Palaeodiversity, palaeobiology and palaeoecology of Middle Devonian crinoids from the Eifel type region

Inaugural - Dissertation

zur

Erlangung des Doktorgrades

der Mathematisch-Naturwissenschaftlichen Fakultät

der Universität zu Köln

vorgelegt von

Jan Bohatý

aus Köln

Köln 2009

Berichterstatter:	Prof. Dr. Hans-Georg Herbig
	Prof. Dr. Ralph Thomas Becker
	PD Dr. Stefan Schröder

Tag der mündlichen Prüfung: 26.11.2009

Kurzfassung

Die vorliegende Dissertation befasst sich mit den Crinoiden des Mittel-Devons (U.-Eifelium bis U.-Givetium) der Eifeler Kalkmuldenzone (Linksrheinisches Schiefergebirge, Deutschland) sowie ergänzend mit mittel- und obergivetischen Crinoiden des Rechtsrheinischen Schiefergebirges. Untersucht wurden neu aufgesammelte Faunen und historische Kollektionen. Seit den klassischen Monographien des frühen 19. Jhdts. blieben die Eifelcrinoiden modern nahezu unbearbeitet. Sie werden in Standardwerken „*Treatise on Invertebrate Paleontology*" und „*Fossil Crinoids*" nur peripher berücksichtigt. Die Eifel ist ein globaler Paläodiversitäts-Hotspot mitteldevonischer Crinoiden. Aufgrund der hohen Diversität wird in dieser Arbeit von jeder der vier paläozoischen Unterklassen jeweils eine charakteristische „Mustergruppe" untersucht: 1. Die U.-Familie Cupressocrininae (U.-Klasse Cladida); 2. die Familie Hexacrinitidae (U.-Klasse Camerata); 3. die Gattung *Stylocrinus* (U.-Klasse Disparida); 4. die Gattung *Ammonicrinus* (U.-Klasse Flexibilia). Insgesamt werden vier Familien, acht Gattungen und 66 Arten taxonomisch behandelt. 10 Arten werden neu beschrieben. Durch die exzellente körperliche Erhaltung teilweise autochthon überlieferter Skelette sowie ihres ökologisch-faziellen Rahmens, wurden wertvolle Erkenntnisse über die Paläodiversität, Paläobiologie und Paläoökologie der Eifelcrinoiden gewonnen: Regenerationsprozesse bei Cupressocrinitiden und Hexacrinitiden entsprechen dem im Rezenten beschriebenen Muster. Aufgrund ihrer wichtigeren Funktion wurde die Regeneration verletzter Armen im Gegensatz zu Kelchen morphologisch perfektioniert. Die generelle Kleinwüchsigkeit der Regenerativarme wurde bei *Hexacrinites* durch eine höhere Anzahl der Pinnulae in Hinblick auf den Nahrungserwerb ausgeglichen. Prä- und postmortale Skelettmodifikationen können durch das Vorhandensein oder Fehlen einer stereomalen Reaktion differenziert werden. Bei Cupressocrinitiden müssen genetisch angelegte Anomalien von extern bedingten Verletzungen und weiteren Wachstumsveränderungen unterschieden werden. Die Funktionsmorphologie von *Ammonicrinus* legt nahe, dass der Nahrungsstrom über einen Pumpmechanismus, nämlich dem aktiven Versteifen und Entspannen des Stielligaments, erzeugt wurde. *Stylocrinus* konnte seine Arme lateral verzahnen, um eine geschlossene Armkrone zu stabilisieren und hydrodynamisch turbulentere Habitate zu besiedeln. *Hexacrinites* bildete in hydrodynamisch turbulenten Environments schräge Kelche aus. Phylogenetische Trends bei *Hexacrinites* und *Ammonicrinus* deuten auf eine von räuberischen Organismen (platyceratide Gastropoden) gesteuerte Evolution hin. Biogen verursachte Skelettanomalien auf Hexacrinitiden-Kelchen können auf platyceratide Gastropoden zurückgeführt werden. Epizoen-Inkrustationen von Bryozoen, Microconchiden, Korallen und Poriferen erfolgten überwiegend postmortal. Im Gegensatz hierzu wuchs die Bryozoengattung *Cyclopelta* zu Lebzeiten um Cupressocrinitiden-Stiele. Kelchmorphotypen bei *Stylocrinus* wurden von ökologischen und faziellen Rahmenbedingungen gesteuert. Die stratigraphische Verbreitung mancher Taxa, z.B. bei *Robustocrinites*, ist Event-gesteuert. Dies hatte Auswirkungen auf die Fluktuation der Paläodiversität. Für den rheno-ardennischen Raum zeigt sich, dass die an karbonatische Flachwasserhabitate adaptierten, mitteldevonischen Crinoiden der Eifelkalkmulden die morphologisch filigranen Crinoiden tieferer Meeresbereiche des O.-Pragiums bis U.-Eifeliums, z.B. des Hunsrückschiefers, ablösten. Mit der Etablierung biostromaler Bildungen in der Eifel dominierte diese Assoziation bei sukzessiver Zunahme der Diversität und Individuenanzahl. Noch im U.-Givetium brach die Paläodiversität vermutlich aufgrund des kontinuierlichen Meeresspiegelanstiegs drastisch ein („*Lower Givetian Crinoid Decline*"), obwohl sie außerhalb der Eifeler Kalkmuldenzone (Bergisches Land und Lahn-Dill Gebiet) bis in das O.-Givetium zu verfolgen ist. Im Frasnium setzte eine von der U.-Klasse Camerata dominierte Crinoiden-Vergesellschaftung ein. Diese *Melocrinites*-*Megaradialocrinus*-Assoziation kann im rheno-ardennischen Raum bis zur Grenze Frasnium/Famennium verfolgt werden und wird abrupt durch eine geringdiverse Amabilicrinitiden-Assoziation abgelöst. Diese zeichnet sich bereits durch einen karbonischen Faunencharakter aus und ist die Reaktion auf das Frasnium-Famennium-Event („*Frasnian-Famennian Crinoid Decline*").

Abstract

This doctoral thesis deals with crinoids from the Middle Devonian (U. Eifelian to L. Givetian) of the Eifel Synclines (western Rhenish Massif, Germany) and secondary with U. Eifelian to U. Givetian crinoids of the eastern Rhenish Massif. The study focuses on new recovered material and on material deposit in historical collections. Since the classic monographs of the early 19^{th} century, crinoids are nearly unstudied in modern view. They are only periphery mentioned within the standard works "*Treatise on Invertebrate Paleontology*" and "*Fossil Crinoids*". The Eifel has to be characterised as the global hotspot of Middle Devonian crinoids. Because of the high diversity, selected groups of each of the four occurring Palaeozoic subclasses are studied in the course of this work: 1. The subfamily Cupressocrininae (subclass Cladida); 2. the family Hexacrinitidae (subclass Camerata); 3. the genus *Stylocrinus* (subclass Disparida); 4. the genus *Ammonicrinus* (subclass Flexibilia). Altogether, four families, eight genera and 66 species are described taxonomically. 10 new species are erected newly. Based on the excellent three-dimensional preservation of the partly autochthon conserved skeletons and their ecological-/facial response, the Eifel crinoids gave important information about the palaeodiversity, palaeobiology and palaeoecology: Regeneration processes in cupressocrinitids and hexacrinitids correspond with that features defined for recent echinoderms. Because of their important functions, the regeneration of injured arms is more perfect than those of affected cups. *Hexacrinites* contra balanced the general smallness of the regenerative arms by an increased pinnulated surface. Pre- and postmortem skeletal modifications are distinguishable based on the presence or absence of a stereomatic response. In cupressocrinitids, obviously genetically modified anomalies must be separated from external caused skeletal modifications. The function morphology of *Ammonicrinus* indicates that the nutriment flow of several species was obviously enabled by an active ligament pumping mechanism of the stem *via* slowly stiffening and relaxing of their mutable connective tissues under ionic balance. The arms of *Stylocrinus* shows internally inclined edges adjoining laterally with adjacent brachials in an interlocking network to stabilise the closed arm crown and may allow settling in hydrodynamic turbulent environments. The cups of *Hexacrinites* show sloping morphologies in turbulent environments. *Hexacrinites* and *Ammonicrinus* show phylogenetic trends that obviously evince a predator driven evolution (e.g. platyceratid gastropods). Biogenous caused skeletal modifications in hexacrinitid-cups can be attributed to platyceratid gastropods. Epizoan encrusting of bryozoans, microconchids, corals and poriferas mostly occurred postmortem, while the bryozoan genus *Cyclopelta* premortem encrusted the stems of cupressocrinitids. *Stylocrinus*-morphotypes are controlled by the ecological and facial framework. The stratigraphic distribution of several taxa, e.g. of *Robustocrinites*, was controlled by regional-geological events. This have bearing on the fluctuation of the palaeodiversity: Within the Rheno-Ardennic Massif it can be shown that the Middle Devonian crinoids of the Eifel Synclines are linked to carbonatic shelf environments and displaced the crinoid associations of the U. Pragian to L. Eifelian, e.g. of the Hünsrückschiefer, which are adapted to deeper water habitats and show more filigree skeletal morphologies. With the establishment of biostromal developments, this association dominates up to the L. Givetian with successive increasing of the diversity and individual numbers. Within the L. Givetian, this palaeodiversity collapse presumably because of successive increasing of the sea level ("*Lower Givetian Crinoid Decline*"), although, outside the Eifel, this association can be traced up to the U. Givetian of the Bergisches Land and the Lahn-Dill region. With beginning of the Frasnian, a crinoid association, which is dominated by camerates, sets in and can be recognised within the Rheno-Ardennic Massif up to the Frasnian/Famennian boundary. This *Melocrinites-Megaradialocrinus* association was abruptly replaced by an extremely low diverse amabilicrinitid-dominated fauna, which already has a "Carboniferous character", and is the response of the Frasnian-Famennian Event ("*Frasnian-Famennian Crinoid Decline*").

Acknowledgements

First of all, I would like to thank my supervisor, PROF. DR. H.-G. HERBIG (University of Cologne), who introduced me to this exciting field in the geosciences and provided advice, support and motivation throughout the past two years. Likewise, my gratitude is extended to PD DR. S. SCHRÖDER (University of Cologne) for his continuous cooperativeness. The outcome of this thesis work, which was funded by the Deutsche Forschungsgemeinschaft (DFG, projects He 1610/16-1 and -2), benefited greatly from many fruitful discussions with both.

For the great encouragement, without which the outcome of an important part of this thesis would have been unthinkable, I would like to express my deepest gratitude to PROF. DR. W. I. AUSICH (Ohio State University) and PROF. DR. G. D. WEBSTER (Washington State University).

The same gratitude is expressed to DR. A. ERNST (Christian-Albrechts-University of Kiel), DR. R. HAUDE (Georg-August-University of Göttingen), DR. H. HESS (Museum of Natural History, Basel), PROF. DR. J. LE MENN (Université de Bretagne Occidentale), DR. G. C. MCINTOSH (Rochester Museum and Science Center), PROF. DR. R. J. PROKOP (National Museum, Prague) and PROF. DR. G. D. SEVASTOPULO (Trinity College, Dublin).

I would like to thank MR. H.-P. HEIN (Wermelskirchen), MR. U. HEIN (Solingen), MR. E. JANKE (Elsdorf), MR. R. LEUNISSEN (Wollersheim), MR. T. PAUL (Wuppertal), MR. H. PRESCHER (Kerpen-Horrem), PROF. DR. J. SCHREUER (Ruhr-University Bochum) and DR. A. THEISS (Nackenheim) for the recovery and the donation of the studied crinoids as well as for numerous important comments and their continuous encouragement.

DR. D. HEIDELBERGER and MR. F. GELLER-GRIMM (both Naturhistorische Landessammlung, Museum Wiesbaden), DR. F. J. COLLIER and MS. J. D. CUNDIFF (both Museum of Comparative Zoology, Harvard University) as well as DR. G. HEUMANN (Goldfuss-Museum, Bonn) and DR. C. NEUMANN (Museum of Natural History, Humboldt-University of Berlin) permitted access to the GOLDFUSS, JAEKEL, RÖMER, SANDBERGER, SCHULTZE and WANNER collections.

Additional gratitude is extended to MR. R. BÄUMLER, DIPL.-ING. H. CIESZYŃSKI, DR. M. GRIGO, MRS. CH. KRINGS, CAND. GEOL. D. LANGE (Düsseldorf) and DIPL.-GEOL. H. VOGEL (all University of Cologne) – furthermore, to MR. M. BASSE, MR. M. RICKER and DR. E. SCHINDLER (all Senckenberg Research Institute and Natural History Museum), DR. V. EBBIGHAUSEN (Odenthal), MS. CH. SCHMITZ (Cologne), MR. H. G. SCHOPPER (Solingen), DR. G. SCHWEIGERT (Museum of Natural History, Stuttgart) and DR. H.-M. WEBER (Bergisch Gladbach).

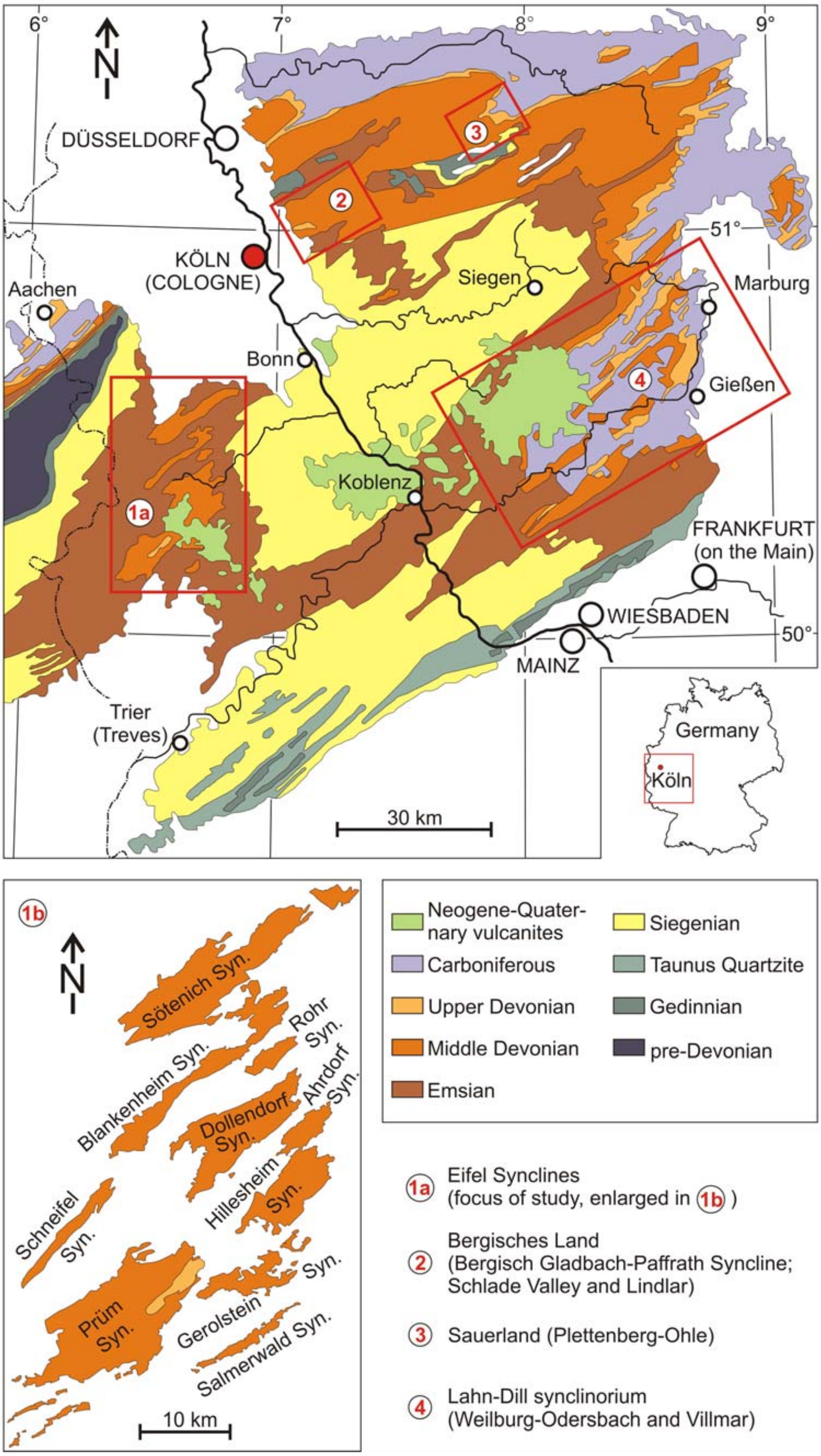
Not least, I am very thankful to my parents, to my mother I. G. R. BOHATÝ and my father PROF. DR. L. P. BOHATÝ (both Cologne), for introducing me to our recent and prehistoric nature and for inspiring my inquisitiveness in so many aspects.

Index of contents

1. INTRODUCTION

Crinoids (phylum Echinodermata) from the Middle Devonian of the western Rhenish Massif, in particular of the Eifel Synclines (North Rhine-Westphalia and Rhineland-Palatinate, western Germany), are studied. The crinoids were found in limy and marly sediments, including some clastic components that were deposited on the south-eastern shelf of the Old Red Continent (Fig. 1.1). The bulk of these crinoids came from the time slice between the base of the Eifelian (391.9 ± 3.4 Ma BP; KAUFMANN 2006) and the lowermost Lower Givetian (~ 388 Ma BP; adapted to KAUFMANN). For the purpose of faunal comparison, the taxa are compared to crinoid genera form the Eifelian to Upper Givetian (391.9 ± 3.4 to 383.7 ± 3.1 Ma BP; after KAUFMANN) of the eastern Rhenish Massif (Sauerland and Bergisches Land within North Rhine-Westphalia; Lahn-Dill Vicinity within Hesse, Germany). Selected taxa are discussed in their supraregional framework (Europe, N-Africa, Asia and Australia).

FIGURE 1.1—Palaeomap, showing likely continent and ocean location during the Middle Devonian (391.9 ± 3.4 to 383.7 ± 3.1 Ma BP; after KAUFMANN 2006), with Siberia, the Old Red Continent, Gondwana, the Panthalassa Ocean, the Rheic Ocean and the Proto- and Palaeotethys oceans. The approximate position of the Rheno-Ardennic Massif is marked by the red dot. Copyright by PROF. DR. RON BLAKEY, Northern Arizona University (permission granted to use in this study).



FUGURE 1.2—Geological overview of the Rhenish Massif (above), showing the studied areas (modified from KORN 2008, after WALTER 1995) and detailed view (below) of the Eifel Synclines (focus of study) [modified after STRUVE 1996a].

This study focuses on skeletal features, mainly observed in recently discovered crinoids from field campaigns within the Eifel Synclines between April 2007 and April 2009, and on specimens deposited in historical collections. These are: The *Forschungsinstitut und Naturmuseum Senckenberg* (Frankfurt on the Main), the *Naturhistorische Landessammlung, Museum Wiesbaden* (both Hesse, Germany), the *Institut für Geologie und Mineralogie der Universität zu Köln* (Cologne), the *Steinmann-Institut für Geologie, Mineralogie und Paläontologie der Rheinischen Friedrich-Wilhelms-Universität Bonn* (both North Rhine-Westphalia, Germany, the *Museum für Naturkunde der Humboldt-Universität zu Berlin* (city state of Berlin, Germany), the *Geowissenschaftliches Zentrum der Universität Göttingen* (Lower Saxony, Germany), the *Laboratoire de Paléontologie de Brest (Université de Bretagne Occidentale)* [Brest, France), the *Pracownia Palezoologiczna Muzeum Ziemi* (Warsaw, Poland), the *Museum of Comparative Zoology (Agassiz-Museum), Harvard University* (Cambridge, Massachusetts), the *National Museum of Natural History (Smithsonian Institution)* [Washington D.C., both U.S.A.), the *Nanjing Institute of Geology and Palaeontology, Academia Sinica* (Nanjing, China) and the *Queensland Museum* (Queensland, Australia). Furthermore, valuable private collections, recovered between 1980-2009, were intensively studied and designated type material was deposited in museum collections.

The fossils embedded in lime rocks or marls were mechanically dissected using preparatory needles, micro sand-streaming methods, as well as fine pneumatic probes. Anionic detergents (e.g. "*Rewoquad*"), caustic soda (NaOH) and acids (e.g. hydrochloric acid, HCL) were used for chemical preparation. Samples from weathered layers were washed over a 63-µm net. The residue >63 µm was analysed. Cleaned samples were studied *via* binocular- and scanning electron microscope analyses (SEM). Photographs of NH_4Cl-whitened crinoids were arranged using digital image editing software.

The Middle Devonian crinoids of the Eifel Synclines constitute one of the most classic Devonian faunas. By erecting numerous species, they were described in the famous monographs of the early-late 19th century (GOLDFUSS 1826-44; 1839; JAEKEL 1895; MÜLLER 1855; RÖMER 1844; SCHULTZE 1866 and STEININGER 1848). A modern scientific revision utilising advanced taxonomic and stratigraphic concepts was lacking. In addition, the description of taxa characterised as identical is under compulsive regress of the *International Code of Zoological Nomenclature* (ICZN) and afflicted with increasing uncertainties. Therefore, historical collections are revised based on investigation and comprehension of unpublished new faunas and new fossil excavation campaigns. Spectacularly preserved individuals are recognised within these new collections, which underlines the important position of the Eifel as one of the world's most famous localities for Middle Devonian crinoids. Following a taxonomical revision, modern geobiological and palaeobiological studies are possible. They focus on diversity- and faunal-changes ("local extinctions") within sedimentological sequences, related to lateral and vertical facies-changes, as well as events. In combination with facies-analyses, functionmorphological analyses of the highly specialised echinoderm skeletons allow aut- and synecological interpretations (e.g. substrate- and hydrodynamic dependency, sedimentological rate and trophic level). In contrast to the crinoids of the Ordovician-Silurian and of the Carboniferous, these analyses were lacking for the Middle Devonian crinoids of the Eifel.

Within the Middle Devonian carbonate shallow shelf-environments were the habitats of a highly diverse echinoderm association. Amongst these, crinoids are of special interest, because in the Palaeozoic their skeletons were variously adapted to the hydrodynamic conditions (MEYER et al. 2002; BOHATÝ 2005a; 2006a), to the substrate (e.g. SEILACHER & MACCLINTOCK 2005) and to the trophic level (e.g. AUSICH 1980; MANNIFIELD & SEVASTOPULO 1998). Numerous groups of the sessile and vagile benthos, especially stromatoporoids, rugose and tabulate corals, brachiopods, bryozoans and trilobites are associated with the crinoids.

The composition of the mesodermal echinoderm-skeleton is characterised by isolated ossicles, which are united by organic material. Postmorten disarticulation resulted in a poor preservation record and, accordingly, in a poor status of documentation compared to some other invertebrate-groups. In many cases, rich crinoid associations are only known from "fossil-Lagerstätten regions". Focussing on crinoids, beyond or outside the Eifel the following regions have to be stressed in the Middle Devonian (Eifelian-Givetian): Bohemia (PROKOP 1987), the Polish Holy Cross Mountains (GŁUCHOWSKI 1993), the Kuznez Basin (DUBATOLOVA 1964), Sibiria (DUBATOLOVA & YELTYSHEVA 1967), the western Yunnan Province of China (CHEN & YAO 1993; also see WEBSTER et al. in press), the Nothern Shan States of Burma (REED 1908) as well as Queensland (E-Australia) [JELL et al. 1988] and the State of New York (U.S.A.) [GOLDRING 1923]. Slightly older is the rich- but particularly endemic crinoid-fauna of the Upper Emsian La Vid Formation of the Kantabrian Mountains of N-Spain (BREIMER 1962).

Based on the famous monographs of the 19th century (see above), the Eifel was one of the world's most classical regions where the research of fossil crinoids began. SCHULTZE (1866) first summarised the state of knowledge of these isolated earlier works. The taxa were systematised according to the former knowledge, without integrating them into the stratigraphic or facial framework. Shorter publications of KRAUSE (1927), WANNER (1942), SIEVERTS (1934), SIEVERTS-DORECK (1950; 1953; 1957; 1963), PRICK (1983) and HAUDE (2007) expanded that knowledge only slightly. The necessity of the herein presented study can furthermore be explained because the discovery of Middle Devonian crinoids focused on other parts of the world after publication of the classic monographs. Therefore, from a modern viewpoint, the crinoids from the Eifel have to be revised incorporating the views of modern palaeontology. This is particularly emphasised by the periphery mentions of the crinoids from the Eifel within the standard works *Treatise on Invertebrate Paleontology* (MOORE & TEICHERT 1978) and *Fossil Crinoids* (HESS et al. 1999). The herein presented work should contribute to this by interpreting and revising these marine invertebrates.

Devonian taxa described in the 19th century constitute the foundation of all later studies, however, later taxonomic revisions, integration of taxa within the modern staratigraphic and facial framework of the Eifel Middle Devonian, and phylogenetic analyses are missing.

More recently, privately published monographs of HAUSER (e.g. 1997; 2001) as well as single works of the author (see ‹http://www.devon-crinoiden.de›) are not comprehensive in scientific content, as exemplified by BOHATÝ (2005a-b; 2006a-c) and BOHATÝ & HERBIG (2007). Unfortunately, this also includes the voluminous plates in which numerous previously only lithographed taxa were photographed for the first time.

Because of the deficient knowledge of the Middle Devonian crinoids from the Eifel, the region is, therefore, out of the focus of modern crinoid studies. Because of the binding concepts of priority and types (ICZN), this has consequences of passing down taxonomic errors of recognised or unrecognised Eifel-taxa into other regions which may be of significance for recognition of new taxa. As a consequence, e.g. the stratigraphic distributions and biostratigraphic applications of the taxa, gradients of the palaeodiversity in time and space as well as palaeogeographical relations and further derivative conclusions, such as sea level- and climate-changes, are still blurred. At this point, SCHRÖDER (e.g. 1995; 1997; 2001) has to be mentioned, exemplifying the taxonomic usefulness of taxonomic reappraisals. Based on the former "well known" described rugose corals, he pointed out several previously unidentified palaeogeographical relations to Morocco and N-America, expressed in faunal-migrations during high sea-levels.

The state of the art of the knowledge about the invertebrates of the Middle Devonian Eifel Synclines is extremely heterogeneous. Only several key works that contribute to the Eifel palaeontological data base can be mentioned within the frame of this introduction. The brachiopods were intensively studied by STRUVE; a bibliography of the numerous publications is given in WEDDIGE & ZIEGLER (2000), and a compilation of the stratigraphic results in STRUVE (1996b). The rugose corals were revised by LÜTTE (e.g. 1984; 1987; 1990), COEN-AUBERT & LÜTTE (1990), SCHRÖDER (e.g. 1995; 1997; 2001) as well as SCHRÖDER & SALERNO (2001). Concerning tabulate corals, especially BYRA (1983) and BRÜHL (1999) have to be mentioned. The stratigraphic distribution of trilobites is based on several preliminary works of RICHTER & RICHTER and STRUVE, summarised in STRUVE (1996c). Recently, BASSE (2002; 2003; 2006) and BASSE & MÜLLER (2004) restudied the trilobites from the Eifel monographically. The bryozoans, also nearly undescribed until recently, are now in the focus of modern science (ERNST 2008; ERNST & SCHRÖDER 2007; ERNST & BOHATÝ, in press).

The knowledge about the Devonian of the Eifel is recorded in an unmanageable number of palaeontological, stratigraphical and regional geological publications. Regarding stratigraphy and regional geology, the monograph of MEYER (1986) is the indispensable standard work; several important regional studies are also given in HEESEMANN & DAHM (1965). In the following, only a short summary of the most background important of the facies and lithostratigraphy is given.

The carbonate Middle Devonian of the Eifel is only preserved within the “Eifel Limestone Synclinorium” (Fig. 1.3) because it can be interpret as N-S trending axial depression of the Rheno-Ardennic Massif. A palaeogeographic-facial interpretation is difficult to make based on the relic preservation. In general, the sedimentary input occurred from northern directions, respectively from the Old Red Continent (Fig. 1.1). The input accumulated from the Lower to the Upper Devonian with a retreating coastline toward the north. STRUVE (1961; 1963) proposed the first palaeogeographic reconstruction of the Eifel Middle Devonian and considered the depositional region as an isolated N-S trending basin surrounded by landmasses, which he denoted as “Eifel Sea Street”. WINTER (in MEYER et al. 1977, p. 327; also see MEYER 1986, fig. 37) and FABER (1980) modified the actual palaeogeographic view (compare to MEYER 1986); in particular, the isolated palaeogeographic position of the depositional basin as well as the accentuation of distinctively developed boundaries in the form of barriers and islands is reinterpreted differently.

WINTER (in MEYER et al. 1977) defined three characteristic facies realms (facies types A-C; compare to Fig. 1.3 of this work), which are of considerable importance for the faunal-distribution and -associations.

Facies type A, distinguished by clastic sediments, is developed within the northern Eifel Limestone Synclinorium. Carbonates are proportionally rare. In the northern part of the synclinorium, the sediments were not deposited under normal marine conditions. Normal marine conditions occurred toward the south. Southwards, the changeover to facies type C occurred. Type C is characterised by limestones and marls. Clastic components are sparse. Toward the south, the clay content increases, and type C facies passes into the clay-rich facies of the Moselle Trough (= "Wissenbach Slate"). The third facies type (type B) is developed within the eastern part of the Eifel Limestone Synclinorium. It is characterised by pure, commonly biostromal limestones; marly as well as silty sediments are secondary. This facies characterise a shallow water realm and was positioned close to a shallow-marine barrier at the NE-Eifel ("Mid-Eifelian High" sensu WINTER in MEYER et al. 1977). For the Lower Eifelian, FABER (1980, p. 1122) characterised this shallow-marine realm as a two-phase carbonate platform, which was temporarily interrupted during regressive conditions. Toward the west, he interpreted a relatively undifferentiated open shelf, which is characterised by SW-NE trending facies belts.

This basic division of the facies types A-C applies at least to the Upper Eifelian (Junkerberg Formation; see Tab. 1.1), but because of transgressive or regressive phases within some time slices, it was modified by a lateral facies displacement or even termination of the facies boundaries. In the Upper Eifelian, with the beginning of the Freilingen Formation (Tab. 1.1), the facies differences become indistinct; facies type C was established all over the depositional area. In the Givetian, stromatoporoid coral biostromes extended all over the Eifel Sea. Accordingly, KREBS (1974) characterised the whole Eifel as a shelf lagoon, harboured by a southern barrier.

