 26–28, pl. 2, Fig. 14.

1891 *Encrinus aculeatus*; Wagner, p. 890–898, pl. 44, Fig. 5.

v 1893 *Encrinus* sp. Michael, p. 500–502, Figs. 1, 2.

v 1894 *Encrinus spinosus*; Michael, p. 23.

1903 *Encrinus aculeatus*; Wysogorski, p. 37, 59–60, pl. 6, Figs. 3a, b.

v 1926 *Encrinus spinosus*; Assmann, p. 507–508, fig. p. 507, pl. 9, Fig. 11.

v 1926 *Encrinus aculeatus*; Assmann, p. 509–511, pl. 8, Figs. 1–4.

1929 *Encrinus aculeatus*; Hildebrand and Pia, p. 131, 134–136, 138, Fig. 1.

v 1937 *Encrinus spinosus*; Assmann, p. 17, pl. 4, Fig. 3.

v 1937 *Encrinus aculeatus*; Assmann, p. 17–18, pl. 4, Figs. 4–7.

1938 *Encrinus aculeatus*; Gasche, p. 89–96, pl. 4, Fig. 2.

v 1972 *Encrinus aculeatus*; Emmert, Horstig and Bayern, pl. 1, Fig. 1.

1986 *Encrinus aculeatus* + *brahli*; Głuchowski and Boczarowski, p. 193, pl. 1 figures 1–3.

1986 *Encrinus* + *Chelocrinus*; Głuchowski and Boczarowski, p. 193, pl. 1 Figs. 4–9.

v 1993 *Encrinus aculeatus*; Hagdorn and Głuchowski, p. 172, Fig. 10, 2–5.

1995 *Encrinus aculeatus*; Bielert and Bielert, p. 23–31, Figs. 3, 4.

v 1996 *Encrinus aculeatus*; Hagdorn, Głuchowski and Boczarowski, p. 52, pl. 1a–e.

v 1996 *Encrinidae* gen. et sp. indet.; Hagdorn, Głuchowski and Boczarowski, p. 55–57, pl. 2a–d.

2000 *Encrinus* sp. *aculeatus*; Bielert and Bielert, p. 138–140, pl. 1, Fig. 1.

? 2011 *Encrinus aculeatus*; Niedzwiedzki et al., p. 166–167, Fig. 3.

2014 *Encrinus* cf. *aculeatus*; Billert & Linde, p. 56–64, Fig. 4, 11, 14.

*Holotype by monotypy* The fragmentary juvenile crown from the Lower Muschelkalk uppermost Gogolin Formation (3. Wellenkalkhorizont) of Tarnowitz, Upper Silesia (now Tarnowskie Góry, Poland) mentioned by von Meyer (1847, p. 576–577) and described and figured by von





**Fig. 8** *Encrinurus aculeatus* with purplish colour pigmentation preserved. **a** Complete crown with proximal column, Upper Gogolin Formation, 3. Wellenkalkhorizont, Tarnowitz, Aurora Eisenförderung Mine, crown length ca. 60 mm, BGR × 13005 (ex coll. M. Grundey). **b** Complete crown, immature biseriality from secundibrachial 7–9, brachials with blade-like dorsal extensions, crown length 43.5 mm,

NLH 52044 (ex coll. O. Klages). **c–d** Crowns with long cirrals at proximal nodals, Jena Formation (Bereich Basiskonglomerate), Weißenborn (Lower Saxony, Germany), SBH uncatalogued; **c** polished section, **d** one arm regenerating, barrel-shaped cirrals (photos Dr. F. Bielert)

Meyer (1849: 262–265, pl. 32 Fig. 1): BGR × 6165 (Fig. 6).

**Diagnosis** Medium-sized *Encrinurus*; crown length up to 100 mm. Cup low bowl-shaped with subhorizontal or slightly convex base. Articulations of basals and radial synostosomal, radials dorsally strongly inflated. Arms of adultus biserial after secundibrachials six to seven. Proximal brachials dorsally strongly inflated, medial and distal brachials ornamented with spines or, rarely, with hooks. Column with strongly thickened proximal nodals which

may bear one to five short cirri; cirrus scars depressed or on protruding lateral extensions of nodals; cirrals barrel-shaped, with faint multiradiate articulations. Pigmentation purplish, if preserved.