PAPROTH & STRUVE (1982, fig. 4) distinguished between N-, W- and S-Eifel faunas based on faunal criteria; the *ostiolata*-Facies includes the W-Eifel and part of the S-Eifel fauna. The justifications of these faunal regions were based on a long ranging thrust fault. The fauna of the N-Eifel correlates with facies Type A; the collectivity of the W- and S-Eifel faunas is coeval with Facies types B-C, which is best approximated with the boundary of the *ostiolata*-Facies.

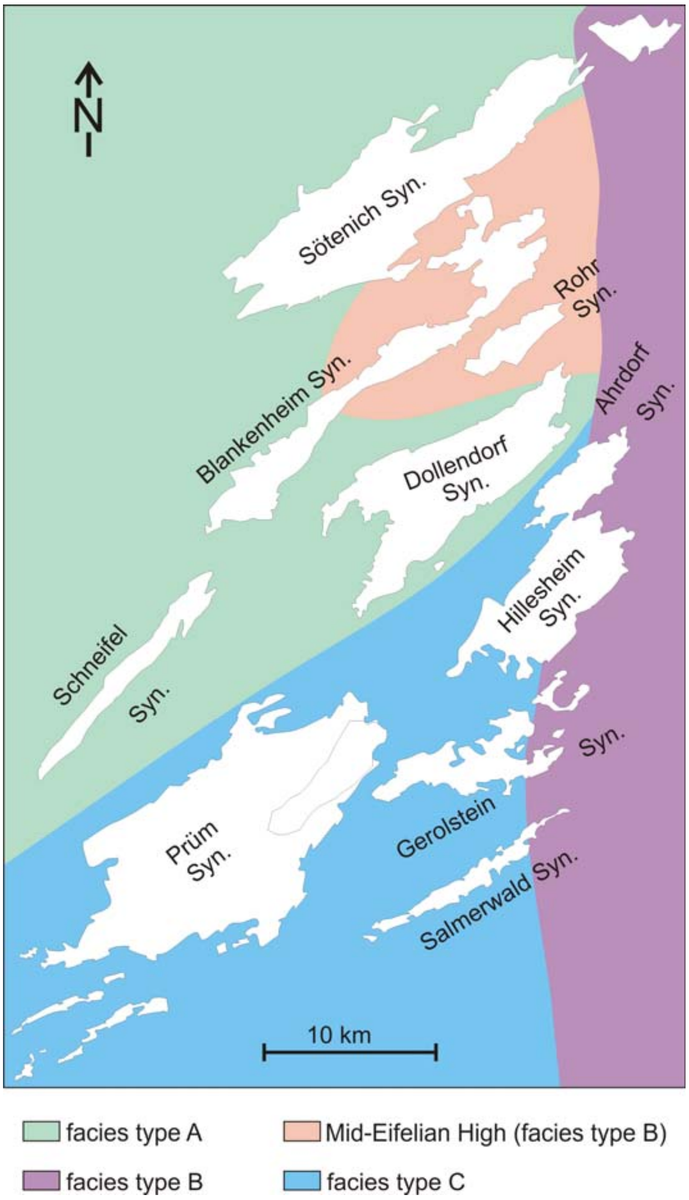


Figure 1.3—Idealised facies model of the Middle Devonian of the Eifel (modified from Winter in Meyer et al. 1977). ***Facies type A***, facies dominated by clastic input; ***Facies type B***, facies characterised by carbonate platforms and biostromal reefs (including the Mid-Eifelian High); ***Facies type C***, reduced clastic input and increasing limy facies.

The most classic fossil localities of Gerolstein, Gees, Niederehe or Büdesheim are situated within the fossil-rich deposits of the Middle Devonian facies Type C of the middle and southern part of the Eifel. Consequently, the deposits within the Hillesheim Syncline were chosen as "Type Eifelian", a reference-profile for all synclines, by Struve

(1982a). Then this lithostratigraphic standard division (HOTZ et al. 1955) had to be correlated with the other synclines – but in the face of numerous bio- and litho-facial differences, this is nearly an unsolvable challenge that blocks further studies concerning this matter, especially within the northern and southernmost Eifel. The erection of regional valid members reflects the complexity of the depositional realm, but leads to a bemusing number of in part uncorrelated formations, subformations and members sensu STRUVE (1961; 1992) not sensu STEININGER & PILLER (1999) [*sic*!; compare to BOHATÝ 2005b, p. 388]. Therefore, e.g. STRUVE tried to correlate the Middle Devonian sequences by using the biostratigraphical value of brachiopods (see compendium in STRUVE 1996d). A summary of the valid lithostratigraphic units is given in STRUVE (1996b).

U-Pb ID-TIMS ages	**Series**	**Stage**	**Formation**	**Subformation**	**Member**	**Conodont Zones**
383.7 ± 3.1 Ma BP	U. Devonian	Frasneian	Wallersheim Fm.			
	Middle Devonian	Givetian	Bolsdorf Fm.			*varcus*
			Kerpen Fm.		Roßberg Mb.	*hemiansatus*
					Bellerophon-Kalk Mb.	
			Rodert Fm.		Korallen-Brachiopoden-Kalk Mb.	
					Stringoc.-Korallen-Kalk Mb.	
					quadr.-ramosa-Kalk Mb.	
					caiqua-Kalk Mb.	
			Dreimühlen Fm.		Galgenberg Mb.	
					Ley Mb.	
					Binz Mb.	
			Cürten Fm.		Meerbüsch Mb.	
					Forstberg Mb.	
					Marmorwand Mb.	
					Felschbach Mb.	
			Loogh-Fm.		Rech Mb.	
					Wotan Mb.	
			Ahbach Fm.	Müllert Sub. Fm.	Zerberus Mb.	
					Olifant Mb.	
388.1 ± 2.6 Ma BP		Eifelian		Maiweiler Sub. Fm.	Lahr Mb.	*kockelianus* and *ensensis*
					Hallert Mb.	
			Freilingen Fm.		Bohnert Mb.	
					Eilenberg Mb.	
			Junkerberg Fm.	Grauberg Sub. Fm.	Giesdorf Mb.	
					Nims Mb.	*kockelianus*
				Heinzelt Sub. Fm.	Rechert Mb.	
					Hönselberg Mb.	
					Mussel Mb.	
					Klausbach Mb.	
			Ahrdorf Fm.	Niederehe Sub. Fm.		*australis*
				Betterberg Sub. Fm.	Wasen Mb.	
					Flesten Mb.	
					Köll Mb.	
					Bildstock Mb.	
			Nohn Fm.	Stroheich Sub. Fm.	Hundsdell Mb.	*costatus*
					Dankerath Mb.	
				Zilsdorf Sub. Fm.	Ahütte Mb.	
					Kirberg Mb.	
			Lauch Fm.		Dorsel Mb.	*paritus*
					Wolfenbach Mb.	
391.9 ± 3.4 Ma BP	L. Devonian	Emsian	Heisdorf Fm.			*patulus*

TABLE 1.1—Biostratigraphy of the Eifel (after STRUVE 1996b); U-Pb ID-TIMS ages after KAUFMANN (2006).

2 DETAILED OBJECTIVES

Because of the high diversity of the Middle Devonian crinoids from the Eifel, only a selected family, subfamily or genus of each of the four occurring Palaeozoic subclasses are studied in the course of this work. Focussing on the palaeodiversity, palaeobiology and palaeoecology, these taxonomic units must exhibit particular potential for comprehensive palaeontological conclusions. Therefore, they must show a widespread stratigraphic and geographic distribution to reflect the ecological and facies context and to indicate morphologic respectively phylogenetic trends through the time. Alternatively, the taxa should show extraordinary skeletal features indicating palaeobiological adaptations respectively response to environmental constraints. The specific results obtained for each taxonomic unit have to be compared with published data to provide a modern view of the Middle Devonian crinoids from the Eifel and other regions of the Rheno-Ardennic Massif.

The four selected groups are discussed in **Chapter 1-4**:

Chapter 1 treats the subfamily Cupressocrininae (subclass Cladida)

Cupressocrinitids are the most characteristic representatives of the Rhenish cladids. They were highly adapted to the biostrome-dominated facies realms of the Eifel and show a wide stratigraphic and geographic range.

Based on the recognition of a new anatomical structure, the "exoplacoid layer" – a second endoskeleton layer, which is developed either mono- or multilamellar, cupressocrinitids were taxonomically revised by BOHATÝ (2005a). In this connection the family Cupressocrinitidae RÖMER, 1854 was subdivided into three genera – *Cupressocrinites* [with type species *C. crassus* GOLDFUSS (1831, p. 212)] – *Abbreviatocrinites* [with type species *C. abbreviatus* GOLDFUSS (1839, p. 333)] – and *Robustocrinites* [with type species *C. scaber* SCHULTZE (1866, pp. 25-26)]. These three genera were assigned to the subfamily Cupressocrininae BOHATÝ, 2006b, who recognised two subfamilies within the Cupressocrinitidae. Because *Rhopalocrinus* WACHSMUTH & SPRINGER, 1880 (previously included in the Cupressocrinitidae) clearly differs from the Cupressocrininae, the genus was designated the type of the subfamily Rhopalocrininae BOHATÝ, 2006b. But the taxonomical status of several genera and species are still afflicted with uncertainty. Furthermore, less is known about the palaeobiology and the palaeoecology of this group.

Continuing studies herein deal with an extended taxonomy, skeletal regeneration patterns as well as pre- and postmortem ossicular modifications and epizoan encrustings. Furthermore, it should be elucidated, if varying palaeodiversity and stratigraphic distribution of the cupressocrinitids provide any response to regional geological events within the Eifel.

Chapter 2 treats the family Hexacrinitidae (subclass Camerata)

Hexacrinitids are cosmopolitan camerate crinoids (WEBSTER 2003). They are among the most characteristic representatives of the Rhenish camerates. The genus "*Hexacrinites*" AUSTIN & AUSTIN, 1843 exhibits highest abundance and diversity within the Eifel Synclines. Therefore, hexacrinitids are of particular interest for this study.

The hitherto discussed species of "*Hexacrinites*" are in urgent need of a comprehensive taxonomical revision, because most obviously differ from the type species by previously unrecognised morphological features of the crown, which are described herein. In consequence, skeletal features will provide information on phylogenetic lineages and morphological changes, such as the development of spines, obviously as defence mechanism against predatory organisms.

Chapter 3 treats the genus *Stylocrinus* (subclass Disparida)

Isolated aboral cups of the genus *Stylocrinus* SANDBERGER & SANDBERGER, 1856 are among the most frequent recoveries of disparids within the Lower Eifelian to Lower Givetian of the Eifel Synclines. The genus is also recovered from the Middle to Upper Devonian of Asia and Australia. But almost nothing is known about the crown-morphology and former taxonomic descriptions dealt with subspecific differentiation of this low diverse genus. Therefore, the taxonomical status of the species and subspecies has to be clarified based on new fossil discoveries and study of specimens in historical collections. The analyses of new recovered material focus on unknown morphological features. Due to the abundance of specimens from the Eifel, this analysis also should propose information of pre- and postmortem ossicular modifications or encrustation by epizoans.

Chapter 4 treats the genus *Ammonicrinus* (subclass Flexibilia)

The genus *Ammonicrinus* SPRINGER, 1926b shows extraordinary skeletal features indicating palaeobiological adaptation as responses to environmental constraints. It is one of the most atypical Palaeozoic crinoids and distinguished by the synarthrial articulation of columnals with fulcra aligned and unequal ligamentary areas on either side of the fulcrum, which produced a planispirally coiled proximal column. Therefore, the enrolled *Ammonicrinus* does not correspond to the erect model of most stalked fossil crinoids, which were attached to the substrate by a diversely designed holdfast followed by an upright stem to elevate the food-gathering system, represented by the arms, above the sea floor (e.g. HESS et al. 1999). The genus is almost entirely known based on columnal descriptions.

This study focuses on the mode of life of this atypical crinoid. It tries to clarify how ammonicrinids provided nutrient filtering without clogging the crown, while laying on soft-bottoms in still-water habitats. The reclined posture also bears the risk of direct contact with predatory benthic organisms that ammonicrinids obviously had to antagonise.

Discussion and conclusion

Within the last chapter of this study, the results of the previous chapters are combined and discussed in their greater context. For that reason they are compared with published data and complemented by own observations on other taxa of the four treated crinoid subclasses. This provides a comprehensive understanding within the Middle Devonian crinoids from the Eifel. It contributes to the general knowledge of Palaeozoic crinoids and their importance as indicators of palaeoecology and facies.

3. GENERAL PART

3.1 CHAPTER I. CRINOIDEA, CLADIDA

PRE- AND POSTMORTEM SKELETAL MODIFICATIONS OF THE CUPRESSOCRINITIDAE

ABSTRACT—The discovery of new specimens and restudy of known collections resulted in revision of some members of the cladid crinoid family Cupressocrinidae. "*Cupressocrinites gracilis*" is generically separated from *Cupressocrinites* whereby "*Procupressocrinus*" is resurrected from synonomy and assigned to the Cupressocrinidae with *C. gracilis* GOLDFUSS, 1831 as the type species. Studies of the SANDBERGER collection presuppose the revision of "*Abbreviatocrinites abbreviatus altus*" (= *A. altus* n. comb.[1]) and *A. nodosus*. Furthermore, the hitherto undetermined cupressocrinitids are described as *Cupressocrinites ahuettensis* n. sp.[2] and *Robustocrinites cataphractus* n. sp.[3] The event-controlled distribution of *Robustocrinites* is discussed and shows similarities to other crinoid genera within the Eifel region. Observed arm-regeneration in *Robustocrinites*, as well as the postmortem incurred ossicular-boring of an indeterminable organism and the skeletal-colonization by a trepostome bryozoan, are further observations of other pre- and postmortem ossicular modifications in cupressocrinitid skeletons.

3.1.1 INTRODUCTION

The famous Devonian crinoid genus *Cupressocrinites* GOLDFUSS, 1831 was revised based on the identification of a new anatomical structure, the mono or multilamellar exoplacoid layer *sensu* BOHATÝ (2005a). Further distinguishing features between the different morphologies of the cupressocrinitid crowns corroborates the generic differentiation of the Cupressocrinitidae RÖMER, 1854 by BOHATÝ (2005a, p. 212, tab. 1; 2006b, p. 153, tab. 1). Studies of the crowns of *Rhopalocrinus gracilis* (SCHULTZE, 1866) required a further differentiation of the family Cupressocrinitidae (see BOHATÝ 2006b). In contrast to other genera of the family, *Rhopalocrinus* WACHSMUTH & SPRINGER, 1880 is distinguished both by possession of an anal plate and a longer anal tube. Therefore, BOHATÝ (2006b) separated the

---

[1] = *A. altus* (SCHULTZE, 1866) *sensu* ICZN
[2] = *Cupressocrinites ahuettensis* BOHATÝ, 2009 *sensu* ICZN
[3] = *Robustocrinites cataphractus* BOHATÝ, 2009 *sensu* ICZN

genera *Cupressocrinites*, *Abbreviatocrinites* and *Robustocrinites* from *Rhopalocrinus* by erecting the subfamily Cupressocrininae BOHATÝ, 2006b, and *Rhopalocrinus* was assigned to the subfamily Rhopalocrininae BOHATÝ, 2006b.

During this research the generic assignment of "*Cupressocrinites gracilis*" GOLDFUSS, 1831 (Fig. 3.1.1) agreed with that recognised by JAEKEL (1918, p. 82) when he designated "**C. gracilis*" the type species of "*Procupressocrinus*" JAEKEL, 1918. Morphological differences (especially the long cup and the extremely long arms of *P. gracilis* contrasts with the flat cup, low brachials with w-shaped cross-section and the significant black-coloured skeleton of *C. crassus*) of the type species **C. crassus* GOLDFUSS, 1831 (Fig. 3.1.3) justified this separation. Furthermore, this is affirmed by the morphological comparison of *Abbreviatocrinites* and *Robustocrinites*. Both genera are distinguished from *Procupressocrinus* by characteristic crown morphology (compare BOHATÝ 2006b, pls. 1, 6-7). Therefore, the genus name "*Procupressocrinus*", previously specified as a junior synonym of *Cupressocrinites* (e.g. MOORE et al. 1978, pp. T657-T658) is resurrected as recognised by JAEKEL (1918).

Studies of the crinoid-collection of the famous palaeontologists GUIDO & FRIDOLIN SANDBERGER, deposited at the *Naturhistorische Landessammlung*, *Museum Wiesbaden*, require the revision of "*Abbreviatocrinites abbreviatus altus*" and *A. nodosus*.

"*A. a. altus*" was originally described as "*Cupressocrinus abbreviatus* var. *alta*" by SCHULTZE (1866, p. 21). The holotype (1866, pl. 2, fig. 2) [Fig. 3.1.2.9] of the subspecies is regarded here to define of the discrete species *A. altus* (SCHULTZE, 1866) n. comb.[4] SCHULTZE assigned a second figured cupressocrinitid-crown (1866, pl. 2, fig. 2a) [Fig. 3.1.2.5] to "*C. a.* var. *alta*" although the specimen clearly differs from the holotype by the development of a smaller crown with shorter arms composed of longer brachials.

SCHULTZE's fig. 2a is judged with the holotype of "*Cupressocrinus nodosus*" SANDBERGER & SANDBERGER, 1856 (Figs. 3.1.2.1-2), figured on their pl. 35, fig 5. SANDBERGER has priority. Herein, "*C. nodosus*" is revised as *Abbreviatocrinites nodosus* (SANDBERGER & SANDBERGER, 1856).

Another specimen figured as "*C. nodosus*" (SANDBERGER & SANDBERGER, 1856, pl. 35, fig. 5a) [Figs. 3.1.2.3-4] is distinguished from the holotype by the development of a wider and lower cup with a larger stem-insertion and is questionably assigned to *A. geminatus* BOHATÝ, 2005a.

Isolated skeletal plates of two species discussed by BOHATÝ (2006b) were

---

[4] = *A. altus* (SCHULTZE, 1866) *sensu* ICZN

listed in open nomenclature. New specimens allow the naming of *Cupressocrinites ahuettensis* n. sp.[5] and *Robustocrinites cataphractus* n. sp.[6]

Stratigraphic and morphologic observations of *Robustocrinites* require further research. Thus, the stratigraphic distribution of the genus is limited by sedimentary events (Fig. 3.1.8). Fossil arms of the new species *R. cataphractus* represent pre- and postmortem ossicle modifications. The holotype exhibits one regenerated, smaller arm (Figs. 3.1.6.1, 3.1.7.1). Another specimen is distinguished by a boring in the ossicle. Furthermore, this trace is encrusted by a trepostome bryozoan (Figs. 3.1.6.3, 3.1.7.2). Based on these cognitions, other skeletal anomalies on cupressocrinitids are classified as: 1, growth anomalies without external influences (Figs. 3.1.9.1-7); 2, growth anomalies without classifiable causes (Figs. 3.1.9.8-15); 3, premortem ossicle anomalies as a reaction of external interferences (Figs. 3.1.9.16-20); 4, pre- and postmortem borings and bite marks (Figs. 3.1.10.1-10); and 5, pre- and postmortem epizoan encrusting (Figs. 3.1.11.1-22).

3.1.2 MATERIAL AND METHODS

Type specimens are deposited in the *Forschungsinstitut und Naturmuseum Senckenberg*, Frankfurt am Main, Germany (SMF) and the *Naturhistorische Landessammlung, Museum Wiesbaden*, Germany (NWNH). Additional original specimens are stored in the collections of the following institutions and museums: *Institut für Geologie und Mineralogie der Universität zu Köln*, Germany (GIK), *Steinmann-Institut für Geologie, Mineralogie und Paläontologie der Rheinischen Friedrich-Wilhelms-Universität Bonn*, Germany (IPB) and *Museum of Comparative Zoology (Agassiz-Museum), Harvard University*, Cambridge, Massachusetts, U.S.A. (MCZ). Other studied crinoids are deposited in private collections (abbreviations CREF, CRBG and R.L.) and are accessible through contact with the author.

In addition to a detailed analysis of previously published data and original material, this study focuses on skeletal features, mainly observed in recently discovered crinoids. They were dissected using micro sand-streaming methods, as well as fine pneumatic probes and studied *via* binocular- and scanning electron microscope analyses (SEM). Photographs of NH_4Cl-whitened crinoids were arranged using digital image editing software.

---

[5] = *Cupressocrinites ahuettensis* BOHATÝ, 2009 *sensu* ICZN

[6] = *Robustocrinites cataphractus* BOHATÝ, 2009 *sensu* ICZN

Higher classification of crinoids followed is that of SIMMS & SEVASTOPULO (1993) as modified by MCINTOSH (2001) and WEBSTER et al. (2003). Morphologic dimensions are given in length and width as defined by WEBSTER & JELL (1999).

The capitalization of the Givetian subdivisions follows BECKER (2005; 2007).

3.1.3 SYSTEMATIC PALAEONTOLOGY

3.1.3.1 Introduction

The order Cladida MOORE & LAUDON, 1943 was originally subordinated to the Inadunata WACHSMUTH & SPRINGER, 1885 (see MOORE et al. 1978). After SIMMS & SEVASTOPULO (1993) recognised the polyphyletical status of the Inadunata, the order was discarded as a subclass. Because MCINTOSH (2001) pointed out the polyphyletic nature of the suborder Poteriocrinina JAEKEL, 1918, several poteriocrinitid taxa were transferred to the Cyathocrinida BATHER, 1899 by WEBSTER et al. (2003). Furthermore, WEBSTER et al. (1999) included the superfamily Cupressocrinitoidea in the Gasterocomoidea, both RÖMER, 1854, for reasons of phylogenetic relations. BOHATÝ (2005a) subdivided the family Cupressocrinitidae RÖMER, 1854 into three genera – *Cupressocrinites* [with type species **C. crassus* GOLDFUSS (1831, p. 212)] – *Abbreviatocrinites* [with type species **C. abbreviatus* GOLDFUSS (1839, p. 333)] – and *Robustocrinites* [with type species **C. scaber* SCHULTZE (1866, pp. 25-26)]. These three genera were assigned to the subfamily Cupressocrininae BOHATÝ, 2006b, who recognised two subfamilies within the Cupressocrinitidae. Because *Rhopalocrinus* WACHSMUTH & SPRINGER, 1880 (previously included in the Cupressocrinitidae) clearly differs from the Cupressocrinitidae, the genus was designated the type of the subfamily Rhopalocrininae BOHATÝ, 2006b. Further study has indicated "*Cupressocrinites gracilis* GOLDFUSS, 1831" belongs to a separate genus (see BOHATÝ 2005a, p. 213; 2006b, p. 161), whereby *Procupressocrinus* JAEKEL, 1918 has priority. *Procupressocrinus gracilis* (GOLDFUSS, 1831) and possibly (?)*P. magnus* (MILICINA, 1977) are assigned to JAEKEL's genus.

3.1.3.2 Crinoid systematic

3.1.3.2.1 Family Cupressocrinitidae

Subclass Cladida MOORE & LAUDON, 1943
Order Cyathocrinida BATHER, 1899
Superfamily Gasterocomoidea RÖMER, 1854
Family Cupressocrinitidae RÖMER, 1854

Included subfamilies.—Cupressocrininae and Rhopalocrininae, both BOHATÝ, 2006b.

Diagnosis.—Distinguished by the robust crown with five atomous arms; primibrachials (“clavicular plate”) low and wide, without pinnules, further brachials pinnule-bearing, with u- (Rhopalocrininae, *Procupressocrinus* and *Robustocrinites*), v- (*Abbreviatocrinites*) or w-shaped (*Cupressocrinites*) cross sections; aboral cup with (*Abbreviatocrinites*, *Cupressocrinites* and *Procupressocrinus*) or without pentamerous basal plate (Rhopalocrininae, *Robustocrinites*) composed of coalesced infrabasals, five basals and radials and either with (Rhopalocrininae) or without a single anal plate (Cupressocrininae); oral view dominated by the “consolidating apparatus” with a rounded mouth opening in the centre and an oval, eccentrically arranged anal opening, with (Rhopalocrininae) or without anal tube (Cupressocrininae); three (*Abbreviatocrinites inflatus*, *A. sampelayoi*) to four axial canals (all the rest of the taxa) around the central canal of the column; endoskeleton either with (Cupressocrininae) or without a second skeletal layer (Rhopalocrininae) – the mono- (*Procupressocrinus*, *Cupressocrinites* and *Robustocrinites*) or multilamellar exoplacoid layer (*Abbreviatocrinites*); colour of fossilised ossicles black (*Cupressocrinites*) or brownish to grey (all the rest of the taxa); preservation of original colour pattern (radiating double-lines) detected in *Procupressocrinus gracilis*.

Occurrence.—Upper Ludlowian (Upper Silurian): Estland; Pragian (Lower Devonian): Australia; Emsian (Lower Devonian), Eifelian and Givetian (Middle Devonian): Germany; Eifelian and Givetian: Great Britain, Russia, Poland, Czech Republic, Morocco, China, N-Burma, Belgium and Spain; Famennian (Upper Devonian): Belgium and United States (supplemented after WEBSTER 2003).

3.1.3.2.2 Subfamily Cupressocrininae

Subfamily Cupressocrininae BOHATÝ, 2006b

Included genera and type species.—*Cupressocrinites* (**C. crassus* GOLDFUSS, 1831); *Abbreviatocrinites* (**C. abbreviatus* GOLDFUSS, 1839); *Robustocrinites* (**C. scaber* SCHULTZE, 1866) and *Procupressocrinus* (**C. gracilis* GOLDFUSS, 1831).

Diagnosis.—Crown ovate and low, cylindrical or lanceolate and elongate with five atomous arms; primibrachials ("clavicular plate") low and wide, without pinnules, further brachials pinnule-bearing, with u- (*Procupressocrinus*, *Robustocrinites*), v- (*Abbreviatocrinites*) or w-shaped (*Cupressocrinites*) cross sections; aboral cup with (*Abbreviatocrinites*, *Cupressocrinites* and *Procupressocrinus*) or without pentamerous basal plate (*Robustocrinites*) composed of coalesced infrabasals, five basals and radials; oral view dominated by the "consolidating apparatus" with a rounded mouth opening in the centre and an oval, eccentrically arranged anal opening, without anal tube; three (*Abbreviatocrinites inflatus*, *A. sampelayoi*) to four axial canals (all the rest of the taxa) around the central canal of the column; endoskeleton with covering mono- (*Procupressocrinus*, *Cupressocrinites* and *Robustocrinites*) or multilamellar exoplacoid layer (*Abbreviatocrinites*); surfaces of plates unornamented to variously ornamented; colour of fossilised ossicles black (*Cupressocrinites*) or brownish to grey (all the rest of the taxa); preservation of original colour pattern (radiating double-lines) detected in *Procupressocrinus gracilis*.

3.1.3.2.3 Genus *Procupressocrinus*

Genus *Procupressocrinus* JAEKEL, 1918

- *Procupressocrinus* JAEKEL, 1918, p. 82.

Type species.—**Cupressocrinites gracilis* GOLDFUSS (1831, p. 213; pl. 64, fig. 5); the holotype (Fig. 3.1.1) is IPB-435b.

Included species.—*P. gracilis* (GOLDFUSS, 1831) and (?)*P. magnus* (MILICINA, 1977).

Diagnosis.—Crown slender, very long, lanceolate; atomous, narrow arms, primibrachials (“clavicular plate”) low and wide, without pinnules, followed by up to 40 pinnule-bearing, narrow brachials with u- to rarely slightly w-shaped cross sections; aboral cup long and cone-shaped to low and globular, with a pentamerous basal plate composed of coalesced infrabasals, forming a long, cone-shaped base, five long basals and radials; oral view dominated by the “consolidating apparatus” with a small, rounded mouth opening in the centre and an oval, eccentrically arranged anal opening, without anal tube; four axial canals around the central canal of the narrow column; endoskeleton with covering monolamellar exoplacoid layer; surfaces of plates unornamented or typically microgranulated; preservation of original colour pattern (radiating double-lines) detected.

Discussion.—According to JAEKEL (1918, p. 82), *Procupressocrinus* developed up to 30 brachials per arm. However, it is now recognised that the number of arm plates reaches up to 40 ossicles (compare DOHM 1930, pl. 1, fig. 1).

3.1.3.2.4 Species *Procupressocrinus gracilis*

Procupressocrinus gracilis (GOLDFUSS, 1831)

Figs. 3.1.1, 3.1.9.11, 3.1.11.(?)1, 3.1.11.(?)3, 3.1.11.6, 3.1.11.(?)13, 3.1.11.(?)19, 3.1.11.(?)22

- *Cupressocrinites gracilis* GOLDFUSS, 1831, p. 213; pl. 64, fig. 5. BOHATÝ, 2006b, pp. 151-153, 156, 160-163, 165; figs. 5.1-3; pl. 6, figs. 1a-c, 2a-b, 3-4, 5a-c, 6-8 (*cum syn.*).
- *Procupressocrinus gracilis* JAEKEL, 1918, p. 82.
- “*Dachsbergcrinites rotundatus* n. gen. n. sp.” HAUSER, 2006b, PDF-publication (genus and species decided *nomen nudum*).
- “*Dachsbergcrinites rotundatus* n. gen. n. sp.” HAUSER, 2007a, pp. 62-67 (= anomal morphotype of *P. gracilis*).

Diagnosis.—A *Procupressocrinus* with a slender, very long and lanceolated crown (see BOHATÝ 2006b, pl. 6, figs. 6-8), narrow arms composed of up to 40 brachials with u- to rarely slightly w-shaped cross sections; aboral cup long, cone-shaped to funnel-like or with long infrabasals and basals, less common with low and globular cup (BOHATÝ 2006b, pl. 6, figs. 1-4) and inflated “consolidating apparatus”; column narrow, with quadrangular to slightly rounded cross section; surface of the skeleton microgranulated; preservation of original colour pattern (radiating double-lines) detected.

Discussion.—Procupressocrinus gracilis clearly differs from the hitherto assigned genus *Cupressocrinites*. Especially are the differences with the type species **C. crassus* (Fig. 3.1.3) distinctive and led to a generic separation by JAEKEL (1918, p. 82). His genus *Procupressocrinus* was rejected by the majority of authors (e.g. BATHER 1926, p. 41; MOORE et al. 1978, p. T658). The splitting of the family into the genera *Abbreviatocrinites, Cupressocrinites* and *Robustocrinites* is based on skeletal features and the overall morphology of the crowns (BOHATÝ 2005a; 2006b). In contrast to the multilamellar exoplacoid layer of genus *Abbreviatocrinites*, *Procupressocrinus* developed a monolamellar layer. Unlike in *Procupressocrinus*, *Cupressocrinites* developed lower cups, lower and wider brachials and significant black-coloured skeletons. *Robustocrinites* developed lower and bowl-shaped cups without an infrabasal plate as well as wider brachials. Therefore, *P. gracilis* was previously assigned to *Cupressocrinites* by BOHATÝ (2005a, p. 213; 2006b, p. 161).

The genus name *Procupressocrinus* JAEKEL, 1918 has priority over the junior synonym "*Dachsbergcrinites*" *sensu* HAUSER (2007a). The junior synonym "*D. rotundatus*" HAUSER, 2007a clearly is a typical morphotype of *P. gracilis* with anomalously three instead of four peripheral axial canals – the most common variation among cupressocrinitids. [Note: The same crinoid, with a holotype deposited in a private collection (*sic*!), was introduced on a private webpage (HAUSER 2006b), which does not meet ICZN regulations for acceptable taxonomic names, and, therefore, "*D. rotundatus* HAUSER, 2006b" is considered *nomen nudum* (pers. information, G. D. WEBSTER; also see critical comments in BOHATÝ & HERBIG (2007, pp. 732-735)]. The transitions between the different morphologies of the cup, as well as variations within cupressocrinitids, were discussed in detail by BOHATÝ (2006b, pp. 160-161).

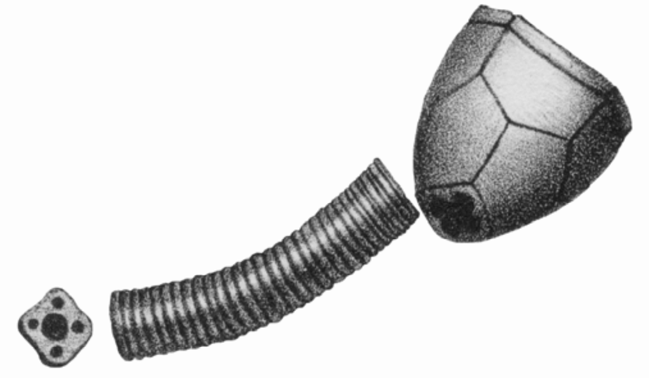


***FIGURE 3.1.1**—Procupressocrinus gracilis* (GOLDFUSS, 1831), **holotype** (IPB.-435b). Scan of the original lithography after GOLDFUSS (1831, pl. 64, fig. 5), ~ x 1.5.

3.1.3.2.5 Genus *Abbreviatocrinites*

Genus *Abbreviatocrinites* BOHATÝ, 2005a

- *pars Cupressocrinites* GOLDFUSS, 1839, pp. 330-335.
- *Abbreviatocrinites* n. gen. BOHATÝ, 2005a, p. 217.

Type species.—**Cupressocrinites abbreviatus* GOLDFUSS (1839, p. 333; pl. 30, fig. 4).

Included species.—*A. abbreviatus abbreviatus* (GOLDFUSS, 1839); *A. abbreviatus granulosus* (SCHULTZE, 1866); *A. altus* (SCHULTZE, 1866) n. comb.[7]; *A. assimilis* (DUBATOLOVA, 1964); *A. geminatus* BOHATÝ, 2005a; *A. gibber* (BATHER, 1919); *A. inflatus inflatus* (SCHULTZE, 1866); *A. inflatus depressus* (HAUSER, 2001); *A. inflatus convexus* (HAUSER, 2001); *A. inflatus cuneatus* BOHATÝ, 2006b; *A. nodosus* (SANDBERGER & SANDBERGER, 1856); *A. rectangularis* (SCHMIDT, 1941); *A. sampelayoi* (ALMELA & REVILLA, 1950); *A. schreueri* BOHATÝ, 2006b; *A. tesserula* (HAUSER, 1997); (?)*A. townsendi* (KÖNIG, 1825) and *A. urogali* (RÖMER, 1850).

Diagnosis.—Crown short, ovate or barrel-like; atomous arms, primibrachials ("clavicular plate") low and wide, without pinnules, further brachials pinnule-bearing, with v-shaped cross sections, brachials with central nodes (e.g. in *A. abbreviatus*), spine-like elongated multilamellar exobrachial layer (e.g. in *A. geminatus*), or distal most exobrachial laminae with central spine (*A. nodosus*); aboral cup bowl-shaped, typically flat and wide (e.g. in *A. abbreviatus*) or slightly longer (e.g. in *A. inflatus cuneatus*), with a pentamerous basal plate composed of coalesced infrabasals (slightly reduced in *A. geminatus* and *A. tesserula*), five basals and radials; oral view dominated by the "consolidating apparatus" with a rounded mouth opening in the centre and an oval, eccentrically arranged anal opening, without anal tube; three (*A. inflatus*, *A. sampelayoi*) to typically four axial canals (all the rest of the taxa) around the central canal of the column; endoskeleton with covering multilamellar exoplacoid layer; surfaces of plates almost unornamented (*A. tesserula*, *A. urogali*) or typically faceted and/or granulated at the exoplacoid margins.

---

[7] = *A. altus* (SCHULTZE, 1866) *sensu* ICZN

3.1.3.2.6 Species *Abbreviatocrinites nodosus*

Abbreviatocrinites nodosus (SANDBERGER & SANDBERGER, 1856)
Figs. 3.1.2.1-2, 3.1.2.5-8, 3.1.11.7-8, 3.1.11.20

- *pars Cupressocrinus nodosus* SANDBERGER & SANDBERGER, 1856, p. 401; pl. 35, fig. 5 only (= holotype), *non* fig. 5a (= *Abbreviatocrinites* cf. *A. geminatus* BOHATÝ, 2005a), *non* figs. 5b-c (= undeterminable cupressocrinitid columnals).
- *pars Cupressocrinites nodosus* WEBSTER, 2003, SANDBERGER & SANDBERGER, 1850-1856, p. 401 only, *non* pl. 35, figs. 5a-5c (fig. 5a = *Abbreviatocrinites* cf. *A. geminatus* BOHATÝ, 2005a, figs. 5b-c = undeterminable cupressocrinitid columnals). MAURER, 1875, p. 609. BASSLER & MOODEY 1943, p. 385.
- *pars Cupressocrinus abbreviatus* var. *alta* SCHULTZE, 1866, p. 21; pl. 2, fig. 2a only, *non* fig. 2 [= *Abbreviatocrinites altus* (SCHULTZE, 1866) n. comb.[8]].
- *Cupressocrinites abbreviatus* var. *alta* MIESEN, 1971, pp. 14-15; pl. 2, fig. 5d; p. 57 unnumbered figure directly below (?).
- *Cupressocrinites abbreviatus alta* HAUSER, 1997, p. 63; pl. 10, figs. 4-5.
- *Cupressocrinites abbreviatus altus* BASSLER & MOODEY, 1943, p. 384. HAUSER, 2001, p. 149.
- *Cupressocrinites schlotheimi alta* WEBSTER, 1973, p. 91.
- *Abbreviatocrinites abbreviatus altus* BOHATÝ, 2005a, pp. 203, 206, 208, 212, 217. BOHATÝ, 2006b, pp. 153, 163, 165; pl. 3, figs. 1a-c, 2a-b, 3.

Diagnosis.—An *Abbreviatocrinites* with elongated, ovate crown, long cone-shaped cup (rarely long bowl-shaped) with small insertion for stem and slender arms composed of few, long brachials (Figs. 3.1.2.5-8, 3.1.11.7); with nodes on proximal and middle brachials which are restricted to the centres of the plates, distal most skeletal layer of the multilamellar exobrachial laminae with central spine (Figs. 3.1.2.7-8).

Holotype.—Partly preserved crown; NWNH-297 (Figs. 3.1.2.1-2). Original of SANDBERGER & SANDBERGER (1856, p. 401; pl. 35, fig. 5 only). The holotype was discovered at the “Roteisenstein” (lower Upper Givetian, upper Middle Devonian) of the “Grube Lahnstein” near Weilburg-Odersbach, NE of Limburg an der Lahn (SE-Rhenish Massif, Lahn-Dill Syncline, Germany).

---

[8] = *Abbreviatocrinites altus* (SCHULTZE, 1866) *sensu* ICZN

Other material examined.—MCZ-102980 (*vidi*), original of SCHULTZE (1866, pl. 2, fig. 2a) [Fig. 3.1.2.5]; CREF84-2 (LEUNISSEN collection) [Fig. 3.1.2.6]; CREF180-1 (HEIN collection) [Figs. 3.1.2.7-8]; GIK-1938 (Figs. 3.1.11.7-8); GIK-1947 (Fig. 3.1.11.20) and CRBG7-1 (HEIN collection; unfigured).

Occurrence.—Middle Devonian, Germany. Upper Middle Eifelian: Eifel (Junkerberg Formation of the Hillesheim and Prüm synclines), lower Middle Givetian: Bergisches Land (Büchel Formation of the Bergisch Gladbach-Paffrath Syncline, Rhenish Massif), lower Upper Givetian: Weilburg-Odersbach ("Roteisenstein" of the Lahn-Dill Syncline, SE-Rhenish Massif).

Discussion.—*A. nodosus* was described by SANDBERGER & SANDBERGER (1856) referring to the figured holotype (1856, pl. 35, fig. 5 only) [Figs. 3.1.2.1-2]. The authors assigned an additional cupressocrinitid-cup to the species (pl. 35, fig. 5a) [Figs. 3.1.2.3-4] that differs from *A. nodosus*. This theca, identified in the unlabelled SANDBERGER material, is most likely attributed to *A. geminatus* BOHATÝ, 2005a.

Also the multilamellar exoplacoid layer of the Lahn-Dill *A. nodosus* is exiguous coarser, its overall morphology, especially of the arms, clearly corresponds with the Eifel material. Hitherto, the Eifel *nodosus* material was ascertained to refer to SCHULTZE's lithography of "*Cupressocrinus abbreviatus* var. *alta*" (= *A. altus*) [1866, pl. 2, fig. 2a; see Fig. 3.1.2.5], although this crown clearly differs from the holotype of *A. altus*, which is figured on SCHULTZE's pl. 2, fig. 2 only (Fig. 3.1.2.9).

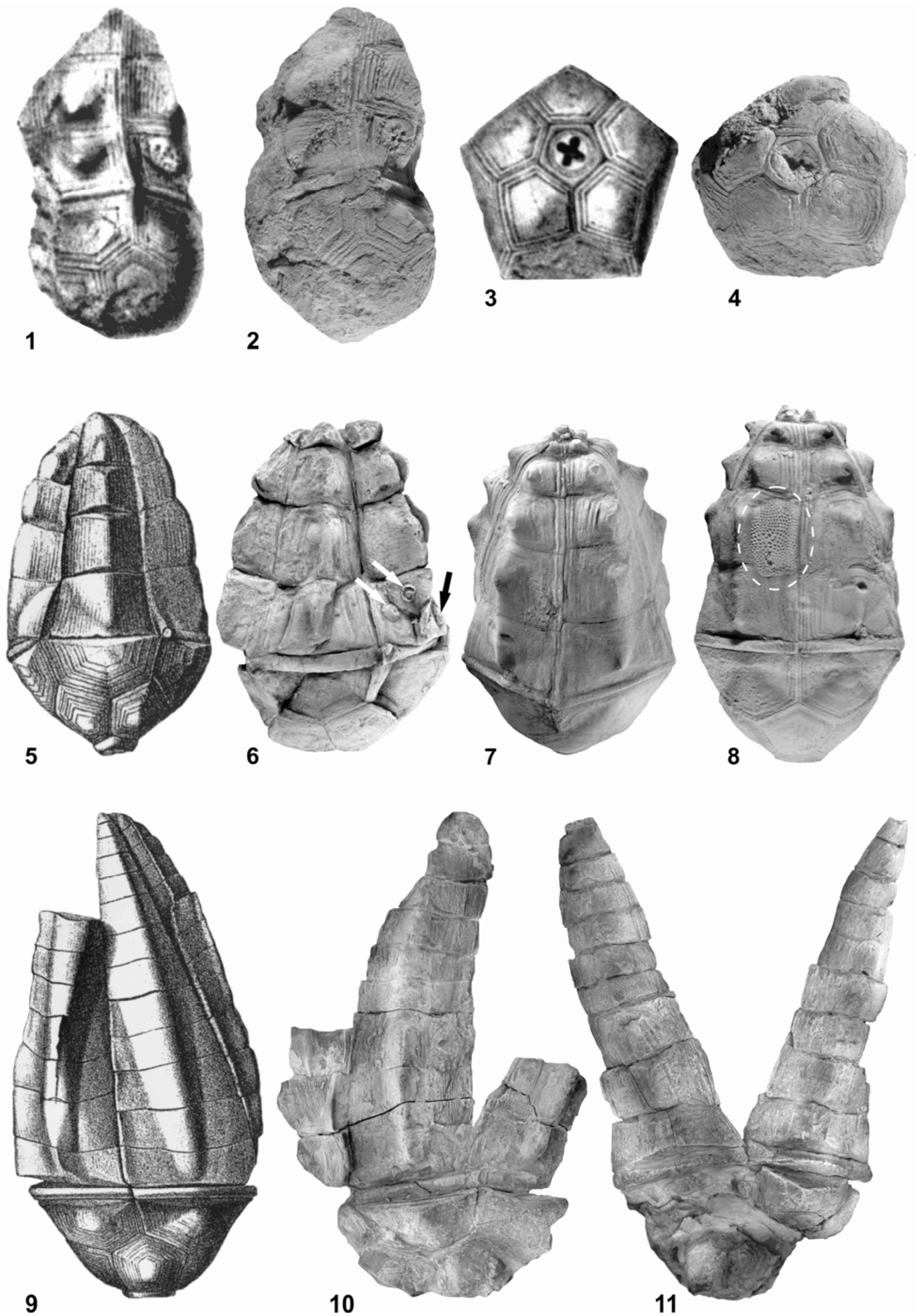
The holotype of *A. altus*, as well as two additional studied crinoids (Figs. 3.1.2.10-11), is clearly different from *A. nodosus*. *A. altus* developed a larger crown with longer arms, composed of numerous wide, lower brachials. In contrast, *A. nodosus* is distinguished by a smaller crown, with a longer cup and slender arms with fewer (4-6) higher brachials per arm. SANDBERGER's lithography seems to have an aborted distal crown. However, from the present study, it is evident that the three preserved arms are complete and consist of primibrachials ("clavicular plate") as well as four subsequent pinnule-bearing brachials.

Also, SANDBERGER's original represents the youngest *A. nodosus* specimen; it is not the only Givetian evidence of this abbreviatocrinid species. Besides numerous cups and crowns from the upper Middle Eifelian of the Eifel, another aboral cup demonstrates its occurrence in the Givetian. That cup CRBG7-1 (HEIN collection, unfigured) was recovered from an abandoned quarry at the "Schlade Valley", near Bergisch-Gladbach (Bergisch Gladbach-Paffrath Syncline, Bergisches Land, Rhenish Massif, Germany) within the deposits of the Büchel Formation (lower Middle Givetian) [BOHATÝ & HERBIG in review].

In addition to *A. nodosus*, *A. abbreviatus abbreviatus*, *A. geminatus* and *A. sampelayoi* were identified in the SANDBERGER collection. Together with typical Upper Eifelian and Lower Givetian sphaerocrinids, stylocrinids, gasterocomids and hexacrinids, the studied crinoids document the youngest known Middle Devonian occurrences of the mentioned species within the Rhenish Massif (Germany). That fact does not reflect the actual stratigraphical and/or geographical distribution of the crinoids but is a result of the lithologic framework. Equivalent deposits to the upper Middle to lower Upper Givetian Lahn-Dill-strata are typically dominated by dolomite or "Massenkalk" within the Eifel and the Bergisches Land and yield only infrequent well-preserved macrofossils.

FIGURE 3.1.2 (see p. 25)—1, *Abbreviatocrinites nodosus* (SANDBERGER & SANDBERGER, 1856), **holotype**, NWNH-297 – lateral view of the partly preserved crown, lithographed by SANDBERGER & SANDBERGER (1856, pl. 35, fig. 5 only); ***2***, Same view as 1, photograph of the **holotype**, x 1.6; ***3***, *Abbreviatocrinites* cf. *A. geminatus* BOHATÝ, 2005a, aboral view of the cup NWNH-408 – original lithography of SANDBERGER & SANDBERGER (1856, pl. 35, fig. 5a); ***4***, Same view as 3, photograph of the poorly preserved specimen, x 1.2; ***5***, *Abbreviatocrinites nodosus* (SANDBERGER & SANDBERGER, 1856), lateral view of the crown MCZ-102980, lithographed by SCHULTZE (1866, pl. 2, fig. 2a). Locality: "Prüm" (W-Rhenish Massif, Eifel, Prüm Syncline, Germany), stratigraphy (supposed): Junkerberg Formation (upper Middle Eifelian); ***6***, *Abbreviatocrinites nodosus* (SANDBERGER & SANDBERGER, 1856), CREF84-2 (LEUNISSEN collection) – lateral view of a compressed crown, encrusted by *Microconchus* sp. (arrows), x 1.7; ***7***, *Abbreviatocrinites nodosus* (SANDBERGER & SANDBERGER, 1856), CREF180-1 (Hein collection) – lateral-oral view of a consummate three-dimensional preserved crown; distal brachials with exobrachial-spines; proximal and middle arm plates with central nodes, composed of nodular-shaped exoplacoid laminae which are restricted to the centres of the brachials, x 1.7; ***8***, Same as 7, lateral view; one brachial is encrusted by a trepostome bryozoan (*Eostenopora* sp.) [framed], x 1.7; ***9***, *Abbreviatocrinites altus* (SCHULTZE, 1866) n. comb., lateral view of the **holotype** (MCZ-102979), lithographed by SCHULTZE (1866, pl. 2, fig. 2). Locality: "Prüm" (W-Rhenish Massif, Eifel, Prüm Syncline, Germany), stratigraphy (supposed): Uppermost part of the Ahbach Formation (lowermost Lower Givetian); ***10***, *Abbreviatocrinites altus* (SCHULTZE, 1866) n. comb., CREF16c-1 (HEIN collection) – lateral view of a partly preserved crown with thin plates and exoplacoid layer, x 1.1; ***11***, *Abbreviatocrinites altus* (SCHULTZE, 1866) n. comb. (SMF-75461) – lateral view of a partly preserved crown, x 0.9.

***FIGURE* 3.1.2 (legend p. 24)**



3.1.3.2.7 Species *Abbreviatocrinites altus*

Abbreviatocrinites altus (SCHULTZE, 1866) n. comb.[9]

Figs. 3.1.2.9-11

- *pars Cupressocrinus abbreviatus* var. *alta* SCHULTZE, 1866, p. 21; pl. 2, fig. 2 only (= holotype), *non* fig. 2a [= *Abbreviatocrinites nodosus* (SANDBERGER & SANDBERGER, 1856)].
- *Cupressocrinites schlotheimi* var. *alta* SCHMIDT, 1941, p. 104.
- *Abbreviatocrinites geminatus* BOHATÝ, 2006b, p. 174; pl. 4, figs. 3, 12.

Diagnosis.—An *Abbreviatocrinites* distinguished by an elongate, ovate crown with spearhead-like shape of closed distal arms (SCHULTZE 1866, pl. 2, fig. 2) [Figs. 3.1.2.9-11]; the wide arms are composed of numerous (10-15) wide brachials, which are covered by a straticulate, multilamellar exobrachial layer, without central nodules or spines; cup bowl-shaped to patelliform; insertion of stem wide.

Holotype.—Adult crown no. MCZ-102979 (*vidi*), original lithography by SCHULTZE (1866, pl. 2, fig. 2 only) [Fig. 3.1.2.9]. According to the original designation, the holotype was discovered at "Prüm". Most likely, the crown was found within the upper part of the Ahbach Formation (lowermost Lower Givetian, Middle Devonian) in the vicinity of Rommersheim and Brühlborn, to the east of Prüm (Prüm Syncline, Eifel, Rhenish Massif, Germany).

Other material examined.—Nos. SMF-75461 (Fig. 3.1.2.11) and CREF16c-1 (HEIN collection) [Fig. 3.1.2.10].

Occurrence.—*Stratum typicum* of the type region (Prüm Syncline) and of the abandoned "Müllertchen Quarry", S of Ahütte (Hillesheim Syncline, Eifel, Rhenish Massif, Germany).

Discussion.—In addition to the adult holotype of *A. altus* (SCHULTZE 1866, pl. 2, fig. 2) [Fig. 3.1.2.9], SCHULTZE assigned a second specimen, a juvenile crown, to the species (1866, pl. 2, fig. 2a) [Fig. 3.1.2.5]. After restudy of the SANDBERGER collection, this

---

[9] = *Abbreviatocrinites altus* (SCHULTZE, 1866) *sensu* ICZN

cupressocrinitid is assigned to *A. nodosus*. The few newly-discovered crowns (Figs. 3.1.2.10-11), which are clearly associated with *A. altus*, were spuriously regarded as morphotypes of *A. geminatus* (BOHATÝ 2006b, p. 164; pl. 4, figs. 3, 12). The distinction of *A. geminatus*, *A. nodosus* and *A. altus* is based on the morphologic differences of the crowns: *A. nodosus* developed an ovate crown with a long cup and slender arms, composed of few, long brachials bearing central exobrachial-nodules (Figs. 3.1.2.1-2, 3.1.2.5-8, 3.1.11.7); *A. altus* is distinguished by a long crown with spearhead-like shape of closed distal arms (Figs. 3.1.2.9-11) composed of numerous wide brachials, which are covered by a straticulate, multilamellar exobrachial layer, without central nodules; the massive exoplacoid layer of *A. geminatus*, especially the characteristic spine-like exobrachial layers (BOHATÝ 2006b, pl. 4, fig. 10), is the most conspicuous feature distinguishing *A. nodosus* and *A. altus*.

3.1.3.2.8 Genus *Cupressocrinites*

Genus *Cupressocrinites* GOLDFUSS, 1831

- *Cupressocrinites* GOLDFUSS, 1831, p. 212.

Type species.—**Cupressocrinites crassus* GOLDFUSS (1831, p. 212; pl. 64, figs. 4a-i, 4k-m); the holotype (Fig. 3.1.3) is IPB-434a.

Included species.—*C. ahuettensis* n. sp.[10]; *C. crassus* GOLDFUSS, 1831; *C. dohmi* HAUSER, 1997; *C. elongatus* GOLDFUSS, 1839; *C. hieroglyphicus* (SCHULTZE, 1866); *C. longibrachialis* POLYARNAYA, 1973; *C. ornamentus* BOHATÝ, 2006b and *C. steiningeri* BOHATÝ, 2006b.

Diagnosis.—Crown cylindrical (*C. crassus*, *C. elongatus*) or lanceolate and elongate (*C. dohmi*, *C. hieroglyphicus* and *C. longibrachialis*); atomous arms, primibrachials ("clavicular plate") low and wide, without pinnules, further brachials pinnule-bearing, with w-shaped cross sections; aboral cup bowl-shaped, slightly flattened (in *C. crassus*, *C. ornamentus*, *C. elongatus*, *C. steiningeri* and, especially, in *C. ahuettensis*) or cone-shaped (in *C. dohmi* and *C. hieroglyphicus*), with one pentamerous plate composed of coalesced

---

[10] = *C. ahuettensis* BOHATÝ, 2009 *sensu* ICZN

infrabasals and five basals and radials; oral view dominated by the "consolidating apparatus" with a rounded mouth opening in the centre and an oval, eccentrically arranged anal opening, without anal tube; three (*C. dohmi* and *C. hieroglyphicus*) to typically four axial canals (all the rest of the taxa) around the central canal of the column; the crown-ossicles are covered by a monolamellar exoplacoid layer; plate surfaces unornamented (e.g. in *C. crassus*, *C. steiningeri* and *C. dohmi*), or decorated by pustules, tubercles and/or coalesced tubercles (as in *C. elongatus*) or fine and meander adornments (e.g. in *C. hieroglyphicus*, *C. ornamentus*); colour of unweathered fossil skeletons black.

Discussion.—The isolated cup with lost exoplacoid layer, described by HAUSER (2007a, pp. 61-62) as "*C. goldfussi*" is a junior synonym of *C. ornamentus*. Therefore, the species, with a holotype deposited in a private collection (*sic*!), is not listed within the included species of the genus. [Note: The same crinoid was introduced on a private web-page (HAUSER 2006a), which does not meet ICZN regulations for acceptable taxonomic names, and, therefore, considered *nomen nudum* (pers. information, G. D. WEBSTER; also see critical comments in BOHATÝ & HERBIG (2007, pp. 732-735)].

3.1.3.2.9 Species *Cupressocrinites crassus*

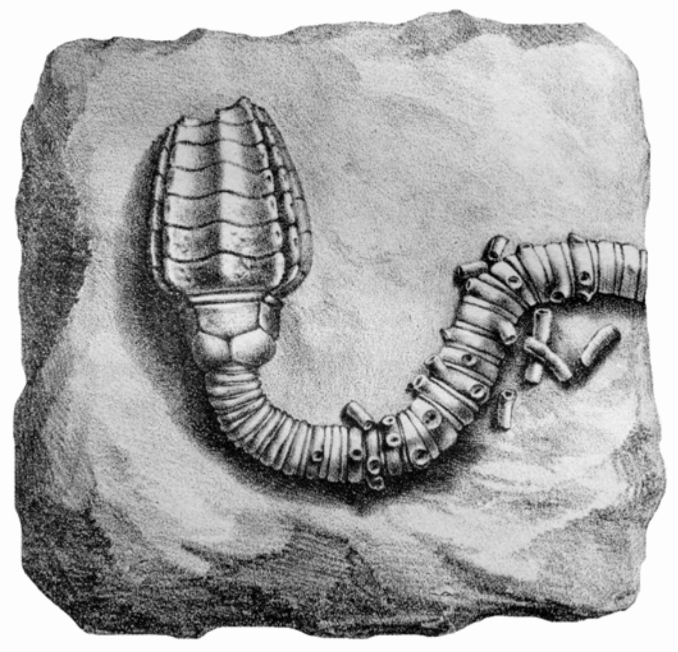


FIGURE 3.1.3—*Cupressocrinites crassus* GOLDFUSS, 1831, **holotype** (IPB.-434a). Scan of the original lithography, idealised and mirror-inverted by GOLDFUSS (1831, pl. 64, fig. 4), ~ x 1.5.

Cupressocrinites crassus GOLDFUSS, 1831

Figs. 3.1.3, 3.1.9.18-19, 3.1.10.9

- *Cupressocrinites crassus* GOLDFUSS, 1831, p. 212; pl. 64, figs. 4a-i, 4k-m.
- *Cupressocrinites crassus* BOHATÝ, 2006b, pp. 151-154, 156-158, 161, 164-165; pl. 10, figs. 4, 7, 8a-b, 9-10 (*cum syn.*).

Diagnosis.—A *Cupressocrinites* with cylindrical crown; arms composed as many as 20 low and wide brachials with distinctive w-shaped cross sections; cup low, bowl-shaped; skeletal elements intensive black-coloured, unadorned.

3.1.3.2.10 Species *Cupressocrinites ahuettensis*

Cupressocrinites ahuettensis n. sp.[11]

Figs. 3.1.4.1-2

- *Cupressocrinites* n. sp. I BOHATÝ, 2006b, pp. 153, 156, 158-159, 165; fig. 2.

Diagnosis.—A *Cupressocrinites* with a discoid, small cup and long arms, distal arm width only slightly narrower than proximal plates; brachials ternary wider than long, w-shaped in cross section. Surfaces of the skeletal elements without ornamentations.

Description.—Crown elongated, cylindric. Cup 20mm wide and 5mm long; infrabasal plate very slender; the unornamented ossicles are covered by the thin-walled, monolamellar exoplacoid layer; proportion of cup diameter to length of crown 1:4.8. Arms of adult crown eight cm long (Fig. 3.1.4.1) composed of 14 brachials, proximalmost brachial 5mm long and 18mm wide, distal plates slightly narrower; cross section of brachials w-shaped, with externally bent fossal grooves of the proximal pinnular; length to width proportion of brachials 1:2.5-3.0. Further skeletal elements unknown.

Etymology.—After the village Ahütte (northwestern Rhineland-Palatinate, southwestern Germany).

---

[11] = *Cupressocrinites ahuettensis* BOHATÝ, 2009 *sensu* ICZN

Holotype.—Isolated arm; SMF-75460 (Fig. 3.1.4.2). The holotype was discovered in the Olifant Member of the Ahbach Formation, lowermost Lower Givetian (Middle Devonian) of the abandoned "Müllertchen Quarry", S of Ahütte (Hillesheim Syncline, Eifel, Rhenish Massif, Germany); UTM 50°20'05.41"N/6°46'16.81"E.

Other material examined.—Partly preserved crown CREF11b (LEUNISSEN collection) [Fig. 3.1.4.1].

Occurrence.—Only in the type region.

Discussion.—*C. ahuettensis* n. sp.[12] is distinguished by the long arms and mainly by the dimensions of the distal plates that are only slightly narrower than the proximal ossicles. In proportion to the arm measurements, the cup of the new species is comparatively small. Those features clearly differentiate *C. ahuettensis* from the type species **C. crassus*, which has eminently similar shaped cross sections of the arms.

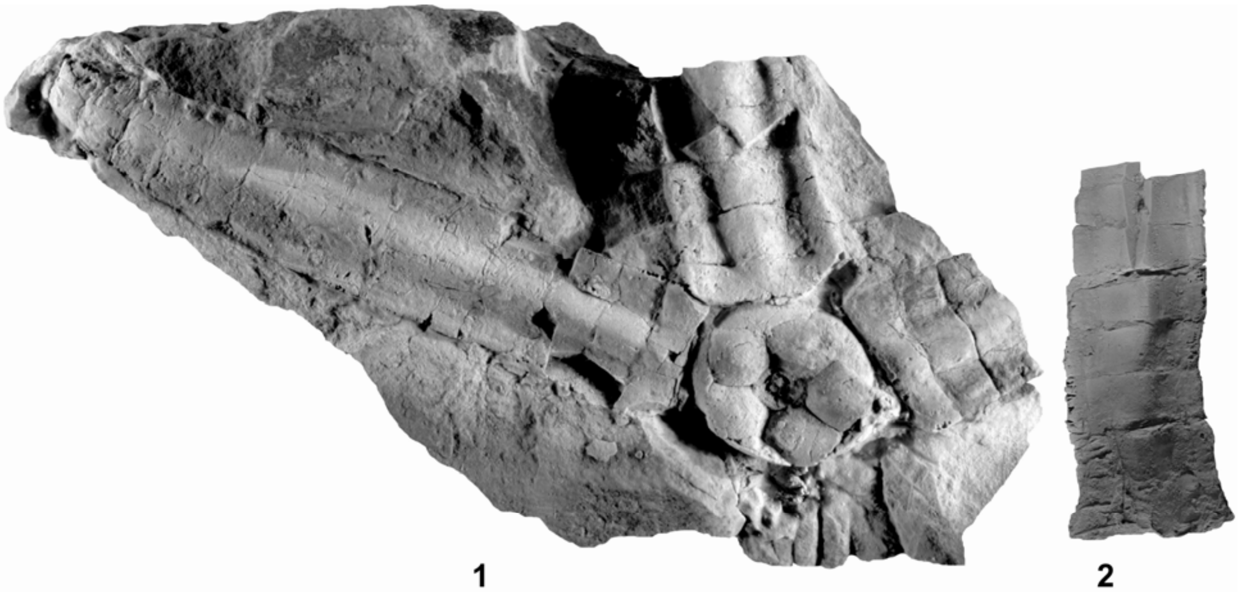


FIGURE 3.1.4—*Cupressocrinites ahuettensis* n. sp. ***1***, CREF11b (LEUNISSEN collection) – aboral view of the disarticulated, weathered exemplar, x 1.2; ***2***, **Holotype**, no. SMF-75460 – lateral view of a typical arm, x 1.1.