**Range** Middle Triassic, middle to late Anisian (Pelsonian, early Illyrian), (?) early Ladinian (Fassanian).

**Occurrence** Lower Muschelkalk: Upper Gogolin, GóraŹdze and Karchowice formations, Upper Silesia, Poland; Jena-Formation, Germany. Middle Muschelkalk: Diplopora



Dolomite, Upper Silesia, Poland. Prags to Perez Formations, Dolomites, Italy; ? Angolo Limestone, ? “Banco a Brachiopodi”, Val Brembana, Orobic Alps, Bergamo, Italy; ? Vászolyi Formation, Veszprém Plateau, Hungary.

**Material Encrinus aculeatus:** two slabs with 36 more or less complete crowns, arm and column fragments from Val Brembana (MPIUM 11758; private collection M. Salmoiraghi); epoxy casts of slabs 1 and 2 MHI 2160/1, MHI 2160/2. Original von Meyer 1849: pl. 32, 1; holotype: BGR × 6165. Originals Assmann 1926: pl. 8, Figs. 1–3 (= Assmann 1937: pl. 4, Figs. 4–6); BGR × 03269; BGR × 03270; BGR 03271. *Encrinus spinosus* zu *E. aculeatus*: Original Michael 1893: Fig. p. 500; holotype: BGR x 6120). Complete crown from Tarnowitz, ex coll. Grundey: BGR x 13005. 3 complete crowns, Tarnów Opolski: MHI 1270/1a, 1270/1b, 1270/2. Juvenile crown with proximal column, Strzelce Opolskie: MHI 1268/1; cup: MHI 1268/2; distal crown fragment: MHI 1268/3. Originals Hagdorn, Gluchowski and Boczarowski 1996: pl. 1a, GIUS-7-21c (first primibrachial), pl. 1b, GIUS-7-21d (primaxillary), pl. 1d, GIUS 7-59-/21b (proximal secundibrachial). Countless isolated sclerites from different localities in Poland (Upper Gogolin, Górażdze and Karchowice Formation) and Germany (Jena Formation): MHI uncatalogued. 2 complete crowns, Jena-Formation, Königsutter am Elm: NLH 52044, NLH 50012/1. Originals of Bielert and Bielert 1995: figs. 3–4. Isolated sclerites from Prags to Perez formations, Dolomites, Italy and Vászolyi Formation, Veszprém Plateau, Hungary: MHI uncatalogued.

**Acknowledgements** This paper is dedicated to the memory of Dr. Dr. h.c. Hans Hess. Over many years, Hans has stimulated and fostered my (H.H.) work on Triassic echinoderms as a senior colleague and he became a paternal friend. It is a pleasure for me to gratefully contribute to this volume in commemoration of his extraordinary echinoderm work. Hans' high scientific professionalism as private paleontologist is admirable and outstanding. Our thanks go to M. Salmoiraghi (Castellanza, Varese, Italy) who donated slab 1 to MPUM and allowed to cast slab 2, after purchasing both slabs from the collector. Thanks are also due to Prof. Dr. Edward Gluchowski (Geological Institute Silesian University Sosnowiec), Drs. W. Lindert and A. Ehling (Bundesanstalt für Geowissenschaften und Rohstoffe, Dienstbereich Berlin), Dr. Annette Richter (Niedersächsisches Landesmuseum Hannover), for allowing to study specimens in their care. We also thank Drs. F. and U. Bielert (Nussloch, Abbesbüttel) for photographs of specimens. H.H. thanks the Paleontological Museum of the Università degli Studi di Milano, for donation of resin casts of the above described *Encrinus aculeatus* slabs to the Muschelkalk-museum. We would also like to thank the companies in Germany and Poland who allowed collecting of crinoid material in their quarries. Drs. Christian Klug, Zürich, and Ben Thuy, Luxembourg, are thanked for their careful reviews and valuable suggestions.

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