---

[12] = *C. ahuettensis* BOHATÝ, 2009 *sensu* ICZN

3.1.3.2.11 Genus *Robustocrinites*

Genus *Robustocrinites* BOHATÝ, 2005a

- *pars Cupressocrinus* SCHULTZE, 1866, pp. 14-26.
- *Robustocrinites* n. gen. BOHATÝ, 2005a, pp. 213-214.

Type species.—**Cupressocrinus scaber* SCHULTZE (1866, pp. 25-26; pl. 1 figs. 4, 4a-b); the holotype (Figs. 3.1.5.1-3) is MCZ-112662.

Included species.—*R. cataphractus* n. sp.[13]; *R. galeatus* (HAUSER, 2001) and *R. scaber* (SCHULTZE, 1866).

Diagnosis.—Crown long, elongated cylindrical; atomous arms, primibrachials ("clavicular plate") low and wide, without pinnules, up to 20 further, pinnule-bearing brachials with u-shaped cross sections; aboral cup bowl-shaped with convex base, one plate composed of coalesced infrabasals is missing, with five basals and radials; oral view dominated by the "consolidating apparatus" with a small, rounded mouth opening in the centre and an oval, eccentrically arranged anal opening, without anal tube; four axial canals around the central canal of the column; the crown-ossicles are covered by a monolamellar exoplacoid layer; plate surfaces unornamented (*R. galeatus*), decorated by fine and meander-like adornments (*R. scaber*) or adorned by roughly developed crinkles (*R. cataphractus* n. sp.[14]).

3.1.3.2.12 Species *Robustocrinites scaber*

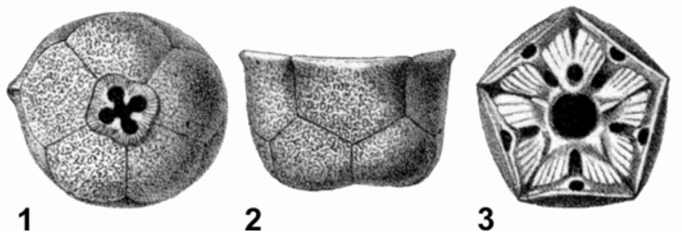


FIGURE 3.1.5—*Robustocrinites scaber* (SCHULTZE, 1866), **holotype**, no. MCZ-112662. Scan of the original lithography after SCHULTZE (1866, pl. 1, fig. 4). ***1***, Aboral-, ***2***, lateral-, ***3***, oral view, ~ x 1.4.

---

[13] = *R. cataphractus* BOHATÝ, 2009 *sensu* ICZN

[14] = *R. cataphractus* BOHATÝ, 2009 *sensu* ICZN

Robustocrinites scaber (SCHULTZE, 1866)

Figs. 3.1.5.1-3

- *Cupressocrinus scaber* SCHULTZE, 1866, pp. 25-26; pl. 1, figs. 4a-b.
- *Robustocrinites scaber* BOHATÝ, 2005a, pp. 206, 212-215, 217.
- *Robustocrinites scaber* BOHATÝ, 2006b, pp. 153, 161-162, 165; pl. 7, figs. 3-4, 5a-b, 6 (*cum syn.*).
- *Cupressocrinites scaber* HAUSER, 2007b, pl. 1, figs. 8-8a.

Diagnosis.—A *Robustocrinites* with long, elongated cylindrical crown and a bowl-shaped aboral cup with convex base; the surface of the skeleton is variously ornamented with low and meander-like ridges and/or fine hieroglyphics.

3.1.3.2.13 Species *Robustocrinites cataphractus*

Robustocrinites cataphractus n. sp.[15]

Figs. 3.1.6.1-4, 3.1.7.1-2

- (?)*Cupressocrinites* n. sp. II BOHATÝ, 2006b, pp. 153, 158-159, 165; fig. 3.

Diagnosis.—A *Robustocrinites* with long, cylindrical crown and a bowl-shaped aboral cup with convex base; crown-ossicles covered by a massive, monolamellar exoplacoid layer; surface of skeleton decorated by few, coarse crinkles that are predominantly oriented horizontally or in idealised x-shaped grooves.

Description.—Adult crown 7.0cm long and 2.5cm wide. Cup bowl-shaped, wider than long; basals and radials (Figs. 3.1.6.2, 3.1.6.4) covered by irregular curly folded exoplacoid laminae; insertion of stem wide and laterally framed by the sculpturing of the exobasal layers. Arms maximally 6.0cm long and 1.3cm wide; up to 12 brachials per arm; brachials wider than long, maximally 1.3cm wide and 0.7cm long; five pinnules on each side of a single brachial; monolamellar exobrachial layer decorated with coarse crinkles, which predominantly run in horizontal or in idealised x-shaped grooves; the exobrachial layer of the

---

[15] = *Robustocrinites cataphractus* BOHATÝ, 2009 *sensu* ICZN

distal brachials is distinguished by blunt spines; primibrachials ("clavicular plate") slender, without pinnules, surface of exoclavicular layer with rough, x-shaped ridges. Further skeletal elements not preserved. Colour of unweathered ossicles intensively dark-grey, weathered plates brownish.

Etymology.—*cataphractus* (lat.): armoured, after the armament-like development of the massive crown-ossicles.

Holotype.—Partly preserved crown; SMF-75459 (Figs. 3.1.6.1-2, 3.1.7.1). The holotype was discovered within the Nims Member of the lower part of the Grauberg Subformation, upper Junkerberg Formation, upper Middle Eifelian (Middle Devonian) at the northern slope of the western access route to the "Weinberg Quarry", NW of Kerpen (Hillesheim Syncline, Eifel, Rhenish Massif, Germany); UTM 50°18'54.24"N/6°42'48.76"E.

Other material examined.—One isolated arm plate (LUEKEN† collection, without repository-number, unfigured), specimen GIK-1924 (Figs. 3.1.6.3, 3.1.7.2) and GIK-1925 (Fig. 3.1.6.4).

Occurrence.—*R. cataphractus* n. sp.[16] is restricted to the Hönselberg, Rechert and Nims members of the Junkerberg Formation (Fig. 3.1.8), although STRUVE et al. (1997, pp. 147-150; figs. 13-14) specified the type locality to be of Giesdorfian age. Contrary to this classification, carbonate microfacies-analysis and the biostratigraphic examination of the fossil assemblage, composed of a diverse spectrum of cladid crinoids (*A. nodosus*, *R. gracilis* as well as robustocrinids and gasterocomoids), rugose and tabulate corals, stromatoporoids and brachiopods [but not containing the Giesdorfian guide species *Spinocyrtia* (*Spinocyrtia*) *ostiolata* (SCHLOTHEIM, 1820)] demonstrates an older biostratigraphic positioning. Based on the correlation with more complete Eifel sections, this position is specified as Nimsian age.

In addition to the type region, *R. cataphractus* was found at the following localities within the Eifel (Rhenish Massif, Germany): Housing subdivision "Wiesenweg", southwestern Gondelsheim (Prüm Syncline), UTM 50°13'58.71"N/6°29'52.66"E; housing subdivision "Im Leimenpeschen", southwestern Schwirzheim (Prüm Syncline), UTM 50°13'47.89"N/6°31'17.50"E and southern slope of the access route to the Ahütte lime works, E of the country road "L10", S of Üxheim/W of Ahütte (Hillesheim Syncline), UTM 50°20'10.73"N/6°45'42.86"E.

---

[16] = *R. cataphractus* BOHATÝ, 2009 *sensu* ICZN

Discussion.—The distinctive ornamentation of *R. cataphractus* clearly separates this new species from *R. scaber*, which has considerably finer ornament. *R. cataphractus* developed wider diameters of the plate cross sections in comparison with *R. scaber* and especially with *R. galeatus*. Furthermore, the plates of the latter species are unsculptured. The arms of *R. scaber* and *R. galeatus* are longer than those of *R. cataphractus*.

R. cataphractus was initially assigned to *Cupressocrinites* (BOHATÝ 2006b, p. 159). The discovery of crowns verifies its affiliation to *Robustocrinites*.

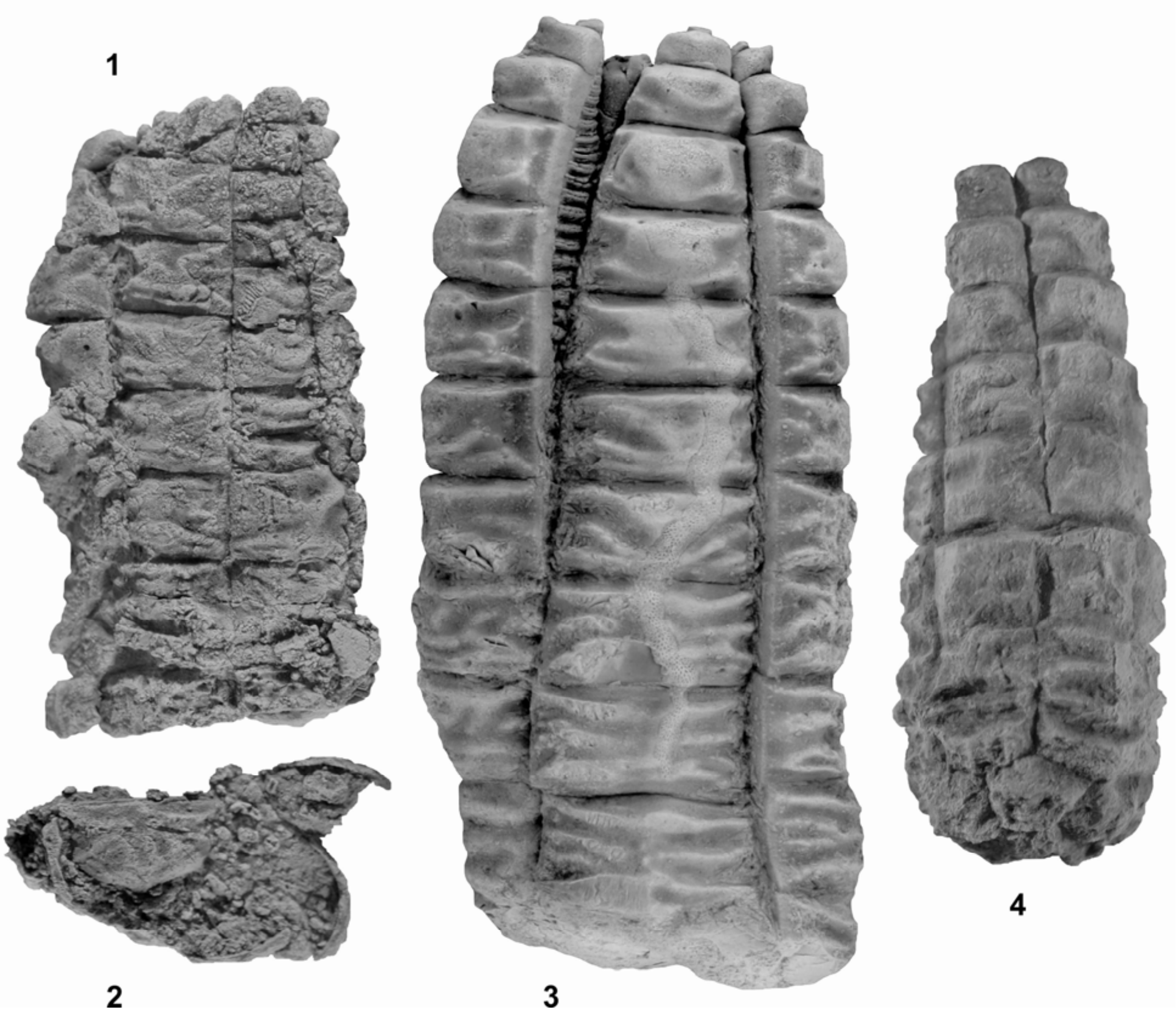


FIGURE 3.1.6—*Robustocrinites cataphractus* n. sp. ***1***, **Holotype**, SMF-75459 – lateral view of a partly preserved and weathered crown with one regenerated arm, x 2.1; ***2***, Same as 1, aboral view of the crown with one preserved radial plate, x 2.1; ***3***, GIK-1924 – lateral view of the adult arm-crown. The boring of an unknown organism is filled by a trepostome bryozoan (?*Eostenopora* sp.), x 2.2; ***4***, GIK-1925 – lateral view of a juvenile crown, x 2.4.

The holotype exhibits distinct skeletal regeneration with one regenerated, smaller brachial (Figs. 3.1.6.1, 3.1.7.1). This typical arm construction could be identified on one crown of *C. ornamentus* BOHATÝ, 2006b (p. 157; pl. 11, fig. 4b) [Fig. 3.1.9.20].

The skeleton GIK-1924 was probably attacked postmortem by a boring organism. A trepostome bryozoan (?*Eostenopora* sp.) secondarily filled the resulting depression (Figs. 3.1.6.3, 3.1.7.2).

Further grows anomalies could be identified on different cupressocrinitid-ossicles from the Middle Devonian of the Eifel. These observations, as well as the encrusting of the skeletal plates by various epizoans, are discussed below.

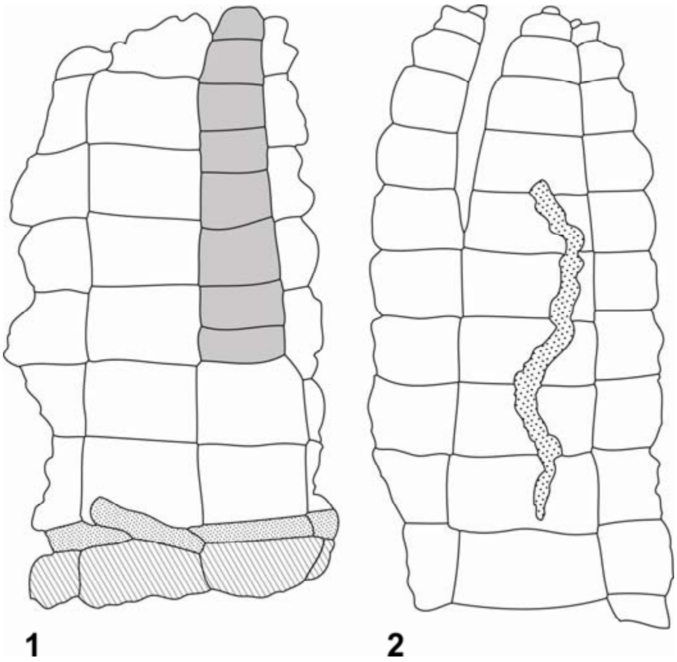


FIGURE 3.1.7*—Robustocrinites cataphractus* n. sp. ***1***, Diagrammatic sketch of the **holotype**; grey: The regenerated, smaller arm; white: Normal brachials; thin-dotted: Primibrachials (“clavicular plates”); hatched: Radials, x 1.9; ***2***, Sketch of specimen GIK-1924; dotted: The boring of an unknown organism is filled by a trepostome bryozoan (?*Eostenopora* sp.), x 1.4.

3.1.4 REGIONAL GEOLOGICAL EVENTS AS A LIMITING FACTOR OF THE STRATIGRAPHIC DISTRIBUTION OF GENUS *ROBUSTOCRINITES* WITHIN THE EIFEL REGION

The stratigraphic distribution of *Robustocrinites* within the Eifel is generally limited to the Eifelian (upper Lower to Upper Eifelian, see Fig. 3.1.8). *R. galeatus* first occurs at the boundary of the Nohn and Ahrdorf formations and has maximum abundance in the

Betterberg Subformation in the lower part of the Ahrdorf Formation. Increased sedimentation rate and the development of expanded mud grounds at the base of the Junkerberg Formation, resulted in a conspicuously retrogressive occurrence of robustocrinids within the Eifel region. This indentation correlates with the beginning and the durability of the “Klausbach Event” (see Struve 1992). During times of moderate sedimentary input, diverse populated hard- and/or firmgrounds were established between the Mussel and Nims members. Between the basal Hönselberg and the top of the Nims Member, the conditions for cupressocrinitids were apparently favourable. This observation is reflected in the high individual and species numbers. During this time interval, the species radiation of *Robustocrinites* occurred. *R. scaber* first occurred within the Mussel Member and has maximum abundance in the Rechert and Nims members. *R. cataphractus* is first recognised in the upper part of the Hönselberg Member and had its maximum abundance during the Nims Member in the lower Grauberg Subformation. All three species became extinct at the top of the Nims Member and, therewith, at the basis of the “*otomari* Event” (Struve et al. 1997). The *otomari* Event is a transgression that resulted in sedimentary changes within the Eifel region. Like the Klausbach Event at the base of the Junkerberg Formation, the *otomari* Event was not favourable for robustocrinids, as demonstrated for *Bactrocrinites* Schnur, 1849 (Bohatý 2005b).

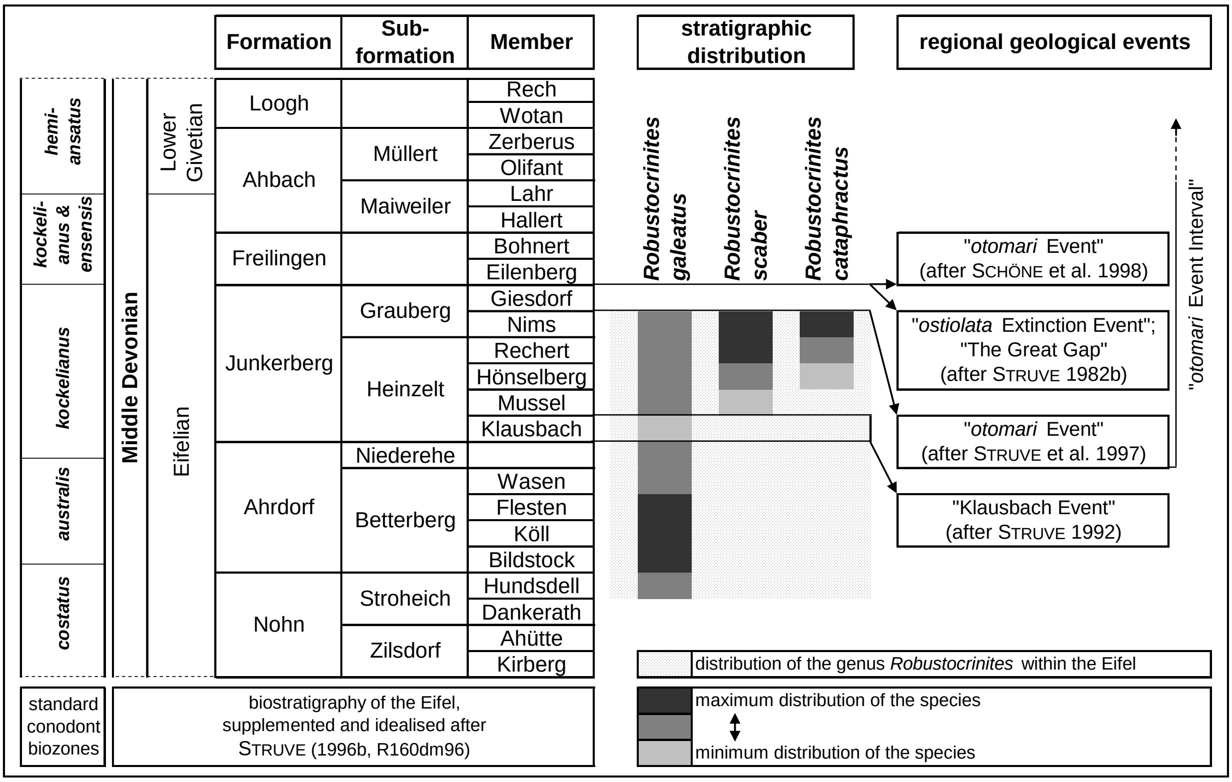


Figure 3.1.8—Biostratigraphic distribution of genus *Robustocrinites* Bohatý, 2005a and regional geological events within the Eifel.

The morphology of robustocrinid crowns changed from the upper Lower to the Upper Eifelian. In the Lower Eifelian, slender crowns with long arms and undecorated plate surfaces dominated. These forms (*R. galeatus*) have a comparatively long stratigraphic duration. Crowns with a finely ornamented surface and slightly shorter arms (*R. scaber*) appeared in the Upper Eifelian. They had a shorter stratigraphic distribution in comparison to *R. galeatus*. *R. cataphractus* has the shortest stratigraphic occurrence, limited to the Rechert/Nims boundary interval. This species exhibits the lowest crown and the plate surface is ornamented by the coarsest sculpture.

3.1.5 CLASSIFICATION OF PRE- AND POSTMORTEM OSSICULAR MODIFICATIONS OF THE CUPRESSOCRINITID SKELETONS

3.1.5.1 Growth anomalies without recognisable external influences – “generic” abnormalities

Growth anomalies without recognisable external influences are predominantly distinguished by the reduction of thecal or brachial-ossicles respectively by additional intermediary plates. These abnormalities could not be attributed to injuries or involved regeneration and are obviously “genetically modified anomalies” (BOHATÝ 2001). Most common are variances of the columnal axial canal (Figs. 3.1.9.5-7), which occurs at the rate of ~1:30 compared with regular grown axial canals (~1500 skeletons analysed). Further, individuals with additional (Figs. 3.1.9.4, 3.1.9.7) or a reduced number of ossicles (Fig. 3.1.9.5) are recognised. Cupressocrinitids with a developed quadrangular or hexagonal symmetry (Figs. 3.1.9.1-3) are relatively rare and occur at several localities with an average rate of ~1:70 compared with regularly developed skeletons (~700 aboral cups and ~300 crowns analysed). Due to the abundance of anomalously grown axial canals or symmetry aberrations within one fossil-horizon, the genetic basis of these interferences is assumed. In this case, the appropriative rates of detectable growth anomalies compared with normal individuals, could be higher than above-mentioned.

***FIGURE* 3.1.9 (legend p. 39)**

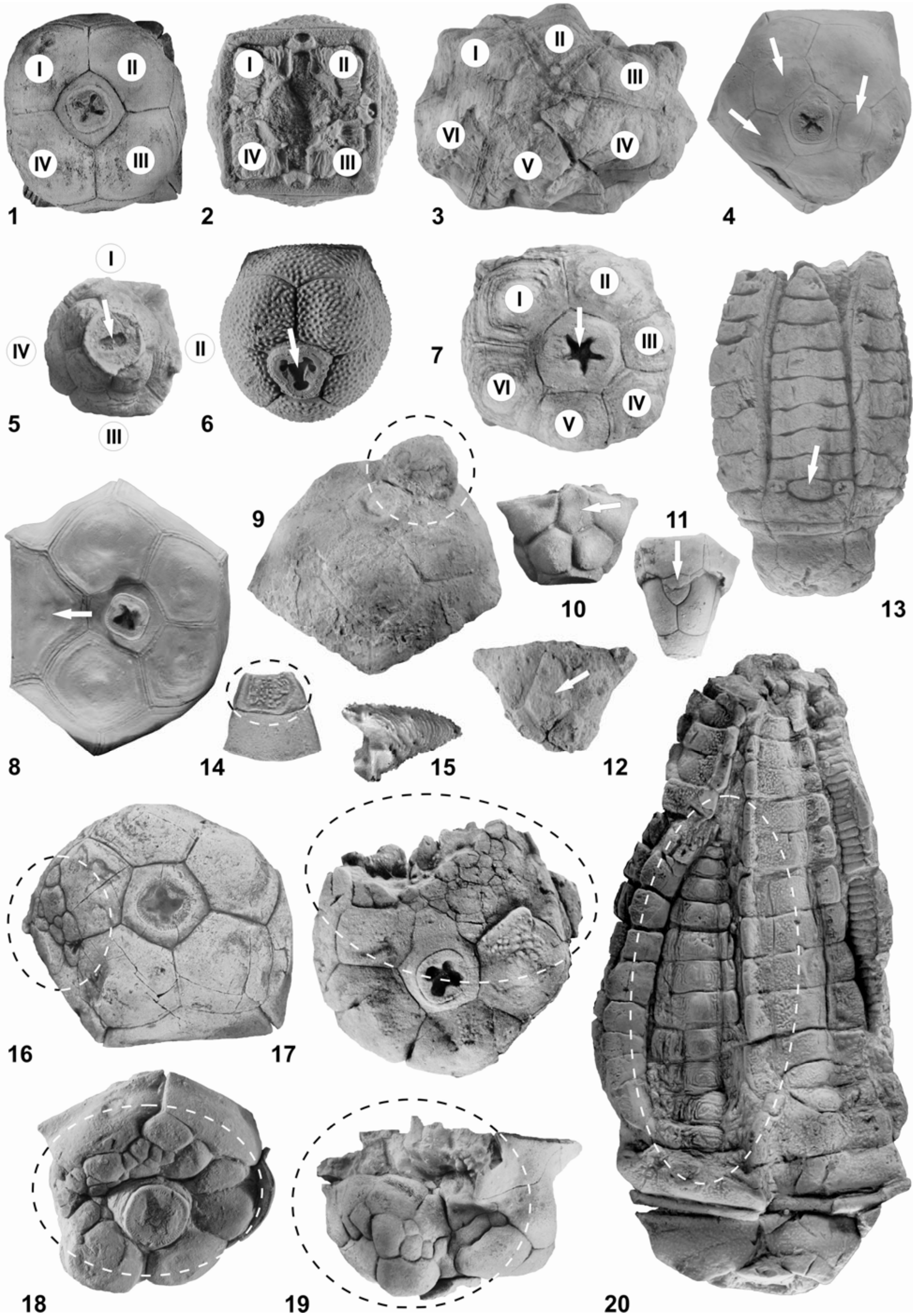


Figure 3.1.9 (see p. 38)—Ossicular modifications observed in cupressocrinitids. ***1-7***, Growth anomalies without recognisable external influences – "genetic" abnormalities; ***8-15***, Growth anomalies without classifiable causes – without indications of external influences; ***16-20***, Premortem ossicular anomalies as a reaction of external interferences – "wound healing" and skeletal regeneration of thecal- or brachial injuries. ***1***, CREF34b-72 (Prescher collection) – aboral view of an anomalous cup of *Abbreviatocrinites abbreviatus abbreviatus* (Goldfuss, 1839) with quadrangular symmetry (lat. I-IV), x 1.2; ***2***, CREF33a-4 (Hein collection) – oral view of an anomalous cup of *Cupressocrinites elongatus* Goldfuss, 1839 with quadrangular symmetry (lat. I-IV), x 1.9; ***3***, CREF34a-1 (Schreuer collection) – oral view of an anomalous crown of *A. a. abbreviatus* with irregularly developed hexagonal symmetry (lat. I-VI), x 1.2; ***4***, GIK-1926 – aboral view of an anomalous cup with additional plates (arrows) and accordingly misshaped basals, radials and infrabasal plate, x 1.0. ***5***, CREF98-57 (Prescher collection) – *A. inflatus inflatus* (Schultze, 1866), anomalous cup with quadrangular radial- (lat. I-IV) and pentamerous basal-symmetry. The columnal axial channel is slit-like shaped (arrow), x 2.4; ***6***, CREF33a-5 (Hein collection) – oblique lateral-aboral view of an anomalous cup of *C. elongatus* with three peripheral axial canals (arrow), x 1.2; ***7***, CREF34b-24 (Prescher collection) – aboral view of an anomalous cup of *A. a. abbreviatus* with six basals (lat. I-VI) and five peripheral axial canals (arrow), x 1.9; ***8***, CREF34a-153 (Prescher collection) – aboral view of an anomalous cup of *A. a. abbreviatus* with one missing basal plate; the imperfection is filled by an accordingly misshaped radial plate (arrow), x 1.2; ***9***, GIK-1927 – adult cup of *A. a. abbreviatus* with one swollen basal plate (framed). The surrounding region is lined with numerous small ossicles, x 0.9; ***10***, CREF116-77 (Prescher collection) – lateral view of an anomalous cup of *C. dohmi* Hauser, 1997 with one additional interradial plate (arrow), x 3.9; ***11***, CREF34a-139 (Prescher collection) – anomalous cup of *Procupressocrinus gracilis* (Goldfuss, 1831) with one additional plate (arrow), x 2.4; ***12***, Lateral view of an anomalous cup of *Abbreviatocrinites gibber* (Bather, 1919) [Hein collection; no repository no.] – with one additional, rhomb-like plate (arrow). Locality: In the Senzeille region (Ardennes, Belgium), stratigraphy: Neuville Formation, Frasnian (lower Upper Devonian), x 1.8; ***13***, IPB-1267 – lateral view of a juvenile crown of *Cupressocrinites crassus* Goldfuss, 1831 with one additional arm plate (arrow), x 1.7; ***14***, GIK-1928 – lateral view of two isolated brachials of *A. a. abbreviatus* with an abnomal exobrachial laminae (framed) covering the upper plate. This ossicle is covered by a single laminae with tubercled surface. The lower brachial is only covered by the regular basal laminae showing an undecorated surface; other exoplacoid layers sheared off, x 1.2; ***15***, GIK-1929 – isolated, misshapen brachial of *Abbreviatocrinites geminatus* Bohatý, 2005a with deformed multilamellar exobrachial layer, x 2.7; ***16***, CREF34b-159 (Prescher collection) – oblique lateral-aboral view of a cup of *A. a. abbreviatus* with a marginal positioned "wound healing" (framed), x 1.6; ***17***, CREF34a-126 (Prescher collection) – a cup of *A. a. abbreviatus* with a large "wound healing" distinguished by numerous regenerative-ossicles (framed), x 2.7; ***18***, CREF33a-6 (Hein collection) – lateral-aboral view of an strongly misshaped cup of *C. crassus*, caused by a large surfaced "wound healing" (framed), x 1.7; ***19***, CREF33a-39 (Prescher collection) – lateral view of an strongly misshaped cup of *C. crassus*, caused by a large "wound healing" (framed), x 1.8; ***20***, R.L.-3 (Leunissen collection) – lateral view of a crown of *C. ornamentus* Bohatý, 2006b. One arm was separated and regenerated above the second regular brachial plate (framed); the two flanked arms distally nestle above the regenerated arm and afford the typical cupressocrinitid defensive or resting posture of the enclosed crown, x 1.1.

3.1.5.2 Growth anomalies without classifiable causes – without indications of external influences.

In some cases it is not possible to determine a cause for a growth anomaly. The figured individuals with one additional or missing plate (Figs. 3.1.9.8, 3.1.9.10-13), with an inexplicable ossicular-swelling (Fig. 3.1.9.9), or a modified exobrachial layer (Figs. 3.1.9.14-15) are not recognisable as regeneration of the skeleton (Figs. 3.1.6.1, 3.1.7.1, 3.1.9.20), "wound healings" (Figs. 3.1.9.16-19), or as documented "generic" abnormalities (Figs. 3.1.9.1-7). No direct evidence of predatory influences like borings or bite marks (compare Figs. 3.1.10.1-10) can be recognised. Therefore, these modifications are summarised as growth anomalies without classifiable causes – without indications of external influences.

3.1.6 PREMORTEM OSSICULAR ANOMALIES AS A REACTION OF EXTERNAL INTERFERENCES – "WOUND HEALING" AND SKELETAL REGENERATION OF THECAL OR BRACHIAL INJURIES

3.1.6.1 "Wound healing"

Different sized anomalies in numerous small ossicles were recognised on ~5% of the studied cupressocrinitids (~700 aboral cups and ~300 crowns analysed). These anomalies are obviously "wound healings" of nonlethal injured individuals. Possible causes of these anomalies could be injuries caused by predators or possibly by impact-injuries with suspended clastic material. The affected regions may be small (Fig. 3.1.9.16) or large (Figs. 3.1.9.17-19). The maxim observed injury affects up to 80% of the surface of the cup.

3.1.6.2 Regeneration

Regenerations of echinoderm skeletons was recently reconsidered by MOZZI et al. (2006), exemplified by the regenerative processes of the "Mediterranean Featherstar" *Antedon mediterranea* (LAMARCK, 1816). AMEMIYA & OJI (1992) described the crinoid regeneration processes. The regeneration in fossil crinoids was also discussed by GAHN & BAUMILLER (2005). For example, they showed arm regeneration of *Rhodocrinites kirbyi*

(Wachsmuth & Springer, 1889) and *Dichocrinus cinctus* Miller & Gurley, 1890. Direct interconnections between the increase of shell-breaking predators and the number of observed arm regenerations of nonlethal injured crinoids were recognised (Gahn & Baumiller 2005, pp. 151-164). Further, Weissmüller (1998) discussed arm regeneration of the Muschelkalk-crinoid *Encrinus liliiformis* Lamarck, 1801 as did Meyer & Oji (1993) for several Eocene metacrinitids.

Arm regeneration in Devonian crinoids is recognised by the conditions specified by Gahn & Baumiller. At the juncture of the injury, the regenerated skeleton has either 1, the insertion of particularly small arms; or 2, the abrupt change in the magnitude of the arm-ossicles (2005, p. 156). The arms recognised as regenerated were all smaller than regularly developed arms (Figs. 3.1.6.1, 3.1.7.1, 3.1.9.20). Nevertheless, the arms of the relevant individuals are enclosed in the typical cupressocrinitid-like resting or avoidance posture, whereas the adjoining, normal longer arms closed about the smaller one and are tangent distally above the regenerated arm.

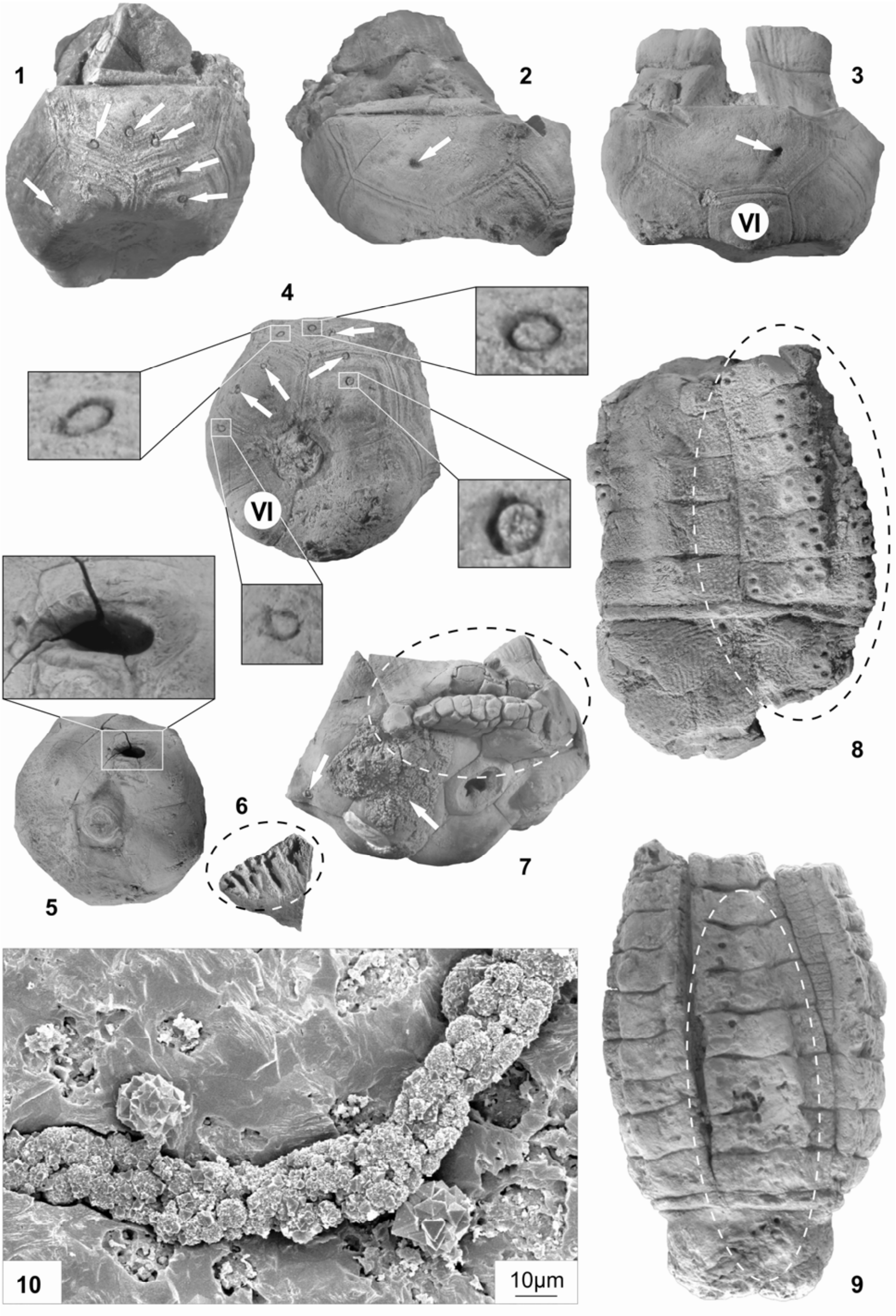
3.1.7 PRE- AND POSTMORTEM BORINGS AND BITE MARKS

3.1.7.1 Postmortem multi-borings

Almost 90% of ~50 analysed skeletons of *C. elongatus* were covered by borings (Sieverts-Doreck 1963; Bohatý 2001, p. 8; 2006b, pl. 10, figs. 1-3) [Fig. 3.1.10.8]. More infrequently, specimens with multiple borings were identified on the crowns of *C. crassus* (2006b, pl. 10, fig. 8b) [Fig. 3.1.10.9]. Both species are covered by a thin and monolamellar exoplacoid layer, which apparently offered less resistance against boring organisms, in contrast to the multilamellar layers of *Abbreviatocrinites*. Generally, these borings were restricted to the non-embedded side of the relevant skeletons and trend in inordinated lines from the cup (or also from the preserved stem) and over one or several arms. Presumably, the borings occurred soon after death. The skeletons are articulated and covered by the unsheared exoplacoid layer on the one hand, but on the other, the borings are restricted to the non-embedded side of the crown. Platyceratid gastropods were discussed as a possible causer of the borings (Sieverts-Doreck 1963). This theory cannot be verified.

Another type of multi-boring of an unknown organism is pictured in Figs. 3.1.10.1 and 3.1.10.4. In this case, several annulus-like (?)borings resulted in a circular boring

FIGURE 3.1.10 (legend p. 43)



with a raised central boss. Less probably, it is also possible that the partial ossicular-ingrowing of e.g. an unpreserved microconchid valve caused the annulus-like depression. Due to an absence of stereomatic reaction of the bored abbreviatocrinid, it is not classifiable, whether the (?)borings occurred pre- or postmortem.

3.1.7.2 Pre- and postmortem incurred single borings

Single borings are present on the ossicles of *A. abbreviatus abbreviatus*, *A. geminatus* and *R. cataphractus*. In abbreviatocrinids, they are normally restricted to the plates with sheared exoplacoid layers (Figs. 3.1.10.2-3) and, therefore, most likely occurred postmortem. The single boring of an unknown organism at the surface of the monolamellar exoplacoid layer, observed in one affected robustocrinid, is filled by a trepostome bryozoan (?*Eostenopora* sp.) [Figs. 3.1.6.3, 3.1.7.2]. Because the boring is positioned on the non-embedded side of the crown and runs across several plate boundaries, it is assumed to have occurred postmortem. Fig. 3.1.10.6 shows a sheared multilamellar exobrachial layer of *A. geminatus* which was affected by a meander-like boring of an unknown organism.

FIGURE 3.1.10 (see p. 42)—Borings [Figs. ***1-4***, ***5***(?), ***6***, ***8-10***] and bite marks (Fig. ***7***) on cupressocrinitids. ***1***, GIK-1930 – aboral-lateral view of a partly preserved crown of *Abbreviatocrinites abbreviatus abbreviatus* (GOLDFUSS, 1839) with several annulus-like borings(?) [arrows], x 1.2; ***2***, Same as 1, lateral view of the opposite side shows a single-boring (arrow), x 1.5; ***3***, Same as 1-2, another single-boring (arrow) of a radial plate with an additional flange caused by an accessory, sixth basal plate (lat. VI), x 1.4; ***4***, Same as 1-3, aboral view (x 1.1) of the additional basal plate (lat. VI) and of the annulus-like borings(?) [arrows], some of them enlarged (x 10.0); ***5***, CREF34b-1 (LEUNISSEN collection) – lateral-aboral view of an *A. a. abbreviatus*-cup (x 1.0) with a deep, oval single-boring(?) [enlarged x 3.5] of an unknown organism; ***6***, GIK-1931 – a sheared multilamellar exobrachial layer of *Abbreviatocrinites geminatus* BOHATÝ, 2005a with a meander-like boring of an unknown causer (framed), x 1.9; ***7***, CREF11c-1 (LEUNISSEN collection) – lateral-aboral view of an *A. a. abbreviatus*-cup with a partly regenerated bite mark (framed) and visible stereomatic response in form of a small bordering bulge surrounding the hole. The most affected region of basal/radial threshold shows the typical stereomatic response by the development of numerous small regenerative-ossicles. The specimen is also encrusted by *Microconchus* sp. and indeterminable tabulate corals(?) [arrows], x 1.2; ***8***, GIK-1932 – lateral view of a partly preserved crown of *Cupressocrinites elongatus* GOLDFUSS, 1839 with numerous borings on the surface of the cup- and brachial-ossicles (framed), x 1.4; ***9***, IPB-1267 – lateral view of a juvenile crown of *Cupressocrinites crassus* GOLDFUSS, 1831 with numerous borings on the surface of the cup- and brachial-ossicles (framed), x 2.2; ***10***, GIK-1933 – cross section of the multilamellar exoplacoid layer of *A. geminatus*. The SEM-picture shows a microendolithic bore trace which presumably was initially lined wih biogenic matter. Under subsequent ionic sulphide-surplus, the boring was secondary filled by marcasite crystal-agglomerates.

Baumiller & Macurda (1995) and Baumiller (1990; 1993) documented borings on Palaeozoic blastoids and crinoids. Also in this case, platyceratid gastropods were discussed as the possible borers. A significant bit of evidence for this theory is perhaps documented in the combined fossil evidence of a borehole, positioned next to a gastropod valve (Baumiller 1990).

SEM-observations of thin cross-sections of the multilamellar exoplacoid layer of *A. geminatus* exhibits potentially premortem microendolithic borings. These meandering single borings have an average proportion of 20µm in width to 300µm length. They were presumably lined with biogenous matter and ultimately resulted in a secondary sulphide-ion surplus. Through this, the borings are lined with marcasite-crystal agglomerates (FeS_2) [Fig. 3.1.10.10]. Microendolithic borings could be observed in ~70% of the studied multilamellar exoplacoid layers, but in less than 20% of the basal, radial, or brachial plates (30 thin sections analysed).

Fig. 3.1.10.5 presumably has a deep, oval (?)boring on the basal plate of *A. abbreviatus*. The visible stereomatic reaction in the form of an annulus-like swelling indicates that the single-boring occurred most likely premortem. But isolated placoderm teeth from the same location also permit the assumption that this trace may to the bite of a larger predator instead of a boring organism, like a gastropod with specialised radula.

3.1.7.3 Premortem bite marks

Bite marks at cupressocrinitids (Fig. 3.1.10.7) are rare and could be observed in less than 3% of the studied individuals (~1500 skeletons analysed). They are possibly attributed to cephalopods, placoderms or arthropods. Premortem bite marks are recognised as nonlethal injuries, because the bite marks are accompanied by "wound healings" (compare Figs. 3.1.10.7 and 3.1.9.16-19).

3.1.8 PRE- AND POSTMORTEM INCURRED EPIZONAL ENCRUSTING

The epibiontic encrusting of Devonian crinoids, exemplified by Upper Eifelian columnals, was recently discussed by Głuchowski (2005). Bryozoa, Microconchida, Crinoidea, Tabulata, Rugosa and Stromatoporida are also identified on the crown-ossicles of cupressocrinitids.

3.1.8.1 Bryozoa

3.1.8.1.1 “Cyclostome bryozoans”

“Cyclostome bryozoans” (*Hederella* sp.) apparently preferentially encrusted the crown-ossicles of *Abbreviatocrinites nodosus*. Unlike other cupressocrinitids, nearly 95% of the observed *A. nodosus*-skeletons from the Klausbach and Nims members (Fig. 3.1.8) bear encrustings (~80 skeletons analysed). The growth of the hederellids most likely occurred instantaneously postmortem, because some articulated crowns retain unsheared exoplacoid layers (Figs. 3.1.11.7-8). In contrast, the “cyclostome bryozoans” settled beyond the primary movable ossicle boundaries of the endoskeleton. Presumably, the hederellids had a rapid rate of growth. GŁUCHOWSKI (2005, figs. 4F-H) also documented the hederellid-encrusting of Upper Eifelian crinoid columnals.

Hederella is presumably not a true bryozoan (pers. information, A. ERNST; also see WILSON & TAYLOR 2001). TAYLOR & WILSON (2007) favoured a close relationship with phoronids, tentatively interpreting hederelloids as colonial, phoronid-like invertebrates with retractable lophophores. Along with microconchids and cornulitids, hederelloids may have been part of a mid-Palaeozoic acme of lophophorate “worms”.

3.1.8.1.2 Trepostome bryozoans

One brachial of a completely preserved *A. nodosus* crown (Fig. 3.1.2.8), one cup of an also entire *Abbreviatocrinites schreueri* crown (Fig. 3.1.11.4) and one theca of *P. gracilis* (Fig. 3.1.11.6) were encrusted postmortem by trepostome bryozoans (?*Eostenopora* sp.). The boring trace of an affected *Robustocrinites* arm is also populated by (?)*Eostenopora* sp. (Figs. 3.1.6.3, 3.1.7.2); in this case, the colony settled in a non-exposed position.

3.1.8.1.3 Fenestrate bryozoans

Especially within the uppermost Ahbach Formation (lowermost Lower Givetian) of the “Wotan Quarry” (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), several longer stems of *A. geminatus* and *P. gracilis* (Fig. 3.1.11.1) were found encrusted by fenestrate bryozoans. The length of the overgrown columnals as well as some observed embedding patterns of bryozoans located underneath the attached stem, allows the presumption of a premortem settlement (compare BOHATÝ 2005a, fig. 3B). In contrast, some shorter stem fragments or other disarticulated cupressocrinitid-ossicles (Fig. 3.1.11.2) were usually encrusted postmortem. This assumption is based on the entire enclosure of some skeletal elements.

Similarly holdfasts of most likely rhomboporid bryozoans attached to the columnals of *Schyschcatocrinus creber* DUBATOLOVA, 1975, as reported by GŁUCHOWSKI (2005, figs. 3A-B). GŁUCHOWSKI indicated that the bryozoans lived attached to the fragmented dead stems that lay horizontally on the sea floor.

Strong evidence for the settlement of a living stem of *C. hieroglyphicus* is given in Figs. 3.1.11.16-18. The example is encrusted by the holdfast of a fenestrate bryozoan (*Cyclopelta* sp.) that grows all around the column without contact to the crenularium. The reticulate bryozoan colony surrounded the stem, whereas the dissepiments built concentric rings characteristic for this genus.

3.1.8.2 Crinoidea

3.1.8.2.1 Cladida

One observed cup of *A. abbreviatus abbreviatus* (Fig. 3.1.11.9) as well as one isolated radial and arm plate of *A. geminatus* were encrusted by the holdfasts of other cladid crinoids (?*P. gracilis*). The roots settled postmortem on the shearing of the multilamelar exoplacoid layer (Fig. 3.1.11.9), at the interior of a radial plate (Fig. 3.1.11.22), or at the multilamellar exobrachial layer of an isolated brachial (Fig. 3.1.11.13). This association was observed on less than 3% of the studied crinoids (~1500 skeletons analysed).

GŁUCHOWSKI (2005, p. 322) documented the postmortem encrusting of several small crinoid holdfasts attached to Upper Eifelian crinoid columnals.

Various attachments of crinoid juveniles to living or dead adults are known from the Silurian to the Mississippian (see MEYER & AUSICH 1983). Coiling stems, modified discoid holdfasts on the columns of crinoid hosts as well as dendritic holdfasts distributed on all sides of the column were reported from Silurian strata by FRANZÉN (1977) and PETERS & BORK (1998).

3.1.8.3 (?)Lophophorata

3.1.8.3.1 Microconchida

Microconchids with unstructured or ornamented valves encrusted the ossicles of nearly 40% of the studied cupressocrinitids (~1500 skeletons analysed). It is remarkable, that larger individuals are rare and isolated (compare BOHATÝ 2006b, pl. 5, fig. 8), whereas numerous smaller microconchids encrusted the crinoids (Figs. 3.1.2.6, 3.1.11.7-8). Most likely, the colonisation occurred immediately postmortem, before shearing of the exoplacoid layers and ossicle disarticulation.

The single-species encrusting of microconchids on the columnals of *Tantalocrinus scutellus* LE MENN, 1985 and *Schyschcatocrinus creber* DUBATOLOVA, 1975, represent additional settlement examples (GŁUCHOWSKI 2005, p. 323; figs. 5I-L).

3.1.8.4 Anthozoa

3.1.8.4.1 Tabulata

The predominantly postmortem settlement of tabulate corals was recognised on 5-10% of the studied cupressocrinitids (~1500 skeletons analysed). The most common epibiontic tabulates were auloporids like *Aulopora* cf. *A. serpens minor* (GOLDFUSS, 1829) [Figs. 3.1.11.5, 3.1.11.7, 3.1.11.20] and *A.* cf. *A. s. serpens* (GOLDFUSS, 1829) [Fig. 3.1.11.11], settling on isolated crown-ossicles, completely preserved cups of *A. geminatus* and on the crowns of *A. nodosus*. Fig. 3.1.11.20 shows a completely overgrown cup of *A. nodosus*.

Furthermore, one cup of *A. a. abbreviatus* with an encrusting favositid coral (*Favosites* cf. *F. goldfussi* D'ORBIGNY, 1850) was found within the lower part of the Loogh Formation (Lower Givetian) in the “Wotan Quarry” (Hillesheim Syncline) [Fig. 3.1.11.12]. GŁUCHOWSKI (2005) documented small colonies of *Favosites* sp. attached to *Pentagonostipes petaloides* MOORE & JEFFORDS, 1968 and *Tantalocrinus scutellus* LE MENN, 1985 and discussed the possible growth along the axis of the upright stalk of a living host. Favositids that lived attached to living crinoid hosts have also been reported from the Upper Silurian (HALLECK 1973; BRETT & ECKERT 1982; PETERS & BORK 1998), Lower Devonian (GALLE 1978; GALLE & PROKOP 2000) and Lower Carboniferous (compare MEYER & AUSICH 1983).

***FIGURE* 3.1.11 (legend p. 49)**

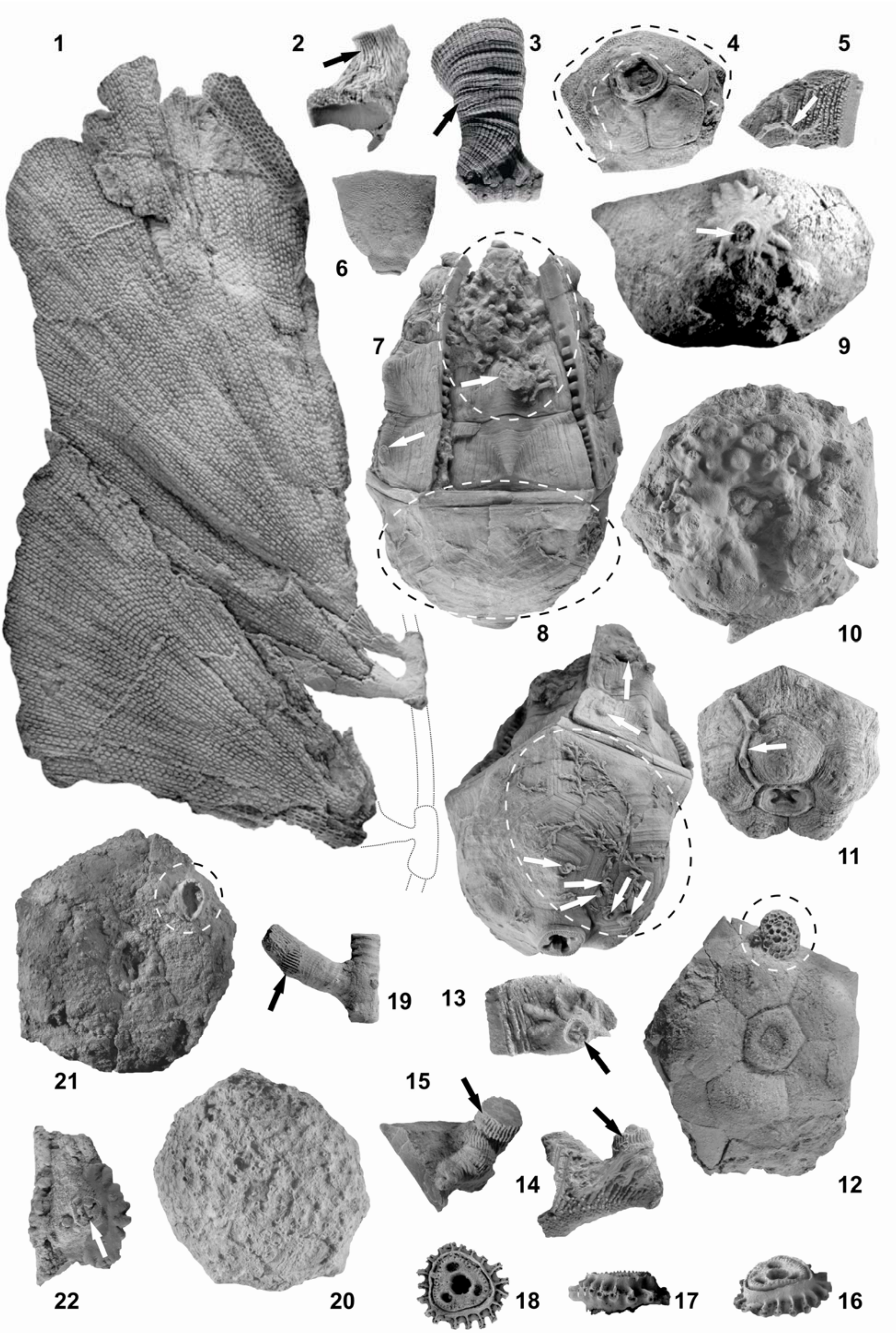


FIGURE 3.1.11 (see p. 48)—Epibiontic encrusting of cupressocrinitid-skeletons. ***1***, GIK-1934 – undetermined fenestrate bryozoans attached to a longer part of the stem of *Procupressocrinus gracilis* (GOLDFUSS, 1831) [?]. Partly reconstructed (dashed lines) accordingly to the preserved imprint, x 1.3; ***2***, GIK-1935-ex-PAgA12.4 – the holdfast of an undetermined fenestrate bryozoan (arrow) encrusted the cracked arm plate of *Abbreviatocrinites geminatus* BOHATÝ, 2005a, x 1.3; ***3***, GIK-1936 – the rugose coral *Glossophyllum soetenicum* (SCHLÜTER, 1885) [arrow] encrusting the stem of *P. gracilis* (?), x 1.4; ***4***, CREF84-1 (LEUNISSEN collection) – aboral view of a cup of *Abbreviatocrinites schreueri* BOHATÝ, 2006b, encrusted by a trepostome bryozoan (?*Eostenopora* sp.), x 1.8; ***5***, GIK-1937-ex-PAgA12.17 – arm plate of *A. geminatus* with preserved multilamellar exoplacoid layer, encrusted by the tabulate coral *Aulopora* cf. *A. serpens minor* (GOLDFUSS, 1829) [arrow], x 1.8; ***6***, CREF33a-9 (HEIN collection) – lateral view of a *P. gracilis*-cup, the specimen is completely overgrown by a trepostome bryozoan (?*Eostenopora* sp.), x 1.5; ***7***, GIK-1938 – lateral view of a closed crown of *Abbreviatocrinites nodosus* (SANDBERGER & SANDBERGER, 1856) encrusted by an epibiontic tabulate coral *Aulopora* cf. *A. serpens minor* (see framing at the centre above), *Hederella* sp. (framing, centre below) and *Microconchus* sp. (arrows), x 1.4; ***8***, Same specimen as 7, oblique lateral-aboral view of the cup with encrusted hederellids (framed) and microconchids (arrows), x 1.4; ***9***, GIK-1939-ex-PAgA11.8 – cup of *Abbreviatocrinites abbreviatus abbreviatus* (GOLDFUSS, 1839) with sheared exoplacoid layer. The specimen is infested by a cupressocrinitid holdfast (?*P. gracilis*) [arrow], x 1.4; ***10***, GIK-1940 – aboral view of a cup of *A. a. abbreviatus*, completely encrusted by indeterminable stromatoporoids, x 0.8; ***11***, CREF34c-8 (SCHREUER collection) – lateral-aboral view of an *A. geminatus*-cup, infested by the tabulate coral *Aulopora* cf. *A. serpens serpens* (GOLDFUSS, 1829) [arrow], x 1.2; ***12***, GIK-1941 – aboral view of a cup of *A. a. abbreviatus*. One basal is encrusted by a favositid coral (*Favosites* cf. *F. goldfussi* D'ORBIGNY, 1850) [framed], x 0.9; ***13***, GIK-1942 – lateral view of an isolated arm plate of *A. geminatus*. The preserved multilamellar exoplacoid layer is encrusted by the holdfast of *P. gracilis* (?) [arrow], x 1.4; ***14***, GIK-1943 – lateral view of an isolated arm plate of *A. geminatus* with preserved multilamellar exoplacoid layer. The exemplar is encrusted by the rugose coral *Thamnophyllum caespitosum* (GOLDFUSS, 1826) [arrow], x 2.1; ***15***, GIK-1944 – lateral view of a fractured arm plate of *A. geminatus*. The exemplar is encrusted by the rugose coral *T. caespitosum* (arrow), x 1.8; ***16-18***, GIK-1945– SEM-pictures of an isolated stem-ossicle of *Cupressocrinites hieroglyphicus* (SCHULTZE, 1866) [***16-17***, lateral view; ***18***, axial view with three peripheral canals and intact partition walls to the central-canal, showing a quartering subdivision]. The segment is entirely encrusted by the holdfast of a fenestrate bryozoan (*Cyclopelta* sp.) growing all around the ossicle, x 5.1; ***19***, GIK-1946 – a stem of *P. gracilis* (?), infested by the epibiontic rugose coral *T. caespitosum* (arrow), x 1.4; ***20***, GIK-1947 – aboral view of an *A. nodosus*-cup. The specimen is completely encrusted by the tabulate coral *Aulopora* cf. *A. s. minor*, x 1.2; ***21***, GIK-1948 – aboral view of a cup of *A. a. abbreviatus*. The specimen is completely encrusted by stromatoporoids and tabulate corals and also by an indeterminable juvenile stadium of a rugose coral, x 0.9; ***22***, GIK-1949-ex-PAgA12.2 – interior side of an isolated radial plate of *A. geminatus*. The plate is infested by the holdfast of *P. gracilis* (?), x 1.2.

Other tabulate corals (e.g. *Antholites*, *Cladochonus* and *Emmonsia*) associated with living crinoids are known from Devonian–Mississippian strata (GŁUCHOWSKI 2005, p. 319; also see MEYER & AUSICH 1983; POWERS & AUSICH 1990 and DONOVAN & LEWIS 1999).

3.1.8.4.2 Rugosa

Within the Ahbach and Loogh formations (Eifelian/Givetian threshold) in the "Wotan Quarry" (Hillesheim Syncline), rugose corals settled on disarticulated cupressocrinitid stems and isolated ossicles, including *Glossophyllum soetenicum* (SCHLÜTER, 1885) [Fig. 3.1.11.3] and *Thamnophyllum caespitosum* (GOLDFUSS, 1826) [Figs. 3.1.11.14-15, 3.1.11.19]. The additional recovery of a completely overgrown theca (stromatoporoid suffusions, see below) documents a further epibiontic settlement by an indeterminable juvenile stadium of a rugose coral (see encircling in Fig. 3.1.11.21). All settlements occurred postmortem.

GŁUCHOWSKI (2005, pp. 317-319) detected the premortem encrustings of the rugose coral (?)*Adradosia* sp. on *Schyschcatocrinus creber* by the stereomic response of the crinoid.

3.1.8.5 (?)Porifera

3.1.8.5.1 Stromatoporida

Some non-disarticulated cups of *A. a. abbreviatus* were completely encrusted by indeterminable stromatoporoid suffusions (Figs. 3.1.11.10, 3.1.11.21). These encrustings could be settled again by chaetetids, tabulate and rugose corals, microconchids and bryozoans.

3.1.9 DISCUSSION

With intensive fossil collecting within the Eifel synclines, hitherto undescribed members of the subfamily Cupressocrininae were determined. Also, research on several classical collections, especially of the SANDBERGER collection at the NWNH, added significantly to the revision of the Cupressocrinitidae.

Biostratigraphical distributions were also studied. As one result it is demonstrated, that *Robustocrinites* was limited to regional geological events as was *Bactrocrinites* within the Rhenish Massif (Germany) [compare BOHATÝ 2005b]. Furthermore, the SANDBERGER cupressocrinitids from the Lahn-Dill Syncline had a longer stratigraphical range of *A. nodosus, A. a. abbreviatus*, *A. geminatus* and *A. sampelayoi* than previously known.

Ossicular-modifications recognised on the subfamily Cupressocrininae were predominantly classified on the basis of pertinent literature.

According to the diagnostic features of GAHN & BAUMILLER (2005), arm regeneration could be identified by the insertion of particularly small arms and/or abrupt changes in the magnitude of the arm-ossicles. Regeneration in the cupressocrinitid arm is presumably superior to the cup regeneration. Whereas a regenerated arm is smaller, the brachial is nearly as perfectly shaped as the primary one. The regeneration of the cup mostly leads to distorted cups. This difference may be attributed to the significant arm functions of ingestion and reproduction. In opposition, the thecal-ossicles were mainly responsible for the soft body protection. This basic function does not require "perfect shapes".

Studied growth anomalies without recognisable external influences are distinguished by the reduction of thecal or brachial-ossicles respectively by additional small plates. These anomalies are not attributed to injuries and are considered genetically modified anomalies. The majority of these thecal anomalies are equivalent to similarly modified specimens of other crinoid-subclasses. The most common anomalies in cupressocrinitids are modified peripheral axial canals of the stem. This observation is similar to other Gasterocomoidea, which were distinguished by three to four peripheral axial canals.

Borings and bite marks were mostly identified as pre- or postmortem incurred events, whereas the causers are predominantly unknown. Different borings of crinoid skeletons were previously described by SIEVERTS-DORECK (1963), BAUMILLER & MACURDA (1995) and BAUMILLER (1990; 1993). Although these traces were associated with platyceratid gastropods, definite proof of this theory is still missing. The typical marks on effected crinoids (e.g. observed in the camerate family Hexacrinitidae WACHSMUTH & SPRINGER, 1885) from the Middle Devonian of the Eifel have other patterns that will be discussed in a separate publication.

Most of the recently described epibionts on Devonian crinoid columnals (GŁUCHOWSKI 2005) could also be observed on Middle Devonian cupressocrinitid skeletons from the Rhenish Massif. In this connection, especially the encrusting of articulated cups and of completely preserved crowns is remarkable. This fact requires either high growth accelerations of the epibionts or an immediate microbial cladding related to a possible ossicular preservation.

The majority of the epibiontic encrustations most were probably postmortem. Only a few examples of individuals that were potentially premortem encrusted were observed. This is confirmed by encrusting of the fenestrate holdfast growing around the entire column without contact to the crenularium.

The preserved or sheared exoplacoid layer of the subfamily Cupressocrininae provide information about pre- or postmortem settling of the different epizoans. Therefore, in addition to the taxonomic relevance of the second skeletal layer, this feature provides insight on the facies (BOHATÝ 2005a) and the ecological conditions.

3.1.10 APPENDIX

3.1.10.1 The fossil localities and stratigraphic positions of the studied crinoids

NWNH-297 and -408, Locality: “Grube Lahnstein” near Weilburg-Odersbach, NE of Limburg an der Lahn (Lahn-Dill Syncline, SE-Rhenish Massif, Germany), stratigraphy: Upper Givetian “Roteisenstein”.

SMF-75459, Locality: N-slope of the western access route to the abandoned “Weinberg Quarry”, NW of Kerpen (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Nims Member of the lower Grauberg Subformation, upper Junkerberg Formation (upper Middle Eifelian).

SMF-75460, Locality: Abandoned “Müllertchen Quarry”, S of Ahütte (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: upper Olifant Member of the lower Müllert Subformation, upper Ahbach Formation (lowermost Lower Givetian).

SMF-75461, Locality: Rommersheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Olifant Member of the lower Müllert Subformation, Ahbach Formation (lowermost Lower Givetian).

IPB-434a, -435b and -1267, Locality: Pelm, E of Gerolstein (Gerolstein Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Hustley Member of the upper Loogh Formation (Lower Givetian).

GIK-1924, -1938 and -1947, Locality: SW-housing subdivision area of village Gondelsheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Nims Member of the lower Grauberg Subformation, upper Junkerberg Formation (upper Middle Eifelian).

GIK-1925, Locality: S-slope of the access route to the Ahütte lime works, E of country road "L10", S of Üxheim / W of Ahütte (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Uppermost Rechert Member of the upper Heinzelt Subformation, middle Junkerberg Formation (upper Middle Eifelian).

GIK-1926, -1927, -1930, -1939-ex-PAgA11.8 and -1940, Locality: "Wotan Quarry" near Ahütte, SE of Üxheim (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Upper Wotan Member of the lower Loogh Formation (Lower Givetian).

GIK-1928, Locality: Commercial area, NE of Blankenheim (Blankenheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Uppermost Bohnert Member of the upper Freilingen Formation (Upper Eifelian).

GIK-1929, -1931, -1933, -1934, -1935-ex-PAgA12.4, -1936, -1937-ex-PAgA12.17, -1942, -1943, -1944, -1946 and -1949-ex-PAgA12.2, Locality: "Wotan Quarry" near Ahütte, SE of Üxheim (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Lowermost Zerberus Member of the upper Müllert Subformation, upper Ahbach Formation (lowermost Lower Givetian).

GIK-1932, Locality: Dasberg, E of Gerolstein (Gerolstein Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Hustley Member of the upper Loogh Formation (Lower Givetian).

GIK-1941 and -1948, Locality: "Wotan Quarry" near Ahütte, SE of Üxheim (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Lower Wotan Member of the lower Loogh Formation (Lower Givetian).

GIK-1945, Locality: NE-slope of the access pathway to the abandoned "Müllertchen Quarry", south of Ahütte (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Lahr Member of the upper Maiweiler Subformation, Ahbach Formation (Eifelian/Givetian threshold).

CREF11b, Locality: Abandoned "Müllertchen Quarry", south of Ahütte (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Olifant Member of the lower Müllert Subformation, Ahbach Formation (lowermost Lower Givetian).

CREF11c, Locality: “Müllertchen Quarry”, stratigraphy: Lowermost Zerberus Member of the upper Müllert Subformation, upper Ahbach Formation (lowermost Lower Givetian).

CREF16c, Locality: Rommersheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Olifant Member of the lower Müllert Subformation, Ahbach Formation (lowermost Lower Givetian).

CREF33a, Locality: NE-slope of the railway cut, 400 m east of railway station Gerolstein (Eifel, Gerolstein Syncline, Rhenish Massif, Germany), stratigraphy: Hustley Member of the upper Loogh Formation (Lower Givetian).

CREF34a, Locality: “Wotan Quarry” near Ahütte, SE of Üxheim (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Lower Wotan Member of the lower Loogh Formation (Lower Givetian).

CREF34b, Locality: “Wotan Quarry” near Ahütte, SE of Üxheim (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Upper Wotan Member of the lower Loogh Formation (Lower Givetian).

CREF34c, Locality: “Wotan Quarry” near Ahütte, SE of Üxheim (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Lowermost Zerberus Member of the upper Müllert Subformation, upper Ahbach Formation (lowermost Lower Givetian).

CREF84, Locality: Gondelsheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Klausbach Member of the lowermost Heinzelt Subformation, lowermost Junkerberg Formation (upper Middle Eifelian).

CREF98, Locality: SW-housing subdivision of village Schwirzheim, SE of Gondelsheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Hönselberg Member of the Heinzelt Subformation, Junkerberg Formation (upper Middle Eifelian).

CREF116, Locality: Weinsheim, N of the “Niesenberg” (Prüm Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Upper Rech Member of the upper Loogh Formation (Lower Givetian).

CREF180, Locality: SW-housing subdivision of village Gondelsheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), stratigraphy: Nims Member of the lower Grauberg Subformation, upper Junkerberg Formation (upper Middle Eifelian).

CRBG7, Locality: Abandoned quarry at the “Schlade Valley”, near Bergisch-Gladbach (Bergisch Gladbach-Paffrath Syncline, Bergisches Land, Rhenish Massif, Germany), stratigraphy: Upper Büchel Formation (lower Middle Givetian).

R.L.-3, Locality: Bou Dib, Nothern-Maider, Jebel Issimour (Morocco), stratigraphy: Lower Eifelian.

3.2 CHAPTER II. CRINOIDEA, CAMERATA

REVISION OF THE HEXACRINITIDAE BASED ON A CLASSICAL LOWER GIVETIAN CRINOID DEPOSIT (GEROLSTEIN, EIFEL/GERMANY)

ABSTRACT—The classic Lower Givetian crinoid occurrence of the northeastern slope of the railway cut near the station of Gerolstein (northwestern Rhineland-Palatinate, westernmost Germany) is famous for yielding an outstanding diversity of the monobathrid camerate family Hexacrinitidae. Following a short palaeogeographical and stratigraphical introduction of the Gerolstein Syncline (Eifel, Rhenish Massif), the previously described "*Hexacrinites*" species of this locality are revised. They clearly differ from the type species **Platycrinus interscapularis* (genus *Hexacrinites*) by the development of uniserial arms, longer aboral cups and other morphological criteria, like a single posterior interradial plate. Therefore, most of the Eifel species are assigned to the genus *Megaradialocrinus* (with **Megaradialocrinus conicus* as its type species), which is herein transferred to superfamily Hexacrinitoidea and family Hexacrinitidae. The extent of morphological differences among other hexacrinitids is discussed and may define further intergeneric differentiation. Five new species are described: *Megaradialocrinus aliculatus* n. sp.[1], (?)*M. bulbiformis* n. sp.[2], *M. piriculaformis* n. sp.[3], *M. theissi* n. sp.[4] and *M. winteri* n. sp.[5] The homonym "*Hexacrinites magnificus*" *sensu* HAUSER (2007a) is renamed: *Megaradialocrinus globohirsutus* n. nov.[6]

3.2.1 INTRODUCTION

The famous Middle Devonian crinoid localities of Gerolstein (Gerolstein Syncline, Eifel, Rhenish Massif, westernmost Germany) [Fig. 3.2.1.1] include several famous deposits of Middle Devonian macrofossils. In addition to corals, stromatoporoids, bryozoans, brachiopods, gastropods, trilobites, cephalopods and placoderms, the diverse spectrum of

---

[1] = *Megaradialocrinus aliculatus* BOHATÝ, in press *sensu* ICZN
[2] = (?)*M. bulbiformis* BOHATÝ, in press *sensu* ICZN
[3] = *M. piriculaformis* BOHATÝ, in press *sensu* ICZN
[4] = *M. theissi* BOHATÝ, in press *sensu* ICZN
[5] = *M. winteri* BOHATÝ, in press *sensu* ICZN
[6] = *Megaradialocrinus globohirsutus* BOHATÝ, in press *sensu* ICZN

mostly well- preserved crinoids is appreciable. At the northeastern slope of the railway cut near the station of Gerolstein [NESG], camerate crinoids of the family Hexacrinitidae WACHSMUTH & SPRINGER, 1885 occur in high diversity and abundance. Well-preserved aboral cups of the genus *Megaradialocrinus* CHEN & YAO (1993, pp. 56-57; figs. 32a-b; pl. 12, figs. 9a-b) are especially abundant within the marly sediments of the Hustley Member (uppermost Loogh Formation, Lower Givetian) at this locality, which is near the type locality of the Hustley Member *sensu* WINTER (1965) [Tab. 3.2.1.2].

3.2.2 PALAEOGEOGRAPHICAL SETTING

Within the central European Variscan fold belt, the Rhenish Massif and the Ardennes are separated by a north-south trending axial depression, the “Eifel Limestone Synclinorium”. Deposits of the Middle Devonian and, in part, of the Upper Devonian are preserved within the synclines, and the anticlines between them are the Lower Devonian strata. The Eifel Limestone Synclinorium is bordered in the northwest and north by the older Palaeozoic “Stavelot-Venn Massif” and in the northeast by the “Mechernich Triassic Bight” (Fig. 3.2.1.1). The eastern boundary is characterised by the western limb of the “Siegerland-Eifel Anticlinorium”. The southern boundary is the older Lower Devonian of the “Manderscheid Anticlinorium”, in which the “Trier Triassic Bight” is adjacent to the south (Fig. 3.2.1.1).

The Devonian marine realm of the Eifel was bordered in the north by the “Old Red Continent”, which was the source area for the clastic sedimentary input. The sedimentary input accumulated from the Lower to the Upper Devonian with a retreating coastline toward the north. Because of massive sedimentary input during the Lower Devonian, essentially only clastic sediments were deposited. With the beginning of the Middle Devonian, carbonate sedimentation occurred in the area of the later Eifel Limestone Synclinorium as well as to the north of the Venn Massif in the Ardennes. The Moselle area, the deepest and most distal part of the sedimentary basin, is characterised by fine-grained siliciclastic sediments. In this palaeogeographical setting a lithostratigraphic/facies trichotomy of the Devonian sequence occurs in the region north of the “Venn Anticline”, the extent of the Eifel Limestone Synclinorium and the “Moselle Trough” (MEYER 1986).

W. STRUVE (1961; 1963) proposed the first palaeogeographic reconstruction of the Eifel Middle Devonian. He considered the depositional region as an isolated north-south trending basin surrounded by landmasses, which he denoted as “Eifel Sea Street”.

Reef growth occurred to the west of the eastern mainland called “Istaevonia” (= “Siegen Block”) and on the “Middle Eifel Barrier” (“Krömmelbein Structure” of Struve 1961, p. 98). The so called “Manderscheid Barrier” was positioned to the south and connected the land of Istaevonia with the mainland of “Arduennia” in the west and separated the comparative shallow Eifel Sea from the deeper Moselle Trough to the south. Struve also presumed that a huge island, on the Venn Massif, divided the Eifel Sea Street in the northwest.

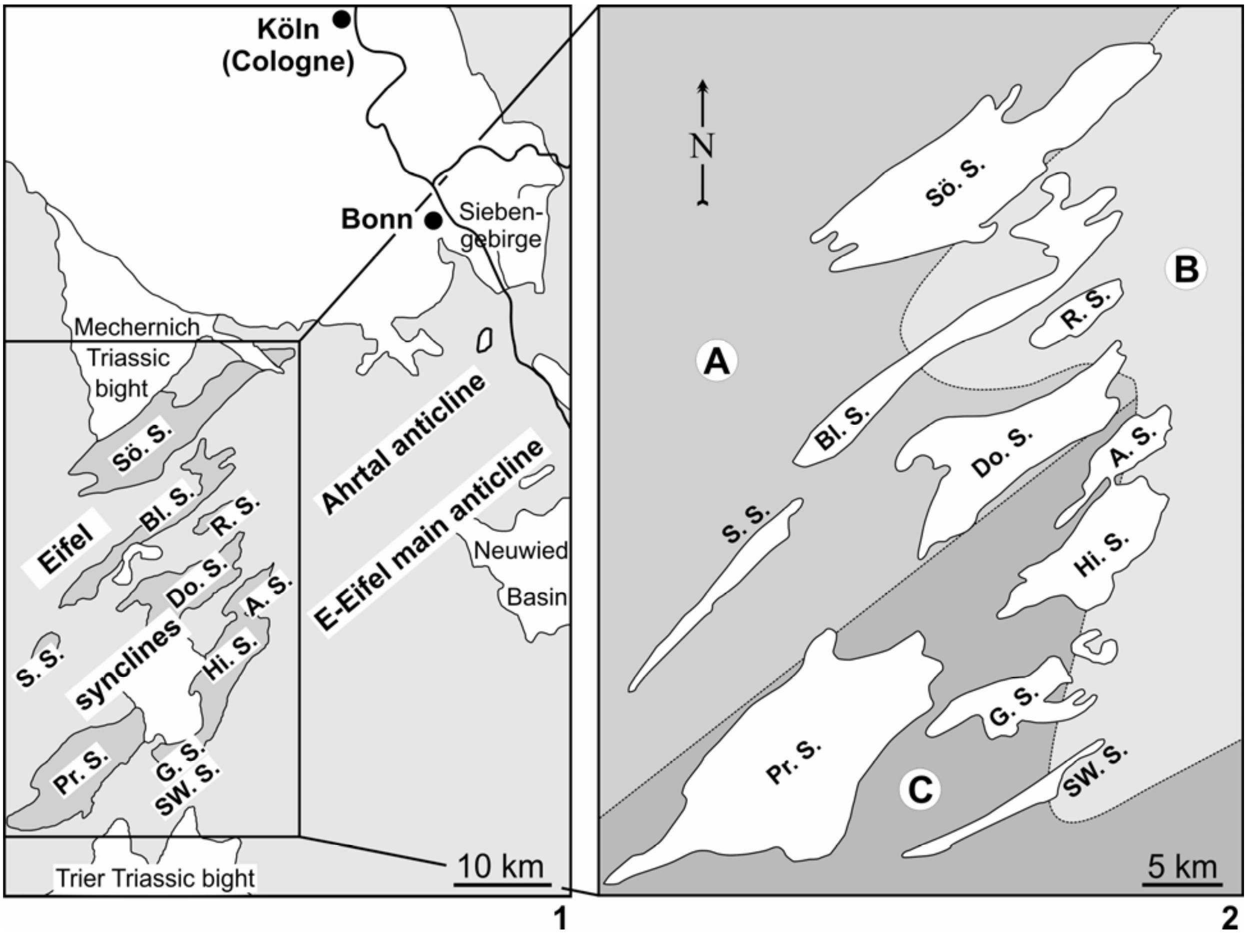


Figure 3.2.1—1, Geological sketch of the Middle Devonian Eifel Limestone Synclinorium (after Walter 1995); legend: **Sö. S.**, Sötenich Syncline; **Bl. S.**, Blankenheim Syncline; **R. S.**, Rohr Syncline; **Do. S.**, Dollendorf Syncline; **S. S.**, Schneifel Syncline; **A. S.**, Ahrdorf Syncline; **Hi. S.**, Hillesheim Syncline; **Pr. S.**, Prüm Syncline; **Ge. S.**, Gerolstein Syncline; **SW. S.**, Salmerwald Syncline; **light grey**, Lower Devonian; **dark grey**, Middle Devonian; **white**, post Palaeozoic strata. ***2***, Idealised facies model of the Middle Devonian of the Eifel according to Winter (1977); **type A**, facies dominated by clastic input; **type B**, facies characterised by carbonate platforms and biostromal reefs; **type C**, reduced clastic input and increasing limy facies.

STRUVE (1961; 1963) provided an important foundation for all later palaeogeographical work. Today, particularly, the isolated palaeogeographic position of the depositional basin as well as the accentuation of distinctively developed boundaries in the form of barriers and islands is reinterpreted differently. Research within the Venn area has shown that the Middle Devonian of the Aachen area (northwest of the Eifel Limestone Synclinorium) is dominated by coarse clastic material up to the Middle Givetian. This sequence was interpreted as coastal sedimentation along the southern edge of the "Brabant Massif" (KASIG & NEUMANN-MAHLKAU 1969, p. 381). The finer clastical sediments of the Eifelian in the northern part of the Eifel Limestone Synclinorium document a gradual ablation of the coast toward the Limestone Synclinorium. Therefore, STRUVE's island cores are no longer necessary. Researches within the "Manderscheid Barrier" (KREBS 1970) to the south of the Salmerwald Syncline demonstrate a transition between a carbonate and a fine-grained siliciclastic facies without an intervening barrier. An explanation for this may be the topography of the sea bottom, perhaps a distal ramp. According to STRUVE (1961; 1963), the west coast of Istaevonia was dominated by a carbonate platform or respectively by a reef barrier. Admittedly, within the eastern part of the Eifel Limestone Synclinorium, there is no evidence of any siliciclastic input. Also because of palaeotectonic reasons, an emergent area that would correspond with the Siegerland Block is implausible.

The current palaeogeography and facies model of the Middle Devonian of the Eifel, especially of the Eifelian, was initially developed by WINTER (in MEYER, STOLTIDIS & WINTER 1977, p. 327), who defined three characteristic facies realms (facies types A-C) [see Fig. 3.2.1.2]. Facies type A, distinguished by clastic sediments, is developed within the northern Eifel Limestone Synclinorium. Carbonates are proportionally rare. In the northern part of the synclinorium, the sediments were not deposited under normal marine conditions. Normal marine conditions occurred toward the south. At about the axis of the Dollendorf Syncline, the changeover to facies type C occurred. Type C is characterised by limestones and marls. Clastic components are sparse. Toward the south, the clay content increases, and type C facies passes into the clay rich facies of the Moselle Trough (= "Wissenbach Slate"). The third facies type (type B) is developed within the eastern part of the Eifel Limestone Synclinorium. It is characterised by pure, commonly biostromal limestones; marly as well as silty sediments are secondary. This facies type characterises a shallow water area, which lay close to a shallow water barrier at the eastern Eifel. Type B facies dominates the eastern parts of the Salmerwald, Gerolstein, Hillesheim, Ahrdorf and Sötenich synclines, as well as parts of the Rohr and the middle and eastern part of the Blankenheim synclines. This basic division of facies types applies at least to the Junkerberg Formation (Eifelian), but within some time slices, it was modified, e.g. at the Niederehe Subformation, biostromal beds were established nearly at the complete northern Eifel sea area during a transgression. Alternatively, facies type A expanded toward the south during times of low sea level. In this case, sedimentation within the upper part of the Nohn Formation and the Junkerberg Formation was dominated by clastic input. Beginning with the Freilingen Formation (Upper Eifelian), facies differences disappear. Because of a transgression, facies type C was established all over the depositional area. In the Givetian, stromatoporoid coral biostromes extended all over the Eifel Sea.

By accentuating the validity of the three facies types, FABER (1980, p. 112) modified WINTER's model. FABER differentiated two palaeogeographical situations within the Lower Eifelian: (a) A relatively undifferentiated open shelf, which is characterised by southwest-northeast trending facies belts; (b) a carbonate platform, which was developed twice within the eastern part of the Limestone Synclinorium, while the western synclinorium was still dominated by "normal" shelf sedimentation. Thus, a second structural control developed, trending north-south. In the Lower Givetian, the whole Eifel region was bounded by a tectonic high within the southern part of the synclinorium (KREBS 1974).

3.2.3 STRATIGRAPHY: "TYPE EIFELIAN" *VS.* REGIONAL STRATIGRAPHIC DENOMINATION OF THE GEROLSTEIN SYNCLINE

The Middle Devonian sequence of the Eifel is subdivided into several formations, subformations and members (Tab. 3.2.1.1), which are separated by lithological as well as faunal criteria. The reference profile is the so called "Type Eifelian Profile" within the Hillesheim Syncline (STRUVE 1982a; STRUVE & WERNER 1982). Because of the facies complexity within the Limestone Synclinorium (see above), several members have a restricted regional extent and detailed stratigraphic nomenclature differ from the Type Eifelian.

The Gerolstein Syncline, from which the crinoids described here were discovered, is dominated by Lower Givetian deposits, which clearly differ from the Type Eifelian area. Therefore, several local members of the Loogh and Cürten formations were established by WINTER (1965) [Tab. 3.2.1.2]. He also differentiated Gerolstein southwestern from a northeastern regional facies, whose differences were clearly visible at the times of the Cürten Formation.

The Lower Givetian of the Gerolstein Syncline is represented by poorly exposed strata of the uppermost Ahbach Formation and by the lime-marl successions of the overlying Loogh and Cürten formations, which together with younger dolomitised formations (Tab. 3.2.1.1-2) dominate the syncline.

The base of the Loogh Formation is distinguished by the Dachsberg Member (Tab. 3.2.1.2) with homogeneous limestones with sparsely preserved macrofossils (WINTER 1965). These limestones were deposited under quiet conditions (1965, p. 307). According to WINTER (1965, p. 289), the Dachsberg Member is restricted to the southwest of the Gerolstein Syncline. Increasing shallowing of the sedimentation area led to incipient biostromal growth and, therefore, to facies differentiation, characterising the Baarley Member of WINTER (1965, pp. 289-290). Massive trochite dominated limestones and "matrix limestones" characterise the member. Regular limestone and marl interbedded strata increase toward the boundary of the Hustley Member (1965, pp. 290-292) and represent a temporary decrease in sedimentation, which was limited by the new appearance of stromatoporoid coral biostromes that distinguish Hustley Member. These biostromes with partly limy and partly marly deposits lead to a maximal facies differentiation at this time.

			Formations	Members of the Type Eifelian within the Hillesheim Syncline (sensu STRUVE 1982a)	regional valid Members of the Loogh Formation within the Gerolstein Syncline (sensu WINTER 1965)	
Middle Devonian	Lower Givetian	*hemiansatus* Conodont Biozone	Rodert Fm.	Korallen-Brachiopoden-Kalk Mb.	**Gerolstein SW facies**	**Gerolstein NE facies**
				Stringoc.-Korallen-Kalk Mb.		
				quadr.-ramosa-Kalk Mb.		
				caiqua-Kalk Mb.	Meerbüsch Mb.	Bungerberg Mb.
			Dreimühlen Fm.	Galgenberg Mb.		
				Ley Mb.	Forstberg Mb.	
				Binz Mb.		
			Cürten Fm.	Meerbüsch Mb.	Marmorwand Mb.	
				Forstberg Mb.		
				Marmorwand Mb.	Felschbach Mb.	Berlingen Mb.
				Felschbach Mb.		
			Loogh Fm.	Rech Mb.	Hustley Mb.	
				Wotan Mb.		
			Ahbach Fm.	Zerberus Mb.	Baarley Mb.	
				Olifant Mb.		
				Lahr Mb.	Dachsberg Mb.	
				Hallert Mb.		
				1		**2**

TABLE 3.2.1—The lowermost Lower Givetian stratigraphy of the "Type Eifelian Profile" sensu STRUVE (1982a) [*1*] and comparison with the regional valid Member of the Cürten and Loogh formations (**grey**) within the Gerolstein SW and NE facies (after WINTER 1965) [*2*].

The type locality of the Hustley Member is close to the NESG and, thus, next to the crinoid localities discussed here. The Hustley Member is generally dominated by encrinitic limestones of minor thicknesses, limestone banks, massive "matrix limestones" and greenish to brighter ochre or brownish marls. Because of the lateral facies interfingering, all rock types were developed side by side. In the study area, local marl packages of several meters are interrupted by isolated stromatoporoid coral biostromes. The biostromes locally interfinger with limestone banks or limestone marl interbedded strata. A diverse macroinvertebrate fauna was recovered, especially within the marly sediments, including the hexacrinitid species described in the present study.

From the base to the top of the Loogh Formation, continuous facies complications, increase of biostromal developments and a successive shallowing of the sea are recorded. This corresponds with the increase in the number of the species and individuals (WINTER 1965, p. 309).

In contrast to the Loogh Formation, the overlying Cürten Formation in the southwestern part of the Gerolstein Syncline can be compared to the Type Eifelian. However, because of distinctive facies peculiarities within the northeastern part of the Gerolstein Syncline, WINTER (1965, pp. 292-304) defined a restructuring of the Cürten Formation in this region (Tab. 3.2.1.2).

He attributed the northeast/southwest differentiation of the Cürten Formation mainly to a lack of the typical limestone-marl interbedded strata (Felschbach and Forstbach members) in the southwestern part of the Gerolstein Syncline within the northeast. He discussed two possible reasons: 1, the different characteristics could be an evidence for a suspected sedimentary adjournment in the northeast; 2, the Felschbach and Forstbach members of the northeastern part could be developed in a Hustley- and/or Meerbüsch-like facies.

3.2.4 FACIES REFLECTING OF THE PRESERVED CRINOID ASSOCIATIONS

The facies complexity of the Lower Givetian deposits in the Gerolstein Syncline is also reflected in the preserved crinoid associations of the Loogh Formation. The higher hydrodynamic turbulence within the biostromal habitats led to a congregation of crinoids with robust skeletons, like cupressocrinitids (BOHATÝ 2005a; 2006b) and some gasterocomoids (BOHATÝ 2006a). Habitats dominated by lower hydrodynamic turbulence were mainly populated by hexacrinitids, rhipidocrinids and eucalyptocrinids. This simplified model must commonly be modified where facies intergrade. Some localities at the NESG are dominated by numerous lateral facies interfingering (see above), which leads to a commingling of the crinoid associations at the marginal areas. However, for practical purposes, WINTER's facies and stratigraphic differentiation can also be traced with crinoids.

3.2.5 CRINOID FAUNA

The crinoid fauna at the NESG is dominated by *Megaradialocrinus elongatus* (GOLDFUSS, 1839) n. comb.[7]; *Eucalyptocrinites rosaceus* GOLDFUSS, 1831; *Rhipidocrinus crenatus* (GOLDFUSS, 1831); *Abbreviatocrinites abbreviatus* (GOLDFUSS, 1839); *A. inflatus* (SCHULTZE, 1866) and *Cupressocrinites crassus* GOLDFUSS, 1831, as reported by BOHATÝ (2006e, p. 263). The locality is most famous for an outstanding diversity of the monobathrid camerate genus *Megaradialocrinus*, which clearly dominates the crinoid association. Other hexacrinitid genera are comparatively rare. The most frequent *Hexacrinites* is *H. pateraeformis* (SCHULTZE, 1866). The bulk of the recorded crinoids consist of isolated aboral cups. Likewise, the new species described below are known only from excellently preserved, isolated aboral cups.

3.2.6 MATERIAL AND METHODS

Type specimens are deposited in the *Forschungsinstitut und Naturmuseum Senckenberg*, Frankfurt am Main, Germany (SMF), the *Steinmann-Institut für Geologie, Mineralogie und Paläontologie der Rheinischen Friedrich-Wilhelms-Universität Bonn*, Germany (IPB) and the *Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing,* China (NIGP). Additional original specimens from the ancient collections are stored in the following institutions and museums: *Institut für Geologie und Mineralogie der Universität zu Köln*, Germany (GIK) and the *Museum für Naturkunde der Humboldt-Universität zu Berlin*, Germany (MB.E.). Other studied crinoids are deposited in private collections (abbreviations CREF and CR.L) and are accessible through contact with the author.

---

[7] = *Megaradialocrinus elongatus* (GOLDFUSS, 1839) *sensu* ICZN

In addition to a detailed analysis of previously published data and original material, this study focuses on skeletal features, mainly observed in recently discovered crinoids. They were prepared using micro sand-streaming methods, as well as fine pneumatic probes, and studied with a binocular microscope. Photographs of NH_4Cl whitened crinoids were arranged using digital image editing software.

Crinoid descriptive terms follows MOORE & TEICHERT (1978) with the following exception: measurement terms follow WEBSTER & JELL (1999). The capitalisation of the Givetian subdivisions follows BECKER (2005; 2007).

3.2.7 SYSTEMATIC PALAEONTOLOGY

3.2.7.1 Crinoid systematic

3.2.7.1.1 Family Hexacrinitidae

Subclass Camerata WACHSMUTH & SPRINGER, 1885
Order Monobathrida MOORE & LAUDON, 1943
Suborder Compsocrinina UBAGHS, 1978
Superfamily Hexacrinitoidea WACHSMUTH & SPRINGER, 1885
Family Hexacrinitidae WACHSMUTH & SPRINGER, 1885

Diagnosis.—Aboral cup medium cone- to bowl-shaped, with low to moderately high tegmen; basals three, subequal; primanal generally of approximately same size as radials or narrower; tegmen stout, composed of small to medium sized plates, orals and ambulacrals commonly distinct; anal opening directly through tegmen or at end of short tube; primibrachials typically not incorporated in aboral cup but commonly joined with interradial tegminal plates; tegmen typically inflated, rarely flat, with one (e.g. in *Megaradialocrinus*) or typically two (e.g. in *Hexacrinites*) posterior interradial plates below the subcentral anal opening; arms two in each ray, branching; uniserial (e.g. in *Megaradialocrinus*) or biserial (e.g. in *Hexacrinites*); column circular in cross section with single subcircular to pentalobate axial canal (modified after UBAGHS 1978, p. T473).

New assigned genera.—(pers. information, G. D. WEBSTER; also see WEBSTER et al. in press): *Megaradialocrinus* (type species **M. conicus*) *sensu* CHEN & YAO (1993, pp. 56-57, 90; figs. 32a-b; pl. 12, figs. 9a-b) from Middle Devonian of the Heyuanzhai Formation (China, western Yunnan Province).

3.2.7.1.2 Genus *Hexacrinites*

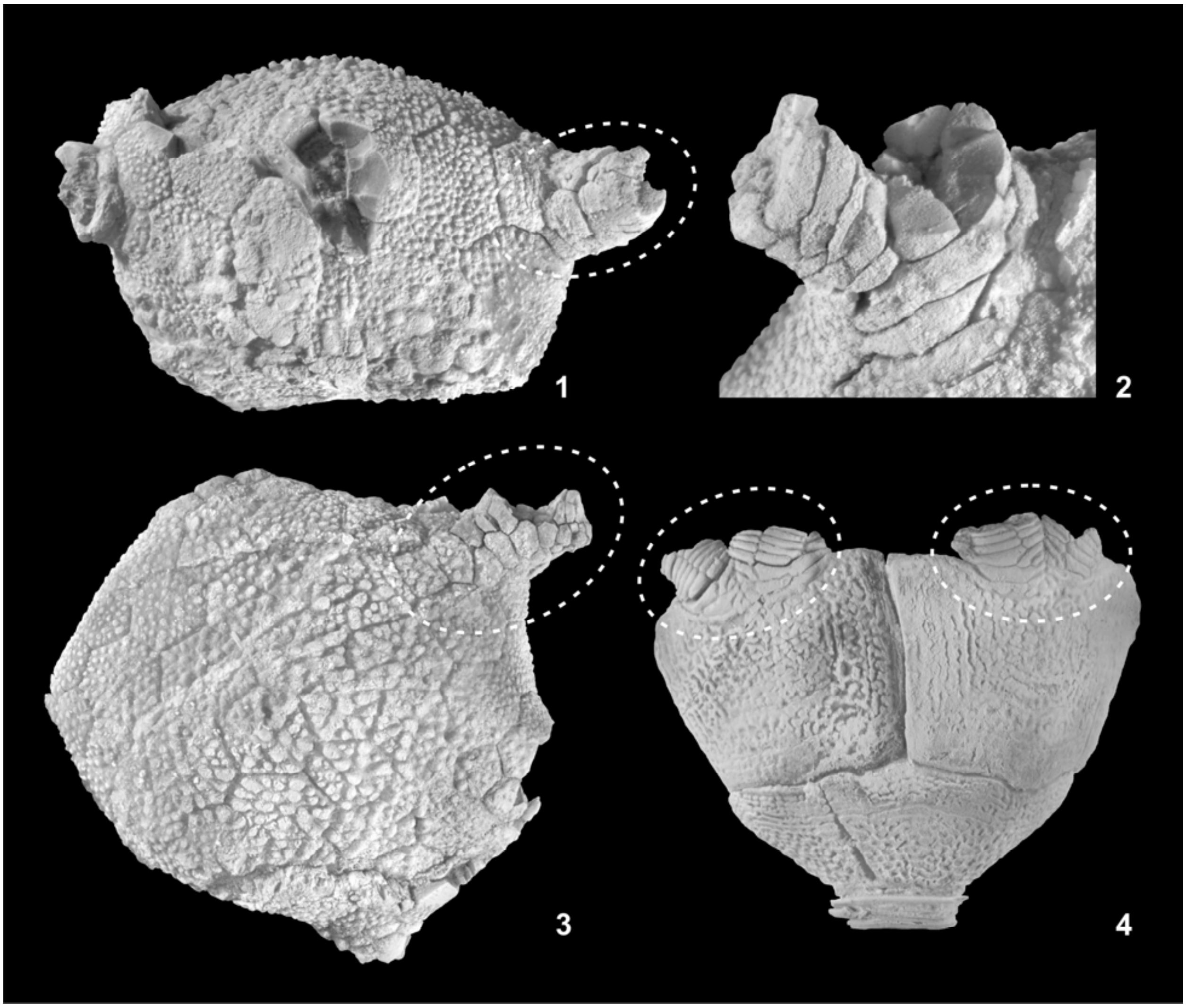


FIGURE 3.2.2—*Hexacrinites* aboral cups. ***1-3***, No. CR.L-1 (col. HEIDELBERGER), *Hexacrinites interscapularis* (PHILLIPS, 1841) from the Givetian of Villmar (Lahn Syncline, eastern Rhenish Massif), basals slightly compressed. ***1***, Left anterolateral view of B ray, rest of biserial arms preserved in A ray (encircled), x 1.3; ***2***, Detail of biserial arms preserved in A ray, x 3.1; ***3***, Oral view, proximal biserial arms encircled, x 1.1; ***4***, No. MB.E.-2429, *Hexacrinites pateraeformis* (SCHULTZE, 1866) from the Hustley Member (upper Loogh Formation, Lower Givetian) of the northeastern slope of the railway cut near the station of Gerolstein (Gerolstein, Gerolstein Syncline, Eifel, Rhenish Massif), lateral view of BA interray with rest of biserial arms preserved in B and A ray (encircled), x 1.8.

Genus *Hexacrinites* AUSTIN & AUSTIN, 1843

Type species.—**Platycrinus interscapularis* PHILLIPS, 1841 (Figs. 3.2.2.1-3).

Occurrence.—After reporting the second Famennian *Hexacrinites*, "*H. persiaensis*" WEBSTER et al., 2007 [= (?)*M. persiaensis* n. comb.[8]] from Iran, the authors reassigned the Silurian (Niagaran) species, "*H. carinatus*" STRIMPLE, 1963, to genus *Oehlerticrinus* LE MENN, 1975 (*non* "*Olertecrinus*" *sensu* WEBSTER et al.). The second Silurian species, "*Hexacrinites adaensis* STRIMPLE, 1952", respectively "*Oehlerticrinus adaensis* (STRIMPLE, 1952) n. comb." *sensu* WEBSTER et al. (2007) [*non* "*Olertecrinus adaensis*" (2007, p. 1104)], is herein reassigned to genus *Megaradialocrinus*.

The Carboniferous "*H. carboniferus* YAKOVLEV & IVANOV, 1956" was placed in the genus *Ivanovaecrinus* by ARENDT (1983), and "*H. mississippiensis* LANE & SEVASTOPULO, 1986" presumably does not belong to the genus. Therefore, *Hexacrinites* is solely Devonian (pers. information, G. C. MCINTOSH). Cosmopolitan (WEBSTER 2003).

Diagnosis.—Crown wide and long; aboral cup wide and bowl-shaped, composed of three typically wider than long basals, forming a very low, wide and bowl-shaped basal circlet and five "spadeblade-shaped" radials (see BOHATÝ 2008, p. 17; figs. 4a-i), which are narrower than the primanal; primibrachials reduced in some species and may be concealed by the first secundibrachials which rest directly on radials; anus subcentral or marginal on tegmen; tegmen wide, composed of pentagonal and/or hexagonal plates, with typically two posterior interradial plates below the subcentral anal opening; free biserial arms (Figs. 3.2.2.1-3), branching, two in each ray, bearing ramuli, arms either directly biserial from the first secundibrachial or in higher secundibrachials after a few uniserial secundibrachials; the distal-most brachials of biserial arms are uniserial, becoming biserial as the arm lengthen; column circular in cross section, smooth or with external sculpturing or spines, with single subcircular to pentalobate axial canal.

Species included.— **(?)*Hexacrinites antares* PROKOP, 1982** [isolated radials]; **(?)*H. ariel* PROKOP, 1982** [isolated radials]; **(?)*H. bacca* (SCHULTZE, 1866)** [a hitherto unconsidered younger synonym is "*Hexacrinites eifeliensis*" HAUSER, 2004; compare HAUSER

---

[8] = (?)*M. persiaensis* (WEBSTER et al., 2007) *sensu* ICZN

(2001, pl. 4; figs. 1, 1a-b) and HAUSER (2004, p. 24; textfig. 19; pl. 2, fig. 12)]; **(?)*H. brownlawi* JELL & JELL, 1999** [ornament very similar to *Arthroacantha mamelonifera* (THOMAS, 1924)]; ***H. granifer* (RÖMER, 1852)**; ***H. interscapularis* (PHILLIPS, 1841)** [a hitherto unconsidered younger synonym (compare to WEBSTER 2003) is *Hexacrinites depressus* (AUSTIN & AUSTIN, 1845), compare to WHIDBORNE (1895, p. 190)]; ***H. pateraeformis* (SCHULTZE, 1866)** [a hitherto unconsidered younger synonym is "*H. magnificus*" *sensu* QUENSTEDT (1866, p. 740; fig. 153); therefore, "*H. magnificus*" *sensu* HAUSER (2006c, published on private web-page = *nomen nudum*; 2007a, p. 13; figs. 4a-c) is an invalid homonym *sensu* ICZN article 10.6. and, herein, renamed as *Megaradialocrinus globohirsutus* n. nov.[9]]; **(?)*H. rosthorni* (CHARLESWORTH in FRECH, 1914)**; ***H. stellaris* (RÖMER, 1851)** [possibly, a younger synonym of *H. interscapularis* (study in progress)]; ***H. symmetricus* (QUENSTEDT, 1866)**; ***H. websteri* HAUSER, 2001** [a hitherto unconsidered younger synonym is "*Hexacrinites johannesmuelleri*" *sensu* HAUSER (2004; compare 2004, p. 32; figs. 33 with 31) with a privately published "holotype" deposited in private collection (*sic*!)]; **(?)*H. yeltyschewae* MILICINA, 1989**.

FIGURE 3.2.3—*Hexacrinites pateraeformis* (SCHULTZE, 1866), aboral cups from the Hustley Member (Loogh Formation, lowermost Lower Givetian) of the northeastern slope of the railway cut near the station of Gerolstein (Gerolstein Syncline, Eifel, Rhenish Massif). ***1***, No. GIK-1950 (field-no. CREF33a-HEIN-10) with a favositid coral encrusted on CB interray (arrow), posterior view of the primanal, x 1.5; ***2***, No. GIK-1951 (field-no. CREF33a-HEIN-11), right anterolateral view of E ray, x 2.6.

---

[9] = *Megaradialocrinus globohirsutus* BOHATÝ, in press *sensu* ICZN

Genera and species excluded from genus Hexacrinites, not assigned to the genus Megaradialocrinus.—“*Hexacrinites carinatus*” STRIMPLE, 1963 = ***Oehlerticrinus carinatus*** **(STRIMPLE, 1952) n. comb.** *sensu* WEBSTER et al. (2007) [*non* “*Olertecrinus*” *carinatus sensu* WEBSTER et al. (2007, p. 1104)]. “*Hexacrintes prescheri*” HAUSER, 2001 = “*H. prescher*” *sensu* HAUSER (2004, appendix, p. 38) = ***Arthroacantha*** **sp.**

HAUSER (2008, p. 32; figs. 72-73; pl. 1, fig. 6) established the species “***Hexacrinites hosticus***” based on a single, atypical aboral cup, deposited in the private collection of Mr. HARALD PRESCHER (Kerpen Horrem, Germany). Contrary to the statement of HAUSER (2008, p. 32) that this crinoid is available for scientific purposes, Mr. PRESCHER briefed the author that he does not know about HAUSER’s assessment and that this fossil is not available for this sort of private publication. It is, therefore, taxonomically not available and decided *nomen nudum*.

3.2.7.2 *Hexacrinites* species from the Gerolstein railroad property

3.2.7.2.1 Species *Hexacrinites pateraeformis*

Hexacrinites pateraeformis (SCHULTZE, 1866)

Figs. 3.2.2.4, 3.2.3.1-2

- *Hexacrinites pateraeformis* (SCHULTZE, 1867). BASSLER & MOODEY, 1943, p. 510. YAKOVLEV, 1964, p. 60; fig. 72. MIESEN, 1971, p. 41; figs. 58, 58a-e; 61, unnumbered figures below right and left. WEBSTER, 1973, p. 148. HAUSER, 1997, p. 13. HAUSER, 2001, p. 12; fig. 8; pp. 145, 195. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*cum syn.*).
- *Hexacrinus pateraeformis.* SCHULTZE, 1866, pp. 87-884; pl. 10, figs. 4, 4a-e. QUENSTEDT, 1866, p. 565. BATHER in LANKESTER, 1900, p. 159; fig. 72. YAKOVLEV, 1930, p. 907; pl. 1, figs. 1a-b. BASSLER & MOODEY, 1943, p. 510.
- *Hexacrinites pateriformis* (SCHULTZE, 1867). HAUSER, 1997, pp. 156-157, 229-230, 256; pls. 54, figs. 3-5; 55, figs. (?)1, 2-3.
- *Hexacrinus magnificus.* QUENSTEDT, 1866, p. 740; fig. 153. QUENSTEDT, 1876, p. 565; pl.

109, figs. 67, 67D-U. *non* “*H. magnificus*” *sensu* HAUSER (2006c, published on private web-page = *nomen nudum* (*vidi*); 2007a, p. 13; figs. 4a-c = invalid homonym *sensu* ICZN article 10.6., herein renamed as *Megaradialocrinus globohirsutus* n. nov.[10]].

- *Hexacrinus hieroglyphicus.* QUENSTEDT, 1876, p. 565; pl. 109, figs. 68, 68d. *non* “*Platycrinites hieroglyphicus*” = *Hexacrinites hieroglyphicus* (GOLDFUSS, 1839) = valid species *sensu* BOHATÝ & HERBIG (2007).
- “*Triplaricrinites exsculptus* GOLDFUSS”. Mentioned *via* SCHULTZE, 1866, pp. 87-88 = unfigured *H. pateraeformis* basals.

Diagnosis.—Crown wide, with bowl-shaped aboral cup, plates very large, “spadeblade-shaped” radials (Figs. 3.2.2.4, 3.2.3.1-2) and bowl-shaped basal circlet; plate sculpturing minor to distinctive meandering crinkles and hieroglyphic impressions, characteristic plate boundaries are uneven and intermesh with each other; radial facet corrigated; tegmen flat, composed of numerous pentagonal to hexagonal plates; with two posterior interradials below the subcentral anal opening; arms biserial (Fig. 3.2.2.4), branching heterotomous; stem facet shallowly impressed, no flange; column circular in cross section, with single axial canal, subcircular to pentalobate in cross section.

3.2.7.2.2 Species (?)*Hexacrinites bacca*

(?)*Hexacrinites bacca* (SCHULTZE, 1866)
for lithographs and photos see SCHULTZE (1866, pl. 10, figs. 5, 5a-c)
and HAUSER (2001, pl. 4, figs. 1, 1a-b)

- *Hexacrinites bacca* (SCHULTZE, 1867). BASSLER & MOODEY, 1943, p. 507. MIESEN, 1971, p. 43; figs. 59, 59a-c. HAUSER, 1997, pp. 141-142. HAUSER, 2001, pp. 29-30; fig. 21; pl. 4, figs. 1, 1a-b. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*cum syn.*).
- *Hexacrinus bacca.* SCHULTZE, 1866, p. 83; pl. 10, figs. 5, 5a-c. BASSLER & MOODEY, 1943, p. 507.

---

[10] = *Megaradialocrinus globohirsutus* BOHATÝ, in press *sensu* ICZN

- “*Hexacrinites eifeliensis*”. HAUSER, 2004, p. 24; fig. 19; pl. 2, fig. 12 [compare HAUSER 2001, p. 29; fig. 21; pl. 4, figs. 1, 1a-b (*vidi*) and HAUSER 2004, p. 24; fig. 19; pl. 2, fig. 12].

Diagnosis.—A *Hexacrinites* with small and comparatively low, “capsule-shaped” aboral cup (see HAUSER 2001, pl. 4, fig. 1; SCHULTZE 1866, pl. 10, fig. 5), composed of a very low, “cloverleaf-shaped” basal circlet (see HAUSER 2001, pl. 4, fig. 1b) with small stem impression in the centre and nearly quadrangular radials, which are arranged at right angles to the basal circlet; radials and primanal sculpturing few strongly developed tubercles and bulges at the raised plate margins that are strongly protruding toward the lateral exterior; arm facets oval in cross section; flat tegmen composed of numerous smooth, mostly pentagonal with some hexagonal plates; with two posterior interradial plates below the subcentral anal opening (see SCHULTZE 1866, pl. 10, fig. 5); column circular in cross section, with single pentalobate axial canal.

3.2.7.3 Genus Megaradialocrinus and its species from the Gerolstein railroad property

3.2.7.3.1 Genus *Megaradialocrinus*

Genus *Megaradialocrinus* CHEN & YAO, 1993

Type species.—**Megaradialocrinus conicus* CHEN & YAO, 1993.

The holotype of *M. conicus* (no. NIGP-346) was discovered within the Heyuanzhai Formation of the Upper Eifelian or Givetian of Heyuanzhai, Shidian County (China). For photos see CHEN & YAO (1993, pl. 12, figs. 9a-b) and WEBSTER et al. (in press, figs. 7k-m).

Remark.—The valid genus name *Megaradialocrinus* is herein declared to have priority over “*Subhexacrinites*”. Genus “*Subhexacrinites*” was established by HAUSER (2004) for two wholly different crinoid species from the Eifel. In 1997 the author described an apparently new "*Hexacrinites*" as "**H. gerolsteiniensis* HAUSER, 1997" (*vidi*), which he defined as the type species of his new genus "*Subhexacrinites*" in 2004. After studying the holotypes (Figs. 3.2.4.1-2), it is clear that species "*S. gerolsteiniensis*" is a typical "*Hexacrinites brevis*" [**Platycrinites brevis sensu* GOLDFUSS (1839, p. 346; pl. 32, figs. 2a-b)] with a (?)platyceratid trace on the radial circlet, wrongly interpreted as laterally positioned anal opening (HAUSER 2004, p. 18). Therefore, "*S. gerolsteiniensis*" is declared a subjective younger synonym of "*H. brevis*".

By separating several species (including "*H. brevis*") from *Hexacrinites*, HAUSER's genus name would have priority if not "*Subhexacrinites*" is herein been declared as junior synonym of the valid older genus name *Megaradialocrinus sensu* CHEN & YAO (1993) [pers. information, G. C. MCINTOSH; G. D. WEBSTER; O. KRAUS]. This is particularly affirmed by the similar aboral cup proportions of *Megaradialocrinus conicus* and (?)*M. piriformis* (SCHULTZE, 1866) n. comb.[11] New findings of (?)*M. piriformis* crowns, with uniserial and heterotomously divided arms, support both hexacrinitids. The arms of *Hexacrinites* are biserial. However, the still unknown arms of CHEN & YAO's type species need to validate these findings.

Note that HAUSER's second species "*Subhexacrinites rommersheimensis* HAUSER, 2004" [with a privately published "holotype" deposited in private collection (*sic*!)] does not belong to the Hexacrinitidae and has to be reappraised after deposition in a museum collection.

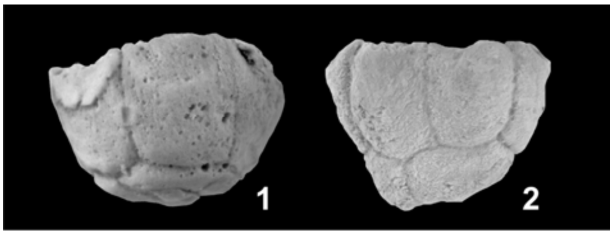


FIGURE 3.2.4—*Megaradialocrinus brevis* (GOLDFUSS, 1839) n. comb., isolated aboral cups. ***1***, No. MB.E.-2579, the cast of the inaccessible original (*sic*!) of "*Hexacrinites gerolsteiniensis* HAUSER, 1997" respectively "*Subhexacrinites gerolsteiniensis* HAUSER, 2004", anterior view of A ray, x 3.6; the aboral cup is concordant with the studied **holotype**, no. IPB-1319 (***2***) of "*Hexacrinites brevis*" [**Platycrinites brevis* sensu GOLDFUSS (1839, p. 346, pl. 32, figs. 2a-b)] = *Megaradialocrinus brevis* (GOLDFUSS, 1839) n. comb., left posterior view of C ray and primanal, x 4.3.

---

[11] = (?)*M. piriformis* (SCHULTZE, 1866) *sensu* ICZN

Species included.—**(?)*Megaradialocrinus aberrans* (WHIDBORNE, 1889) n. comb.**[12]; ***M. adaensis*** **(STRIMPLE, 1952) n. comb.**[13] [*non* "*Olertecrinus*" (= *Oehlerticrinus*) *adaensis* (STRIMPLE, 1952) n. comb. *sensu* WEBSTER et al. (2007, p. 1104)]; ***M. aliculatus*** **n. sp.**[14]; ***M. anaglypticus*** **(GOLDFUSS, 1839) n. comb.**[15]; ***M. angulosus*** **(VON KOENEN, 1886) n. comb.**[16]; ***M. brevis*** **(GOLDFUSS, 1839) n. comb.**[17]; **(?)*M. buchi*** **(RÖMER, 1843) n. comb.**[18]; **(?)*M. bulbiformis*** **n. sp.**[19]; ***M. callosus*** **(SCHULTZE, 1866) n. comb.**[20]; **(?)*M. campaniformis*** **(BOHATÝ, 2008) n. comb.**[21]; **(?)*M. chenae*** **(WEBSTER & BECKER, 2009) n. comb.**[22]; **(?)*M. chirnsidensis*** **(JELL, 1999) n. comb.**[23]; ***M. confragosus*** **(DUBATOLOVA, 1964) n. comb.**[24]; ***M. conicus*** **CHEN & YAO, 1993**; ***M. crispus*** **(QUENSTEDT, 1861) n. comb.**[25] [*non* "*H. crispus*" *sensu* DUBATOLOVA (1964, p. 34; pl. 4, figs. 3-4) = *M. prokopi* n. comb.[26] (n. nov. *sensu* BOHATÝ 2006c); for detailed descriptions of *M. crispus* and *M. prokopi* see BOHATÝ (2006c); hitherto unconsidered younger synonyms of *M. crispus* are: "*Hexacrinites ludwigschultzei*" HAUSER, 2004 and "*Hexacrinites frondosus*" *sensu* HAUSER (2004), compare to BOHATÝ (2006c, pp. 474-480)]; ***M. echinatus*** **(SANDBERGER & SANDBERGER, 1856) n. comb.**[27]; ***M. elongatus*** **(GOLDFUSS, 1839) n. comb.**[28] [hitherto unconsidered younger synonyms are: "*Hexacrinites planus*" *sensu* HAUSER (2005a, published on private web-page = *nomen nudum*; 2007a, p. 6; pl. 1, fig. 1, given without diagnosis/description/differentiation, therefore a *nomen nudum sensu* ICZN; "holotype" deposited in private collection *sic*!) and "*Hexacrinites breimeri*" *sensu* HAUSER (2006d, published on private web-page = *nomen nudum*; 2007b, p. 31; fig. 4]; ***M. exsculptus*** **(GOLDFUSS, 1839) n. comb.**[29]; **(?)*M. faniensis*** **(MAILLIEUX, 1940) n. comb.**[30]; ***M. frechi*** **(CHARLESWORTH, 1914) n. comb.**[31]; ***M. gibbosus*** **(BERGOUGNIOUX, 1939) n. comb.**[32] [a hitherto unconsidered younger synonym is "*Hexacrinites donarius*" HAUSER, 1999 (compare HAUSER 1999, pls. 19, fig. 5; 20, fig. 4)];

---

[12] = (?)*Megaradialocrinus aberrans* (WHIDBORNE, 1889) *sensu* ICZN
[13] = *M. adaensis* (STRIMPLE, 1952) *sensu* ICZN
[14] = *M. aliculatus* BOHATÝ, in press *sensu* ICZN
[15] = *M. anaglypticus* (GOLDFUSS, 1839) *sensu* ICZN
[16] = *M. angulosus* (VON KOENEN, 1886) *sensu* ICZN
[17] = *M. brevis* (GOLDFUSS, 1839) *sensu* ICZN
[18] = (?)*M. buchi* (RÖMER, 1843) *sensu* ICZN
[19] = (?)*M. bulbiformis* BOHATÝ, in press *sensu* ICZN
[20] = *M. callosus* (SCHULTZE, 1866) *sensu* ICZN
[21] = (?)*M. campaniformis* (BOHATÝ, 2008) *sensu* ICZN
[22] = (?)*M. chenae* (WEBSTER & BECKER) *sensu* ICZN
[23] = (?)*M. chirnsidensis* (JELL, 1999) *sensu* ICZN
[24] = *M. confragosus* (DUBATOLOVA, 1964) *sensu* ICZN
[25] = *M. crispus* (QUENSTEDT, 1861) *sensu* ICZN
[26] = *M. prokopi* (BOHATÝ, 2006c) *sensu* ICZN
[27] = *M. echinatus* (SANDBERGER & SANDBERGER, 1856) *sensu* ICZN
[28] = *M. elongatus* (GOLDFUSS, 1839) *sensu* ICZN
[29] = *M. exsculptus* (GOLDFUSS, 1839) *sensu* ICZN
[30] = (?)*M. faniensis* (MAILLIEUX, 1940) *sensu* ICZN
[31] = *M. frechi* (CHARLESWORTH, 1914) *sensu* ICZN
[32] = *M. gibbosus* (BERGOUGNIOUX, 1939) *sensu* ICZN

M. globohirsutus* n. nov.**[33]; **(?)*M. granuliferus* (Römer, 1844) n. comb.**[34] [hitherto unconsidered younger synonyms are: "*Hexacrinus granulifer*" *sensu* Sandberger & Sandberger (1856), "*Hexacrinites microglyphicus*" (Whidborne, 1889) and "*H. vicarii*" (Whidborne, 1889), compare Römer (1844, p. 63; pl. 3, fig. 4) and Sandberger & Sandberger (1856, p. 397; pl. 35, fig. 9) with Whidborne (1889, p. 79) and Whidborne (1895, pp. 196-197; pl. 23, figs. 1-1a, 2-2a)]; ***M. heidelbergeri* (Bohatý, 2008) n. comb.**[35]; ***M. heinorum* (Bohatý, 2006d) n. comb.**[36]; ***M. hieroglyphicus* (Golfuss, 1839) n. comb.**[37] [for detailed description and synonymy see Bohatý & Herbig (2007, p. 734)]; **(?)*M. humei* (Springer, 1926a) n. comb.**[38]; **(?)*M. infundibulum* (von Koenen, 1886) n. comb.**[39]; **(?)*M. inhospitalis* (Schmidt, 1934) n. comb.**[40] [atypical form; further studies are necessary]; ***M. invitabilis* (Dubatolova, 1964) n. comb.**[41]; ***M. iowensis* (Thomas, 1924) n. comb.**[42]; **(?)*M. leai* (Lyon, 1869) n. comb.**[43]; ***M. limbatus* (Müller, 1856) n. comb.**[44]; ***M. lobatus* (Müller, 1857) n. comb.**[45]; **(?)*M. macrotatus* (Austin & Austin, 1845) n. comb.**[46] [a hitherto unconsidered younger synonym is "*Hexacrinites taluxaiensis*" *sensu* Hauser (2006d, published on private web-page = *nomen nudum*; 2007b, p. 32; fig. 8; compare to the typical (?)*M. macrotatus* morphotype in Whidborne 1895, pl. 22, fig. 4)]; ***M. marginatus* (Schultze, 1866) n. comb.**[47] [for detailed description and synonymy see Bohatý & Herbig (2007, pp. 734-735)]; ***M. minor* (Dewalque in Fraipont, 1884) n. comb.**[48] [hitherto unconsidered younger synonyms are: "*Hexacrinites compactus*" Hauser, 1999; "*Hexacrinites gosseleti*" Hauser, 1999; "*Hexacrinites schnuri*" Hauser, 1999 and "*Hexacrinites senzeilleianus*" Hauser, 1999, (compare Hauser 1999, pls. 19, fig. 1; 21, fig. 2; 22, fig. 2). Aboral cup CRBR6-40 figured in Hauser (1999, pl. 19, fig. 4) as "*H. compactus* n. sp." and in the same work (pl. 21, fig. 7) as "*H. glosseti* n sp." (*sic*!)]; ***M. mui* (Xu, 1963) n. comb.**[49]; **(?)*M. neuvilleanus* (Hauser, 2003) n. comb.**[50]; **(?)*M. nitidus

---

[33] = *M. globohirsutus* Bohatý, in press *sensu* ICZN
[34] = (?)*M. granuliferus* (Römer, 1844) *sensu* ICZN
[35] = *M. heidelbergeri* (Bohatý, 2008) *sensu* ICZN
[36] = *M. heinorum* (Bohatý, 2006d) *sensu* ICZN
[37] = *M. hieroglyphicus* (Golfuss, 1839) *sensu* ICZN
[38] = (?)*M. humei* (Springer, 1926a) *sensu* ICZN
[39] = (?)*M. infundibulum* (von Koenen, 1886) *sensu* ICZN
[40] = (?)*M. inhospitalis* (Schmidt, 1934) *sensu* ICZN
[41] = *M. invitabilis* (Dubatolova, 1964) *sensu* ICZN
[42] = *M. iowensis* (Thomas, 1924) *sensu* ICZN
[43] = (?)*M. leai* (Lyon, 1869) *sensu* ICZN
[44] = *M. limbatus* (Müller, 1856) *sensu* ICZN
[45] = *M. lobatus* (Müller, 1857) *sensu* ICZN
[46] = (?)*M. macrotatus* (Austin & Austin, 1845) *sensu* ICZN
[47] = *M. marginatus* (Schultze, 1866) *sensu* ICZN
[48] = *M. minor* (Dewalque in Fraipont, 1884) *sensu* ICZN
[49] = *M. mui* (Xu, 1963) *sensu* ICZN
[50] = (?)*M. neuvilleanus* (Hauser, 2003) *sensu* ICZN

(HAUSER, 2002) n. comb.[51] [privately published "holotype" deposited in private collection (*sic*!)]; ***M. nodifer*** **(SCHULTZE, 1866) n. comb.**[52]; ***M. occidentalis*** **(WACHSMUTH & SPRINGER, 1897) n. comb.**[53]; ***M. ornatus*** **(GOLDFUSS, 1839) n. comb.**[54]; **(?)*M. pentangularis*** **(AUSTIN & AUSTIN, 1845) n. comb.**[55]; **(?)*M. perarmatus*** **(WHIDBORNE, 1889) n. comb.**[56]; **(?)*M. persiaensis*** **(WEBSTER et al., 2007) n. comb.**[57]; ***M. piriculaformis*** **n. sp.**[58]; **(?)*M. piriformis*** **(SCHULTZE, 1866) n. comb.**[59]; ***M. prokopi*** **(BOHATÝ, 2006c) n. comb.**[60]; ***M. rigel*** **(PROKOP, 1982) n. comb.**[61]; ***M. spinosus*** **(MÜLLER, 1856) n. comb.**[62]; ***M. theissi*** **n. sp.**[63]; ***M. thomasbeckeri*** **(HAUSER, 2004) n. comb.**[64]; **(?)*M. trélonensis*** **(HAUSER, 2003) n. comb.**[65]; ***M. triradiatus*** **(SCHULTZE, 1866) n. comb.**[66]; ***M. tuberculatus*** **(VON KOENEN, 1886) n. comb.**[67] [hitherto unconsidered younger synonyms are: "*Hexacrinites ardennicus*" HAUSER, 1999 and "*Hexacrinites ubaghsi*" *sensu* HAUSER (1999, pl. 24, fig. 2 and 2a not the same aboral cup, as wrongly indicated by the author)]; ***M. turritus*** **(BOHATÝ, 2006e) n. comb.**[68]; ***M. unterthalensis*** **(BOHATÝ, 2006d) n. comb.**[69]; ***M. ventricosus*** **(GOLDFUSS, 1831) n. comb.**[70]; **(?)*M. verrucosus*** **(DEWALQUE, 1884) n. comb.**[71] [hitherto unconsidered younger synonyms are: "*Hexacrinites sartenaeri*" HAUSER, 1999, compare HAUSER (1999, pl. 23, figs. 1 and 7) and "*Hexacrinites koeneni*" = (?)*M. verrucosus* aboral cup with lost basals; oral view, figured in HAUSER (1999, pl. 25, fig. 5a) concordant with HAUSER (1999, pl. 23, fig. 1a)]; **(?)*M. villmarensis*** **(BOHATÝ, 2008) n. comb.**[72]; ***M. winteri*** **n. sp.**[73]; ***M. yui*** **(XU, 1963) n. comb.**[74]

---

[51] = (?)*M. nitidus* (HAUSER, 2002) *sensu* ICZN
[52] = *M. nodifer* (SCHULTZE, 1866) *sensu* ICZN
[53] = *M. occidentalis* (WACHSMUTH & SPRINGER, 1897) *sensu* ICZN
[54] = *M. ornatus* (GOLDFUSS, 1839) *sensu* ICZN
[55] = (?)*M. pentangularis* (AUSTIN & AUSTIN, 1845) *sensu* ICZN
[56] = (?)*M. perarmatus* (WHIDBORNE, 1889) *sensu* ICZN
[57] = (?)*M. persiaensis* (WEBSTER et al., 2007) *sensu* ICZN
[58] = *M. piriculaformis* BOHATÝ, in press *sensu* ICZN
[59] = (?)*M. piriformis* (SCHULTZE, 1866) *sensu* ICZN
[60] = *M. prokopi* (BOHATÝ, 2006c) *sensu* ICZN
[61] = *M. rigel* (PROKOP, 1982) *sensu* ICZN
[62] = *M. spinosus* (MÜLLER, 1856) *sensu* ICZN
[63] = *M. theissi* BOHATÝ, in press *sensu* ICZN
[64] = *M. thomasbeckeri* (HAUSER, 2004) *sensu* ICZN
[65] = (?)*M. trélonensis* (HAUSER, 2003) *sensu* ICZN
[66] = *M. triradiatus* (SCHULTZE, 1866) *sensu* ICZN
[67] = *M. tuberculatus* (VON KOENEN, 1886) *sensu* ICZN
[68] = *M. turritus* (BOHATÝ, 2006e) *sensu* ICZN
[69] = *M. unterthalensis* (BOHATÝ, 2006d) *sensu* ICZN
[70] = *M. ventricosus* (GOLDFUSS, 1831) *sensu* ICZN
[71] = (?)*M. verrucosus* (DEWALQUE, 1884) *sensu* ICZN
[72] = (?)*M. villmarensis* (BOHATÝ, 2008) *sensu* ICZN
[73] = *M. winteri* BOHATÝ, in press *sensu* ICZN
[74] = *M. yui* (XU, 1963) *sensu* ICZN

Occurrence.—The genus is almost restricted to the Devonian except of one Silurian species, "*Hexacrinites adaensis* STRIMPLE, 1952", respectively "*Oehlerticrinus adaensis* (STRIMPLE, 1952) n. comb." *sensu* WEBSTER et al. (2007) [*non* "*Olertecrinus adaensis*" (2007, p. 1104)], from the Niagaran (Henryhouse Formation, upper part of Decatur Limestone) of Tennessee (Oklahoma, U.S.A.), which is herein reassigned to genus *Megaradialocrinus*. Cosmopolitan (WEBSTER 2003).

Diagnosis (emend.).—Crown short or elongated and long; aboral cup composed of three subequal basals followed by six plates within radial circlet (primanal generally somewhat narrower than radials), plates rarely smooth, typical moderately or strongly sculptured; aboral cup cylindrical to moderately inverted coniform, long or short; first primibrachials axillary and so reduced in some species as to be concealed by first secundibrachials, which rest directly on radials; anus subcentral or marginal on tegmen; tegmen flat or moderately to strongly inflated, typically composed of moderately to strongly convex polygonal plates (modified proximal ambulacral plates) and either convex or flat polygonal orals, with single posterior interradial plate below the subcentral anal opening; free arms strictly uniserial, two rami in each ray, either straight- or moderately to strongly zigzag (see models, Figs. 3.2.8.1-5); rami branching heterotomously with somewhat narrower, bilateral and unbranched ramules, number and length of ramules variable; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials typically wide and U-shaped, compound, possessing two (bipinnulated) to rarely four pinnules each except on typically asymmetrical to nearly symmetrical, pentagonal or, rarely, triangular axillaries (Fig. 3.2.8.4); number of brachials and axillaries variable; column circular in cross section, smooth or with external sculpturing or spines, with single axial canal, subcircular or pentalobate in cross section.

Differentiation analysis.—In contrast to *Megaradialocrinus*, *Hexacrinites* developed wide, bowl-shaped aboral cups. The wide tegmen, with typically two instead of one posterior interradial plate below the subcentral anal opening, is composed of numerous, mostly flat pentagonal and/or hexagonal plates, in contrast to the fewer, mostly convex plates of *Megaradialocrinus*. The specimens assigned herein to *Megaradialocrinus* are also distinguished by uniserial arms. *Hexacrinites* developed biserial arms either directly from the first secundibrachial or in higher secundibrachials after a few uniserial secundibrachials; the distal-most brachials of biserial arms are uniserial, becoming biserial as the arm lengthens.

Remarks.—A model of known variations of the arms of *Megaradialocrinus* is illustrated in Figs. 3.2.8.1-5. It has to be noted that HAUSER (2008, p. 30; fig. 66) wrongly interpreted those "*Hexacrinites*" with regularly five uniserial arms (= *Megaradialocrinus*) as a genus with four arms and one additional branch, which is only developed in the distal-most part of the right rami in C, B, E and D rays. The latter mistake is presumably based on one anomalous *M. brevis* crown, which was taken as a model in SCHULTZE (1866, p. 71; fig. 14). This developmental anomaly is recognised in one crown of *M. marginatus* (see left rami in B ray of the crown figured in BOHATÝ & HERBIG 2007, p. 733; fig. 4) with one regenerated, smaller and irregularly branched arm. Obviously, the disadvantage of smaller regenerated arms is counterbalanced by additional branching and, therefore, by an increased pinnulated surface.

Megaradialocrinus species from the Gerolstein railroad property.—The following listing is an overview of the previously poorly documented *Megaradialocrinus* species at the NESG and their synonyms; ordered by their abundance – from the most common species *M. elongatus* to the rarer taxa.

3.2.7.3.2 Species *Megaradialocrinus elongatus*

Megaradialocrinus elongatus (GOLDFUSS, 1839) n. comb.[75]

Figs. 3.2.5.1-10

- *Hexacrinites elongatus* (GOLDFUSS, 1839). BASSLER & MOODEY, 1943, p. 508. MIESEN, 1971, p. 39; figs. 54, 54a-g, *non* fig. 54h (= *M.* cf. *exsculptus* n. comb.[76]); p. 59, the two upper figures (unnumbered). WEBSTER, 1973, p. 148. HAUSER, 1997, pp. 144-145; pls. 45, figs. 2-5, *non* fig. 1 (= *M. exsculptus* n. comb.[77]); 46, figs. 1-6; 47, figs. 1-4. HAUSER, 2001, pls. 8, fig. 3; 25, fig. 1. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*cum syn.*).

---

[75] = *Megaradialocrinus elongatus* (GOLDFUSS, 1839) *sensu* ICZN

[76] = *M.* cf. *exsculptus* (GOLDFUSS, 1839) *sensu* ICZN

[77] = *M. exsculptus* (GOLDFUSS, 1839) *sensu* ICZN

- *vidi Platycrinites elongatus*. GOLDFUSS, 1839, p. 345; pl. 32, figs. 1a-c. BASSLER & MOODEY, 1943, p. 508.
- *Platycrinus elongatus* (GOLDFUSS, 1839). BRONN, 1848, p. 993. D'ORBIGNY, 1850, p. 156. DUJARDIN & HUPÉ, 1862, p. 155.
- *Hexacrinus elongatus* (GOLDFUSS, 1839). SCHULTZE, 1866, p. 74; pl. 9, figs. 4, 4a-i. ZITTEL, 1880, pp. 332, 365; figs. 227, 253a-c. QUENSTEDT, 1885, p. 953; pl. 76, fig. 19. ZITTEL, 1895, pp. 119, 128; figs. 230a-b, 242a-c. BEYER, 1896, p. 89; pl. 3, fig. 77. ZITTEL, 1903, p. 130; figs. 242a-b. GÜRICH, 1909, p. 109; pl. 33, figs. 6a-c. BASSLER & MOODEY, 1943, p. 508. SIEVERTS-DORECK, 1950, p. 80; figs. 1a-c. WEBSTER, 1973, p. 148.
- "*Hexacrinites planus*" HAUSER, 2005a [published on private web-page = *nomen nudum*; 2007a, p. 6; pl. 1, fig. 8, given without diagnosis/description/differentiation, therefore decided *nomen nudum sensu* ICZN; ("holotype" deposited in private collection *sic*!)].
- "*Hexacrinites breimeri*" *sensu* HAUSER [2006d, published on private web-page = *nomen nudum* (*sic*!); 2007b, p. 31; fig. 4].

Diagnosis.—A *Megaradialocrinus* with an elongated, cylindrical crown and long, mostly inverted coniform-shaped aboral cup (Figs. 3.2.5.1-4), rarely low and bowl-shaped; very rarely, the cup is sloping in the CD interray or in the A ray direction (Figs. 3.2.5.9-10; also see SIEVERTS-DORECK (1950, p. 81; figs. 1a-c); basal circlet inverted coniform, composed of three basal plates nearly as long as wide, with a smooth stem impression surrounded by tripartite basal flanges; radials five, long and somewhat wider than the primanal, surface of plates moderately sculptured by low ridges or sparsely anastomosing ridges; tegmen either with convex plates (Figs. 3.2.5.4, 3.2.5.10) or with flat orals (Fig. 3.2.5.2) and convex inflated proximal ambulacra and madreporite plates (this results in all transitions between convex and inflated tegmen); with a single posterior interradial plate below the subcentral anal opening; anus opening marginal of tegmen, sometimes surrounded by short and blunt spines; free strictly uniserial arms, two long rami in each ray, straight-lined (see model, Fig. 3.2.8.1); numerous rami branching heterotomously with slender and relatively short, bilateral and unbranched ramules; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials low and wide, U-shaped, compound, possessing (?)two pinnules each (bipinnulated) except on asymmetrical and pentagonal axillaries; column circular in cross section, with single pentalobate axial canal.

3.2.7.3.3 Species *Megaradialocrinus marginatus*

Megaradialocrinus marginatus (SCHULTZE, 1866) n. comb.[78]

Figs. 3.2.5.11-13

- *Hexacrinites marginatus* (SCHULTZE, 1866). HAUSER, 2001, p. 11; fig. 7. BOHATÝ & HERBIG, 2007, pp. 731-736; figs. 1, 2A-C, 4, 6A-C, 7A-K (*cum syn.*). WEBSTER, 2003 (*pars*), *Hexacrinites marginatus*, internet edition of the Bibliography and Index of Palaeozoic crinoids.
- *Hexacrinus ornatus marginatus.* SCHULTZE, 1866, p. 82; figs. 9, 9a-b (referring to the figure at the top of the plate). BASSLER & MOODEY, 1943, p. 510.
- *Hexacrinites ornatus marginatus* (SCHULTZE, 1866). BASSLER & MOODEY, 1943, p. 510.
- *Hexacrinites marginata* (SCHULTZE, 1866). HAUSER, 1997, pp. 152-153. HAUSER, 2001, p. 194.
- *sic*! *vidi Hexacrinites* aff. *marginata* (SCHULTZE, 1866). HAUSER, 1997, pl. 53, fig. 4 (= holotype of *M. hieroglyphicus* n. comb.[79]).
- *sic*! *Hexacrinites hieroglyphicus* (GOLDFUSS, 1839). HAUSER, 2004, p. 28; fig. 26 (= holotype of *M. marginatus* n. comb.[80]).
- *Hexacrinus exculptus* (GOLDF.). DOHM, 1976, p. 36; fig. 25.

Diagnosis.—Crown (BOHATÝ & HERBIG 2007, p. 733; fig. 4) elongate, approximately cylindrical; aboral cup slightly longer than wide; five radials, all longer than wide, bordered by external, sometimes slightly sculptured bulges protruding toward the exterior, centre of radials always concave and smooth (Figs. 3.2.5.11-13); primanal either analogous to radials or with small, elongate, “bead-shaped” spike (2007, p. 735; fig. 7); basals wider than long and lower than radials, either shaped like radials or planar; tegmen moderately inflated; with a single posterior interradial plate below the subcentral anal opening; free strictly uniserial arms, two rami in each ray, zigzag; rami branching heterotomously with long, bilateral, unbranched and long ramules, nearly as wide as rami; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial

---

[78] = *Megaradialocrinus marginatus* (SCHULTZE, 1866) *sensu* ICZN
[79] = *M. hieroglyphicus* (GOLDFUSS, 1839) *sensu* ICZN
[80] = *M. marginatus* (SCHULTZE, 1866) *sensu* ICZN

2, brachials low, wide and U-shaped, compound, possessing two [to (?)four] pinnules each except on characteristically small, symmetrical and triangular axillaries (see model, Fig. 3.2.8.4), which are surrounded by three hexagonal brachials; column circular in cross section, with single pentalobate axial canal; colour of plates black, only in strongly weathered aboral cups brownish (2007, pp. 734-735).

3.2.7.3.4 Species *Megaradialocrinus brevis*

Megaradialocrinus brevis (GOLDFUSS, 1839) n. comb.[81]
Figs. 3.2.4.1-2, 3.2.5.14-24, (?)3.2.5.25

- *Hexacrinites brevis* (GOLDFUSS, 1839). BASSLER & MOODEY, 1943, p. 507. MIESEN, 1971, p. 43; figs. 61, 61a-c. HAUSER, 1997, p. 142; pl. 43, figs. 1-7; *non* pl. 44, fig. 1 (= *Megaradialocrinus* indet.). HAUSER, 2001, pl. 9, fig. 6. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*cum syn.*).
- *vidi *Platycrinites brevis.* GOLDFUSS, 1839, p. 346; pl. 32, figs. 2a-b. BASSLER & MOODEY, 1943, p. 507.
- *Platycrinus brevis* (GOLDFUSS, 1839). BRONN, 1848, p. 993. DUJARDIN & HUPÉ, 1862, p. 155.
- *Hexacrinus brevis* (GOLDFUSS, 1839). SANDBERGER & SANDBERGER, 1856, p. 398; pl. 35, figs. 11-11a. SCHULTZE, 1866, p. 79; pl. 10, figs. 7, 7a-c. HOLZAPFEL, 1895, p. 302. BASSLER & MOODEY, 1943, p. 507.
- *vidi "Hexacrinites gerolsteiniensis".* HAUSER, 1997, pp. 147-148; fig. 44; pl. 49, fig. 1 (= juvenile aboral cup of *M. brevis* n. comb.[82] with a (?)platyceratid trace at the radial circlet).
- *vidi "Subhexacrinites gerolsteiniensis".* HAUSER, 2004, pp. 17-22; fig. 17; pl. 1, fig. 5 (= juvenile aboral cup of *M. brevis* n. comb.[83] with a (?)platyceratid trace at the radial circlet).
- (?)*Hexacrinites brevis* (GOLDFUSS 1839). BOHATÝ, 2008, pp. 10-11; figs. 1a-b.

Diagnosis.—A *Megaradialocrinus* with a low crown (see HAUSER 1997, pl. 43, figs. 1, 4-7) and a small and low aboral cup [Figs. 3.2.4.1-2, 3.2.5.14-24, (?)3.2.5.25], composed of three low and wide basals, five slightly longer than wide radials with maximal width near the radial facet and primanal with maximal width toward the basal circlet; plates

---

[81] = *Megaradialocrinus brevis* (GOLDFUSS, 1839) *sensu* ICZN
[82] = *M. brevis* (GOLDFUSS, 1839) *sensu* ICZN
[83] = *M. brevis* (GOLDFUSS, 1839) *sensu* ICZN

mostly smooth, in some cases, especially the lower regions of the radials, slightly projecting bulges or a few, low tubercles; stem impression relatively wide, impressed and sometimes surrounded by ring-shaped basal flanges; tegmen inflated (Figs. 3.2.5.18-20), composed of smooth, very convex plates; with a single posterior interradial plate below the subcentral anal opening; free strictly uniserial arms, two rami in each ray, zigzag (see model, Fig. 3.2.8.3); rami branching heterotomous with long, somewhat narrower, bilateral and unbranched ramules; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials wide and U-shaped, compound, possessing two pinnules each (bipinnulated) except on asymmetrical and pentagonal axillaries; column circular in cross section, with single pentalobate axial canal.

3.2.7.3.5 Species *Megaradialocrinus ornatus*

Megaradialocrinus ornatus (GOLDFUSS, 1839) n. comb.[84]

Figs. 3.2.5.26, 3.2.6.20

- *Hexacrinites ornatus* (GOLDFUSS, 1839). BASSLER & MOODEY, 1943, p. 510. MIESEN, 1971, p. 35; figs. 48, 48a-c, 48c2, 48f; *non* p. 63, unnumbered figure below right (= *M.* cf. *exsculptus* n. comb.[85]). HAUSER, 1997, p. 154; pl. 52, fig. 1. HAUSER, 2001, pls. 5, fig. 1; 9, fig. 2; 25, figs. 3-(?)3a [= *M.* aff. *hieroglyphicus* n. comb.[86]]. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*cum syn.*). HAUSER, 2004, p. 30; fig. 29.
- *Platycrinites ornatus.* GOLDFUSS, 1839, p. 347. BASSLER & MOODEY, 1943, p. 510.
  Platycrinus ornatus (GOLDFUSS, 1839). BRONN, 1848, p. 993. DUJARDIN & HUPÉ, 1862, p. 155.
- *Hexacrinus ornatus* (GOLDFUSS, 1839). SCHULTZE, 1866, p. 82; pl. 8, figs. 4, 4a-f; 10, fig. 9. HOLZAPFEL, 1895, p. 302. BEYER, 1896, p. 89; pl. 3, fig. 78. BASSLER & MOODEY, 1943, p. 510.
- *sic*! *vidi Hexacrinites exsculptus* (GOLDF., 1838). HAUSER, 1997, pl. 52, fig. 6 (= lectotype of *M. ornatus* n. comb.[87]).
- (?)*Hexacrinites ornatus* (GOLDFUSS, 1839). BOHATÝ, 2008, p. 12; fig. 2e.

---

[84] = *Megaradialocrinus ornatus* (GOLDFUSS, 1839) *sensu* ICZN

[85] = *M.* cf. *exsculptus* (GOLDFUSS, 1839) *sensu* ICZN

[86] = *M.* aff. *hieroglyphicus* (GOLDFUSS, 1839) *sensu* ICZN

[87] = *M. ornatus* (GOLDFUSS, 1839) *sensu* ICZN

***Figure* 3.2.5 (legend p. 81)**

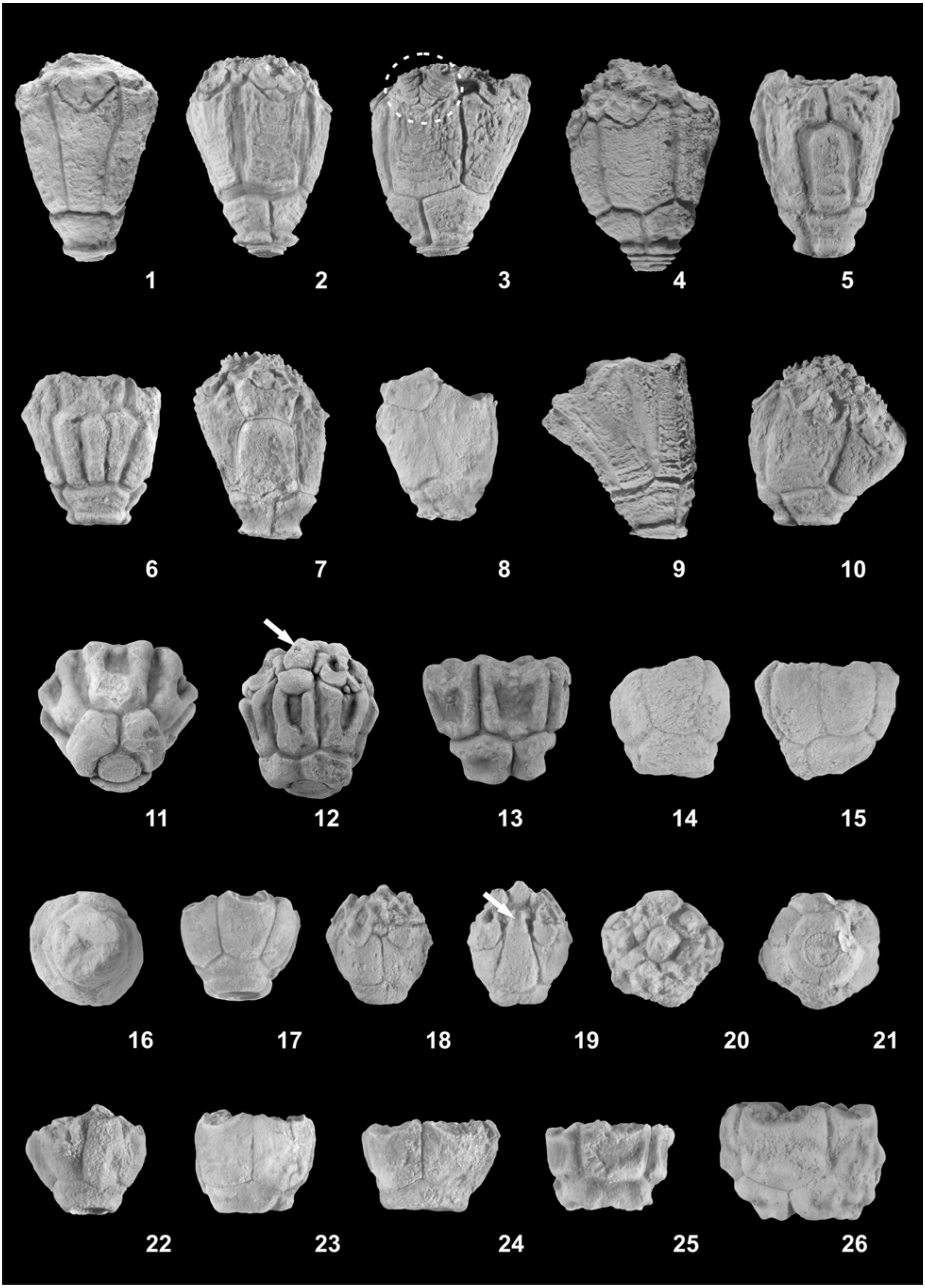


Figure 3.2.5 (see p. 80)*—Megaradialocrinus* aboral cups from the Hustley Member (Loogh Formation, lowermost Lower Givetian) of the northeastern slope of the railway cut near the station of Gerolstein (Gerolstein Syncline, Eifel, Rhenish Massif) [***1-12***, ***17-25***], from the Hustley Member of Pelm, to the east of Gerolstein [***13-16***], and from the Baarley Member (Loogh Formation, lowermost Lower Givetian) of the "Mühlenwäldchen", SW-Gerolstein [***26***]. ***1-10***, *Megaradialocrinus elongatus* (Goldfuss, 1839) n. comb. ***1***, No. GIK-1952 (field-no. CREF33a-Hein-12), right posterior view of D ray, x 1.9; ***2***, No. GIK-1953 (field-no. CREF33a-Hein-13), left anterolateral view of B ray, x 1.5; ***3***, No. GIK-1954 (field-no. CREF33a-Hein-14), right anterolateral view of E ray, showing preserved lowermost part of uniserial arms (encircled), x 1.6; ***4***, No. GIK-1955 (field-no. CREF33a-Hein-15), right anterolateral view of E ray, showing inflated tegmen and proximal part of stem preserved, x 1.6; ***5***, No. GIK-1956 (field-no. CREF33a-Hein-16), lateral view of an abnormal aboral cup, with one shortened radial plate within DE interray, x 1.6; ***6***, No. GIK-1957 (field-no. CREF33a-Hein-17), lateral view of an abnormal aboral cup, with three additional plates within CB interray, x 1.7; ***7***, No. GIK-1958 (field-no. CREF33a-Hein-18), left anterolateral view of an abnormal aboral cup, radial B horizontal divided, x 2.4; ***8***, No. GIK-1959 (field-no. CREF33a-Hein-19), lateral view of an abnormal, juvenile aboral cup, with one additional plate intercalated within CB interray, x 3.1; ***9***, No. GIK-1960 (field-no. CREF33a-Hein-20), lateral view of CB interray, the aboral cup is sloping in anal direction, x 1.4; ***10***, No. GIK-1961 (field-no. CREF33a-Hein-21), lateral view of ED interray, the low aboral cup, showing inflated tegmen, is sloping in anal direction, x 1.3; ***11-13***, *Megaradialocrinus marginatus* (Schultze, 1866) n. comb.; ***11***, No. GIK-1962 (field-no. CREF33a-Prescher), aboral left anterolateral view of stem impression and E ray of aboral cup, x 1.8; ***12***, No. GIK-1963 (field-no. CREF33a-Bohatý-41), posterior view of primanal and posterior interradial plate (arrow) of aboral cup, x 2.0; ***13***, No. IPB-Bohatý-2, left anterolateral view of E ray, showing external bulges protruding toward the exterior, thus resulting in lowered and smooth centre of radials and basals, x 2.7; ***14-24***, *Megaradialocrinus brevis* (Goldfuss, 1839) n. comb. ***14-16***, **Holotype**, no. IPB-1319, right posterior view of D ray (***14***); left posterior view of C ray and primanal (***15***); aboral view (***16***), x 3.7; ***17***, No. GIK-1964 (field-no. CREF33a-Hein-22), right posterior view of D ray, x 3.4; ***18-21***, No. GIK-1965 (field-no. CREF33a-Hein-23), aboral cup with preserved tegmen; lateral view of AE interray (***18***); posterior view of primanal and posterior interradial plate (arrow) [***19***]; oral view (***20***); aboral view (***21***), x 2.5; ***22***, No. GIK-1966 (field-no. CREF33a-Hein-24), posterior view of primanal, x 4.0; ***23***, No. GIK-1967 (field-no. CREF33a-Hein-25), lateral view of AE interray, x 2.4; ***24***, No. GIK-1968 (field-no. CREF33a-Hein-26), lateral view of DE interray, x 4.2; ***25***, No. GIK-1969 (field-no. CREF33a-Hein-27), *Megaradialocrinus* cf. *brevis* (Goldfuss, 1839) n. comb., low and ornamented morphotype(?), anterior view of A ray, x 3.2; ***26***, No. GIK-1970 (field-no. CREF41-Bohatý-1), *Megaradialocrinus ornatus* (Goldfuss, 1839) n. comb., left anterolateral view of B ray, x 1.4.

Diagnosis.—A *Megaradialocrinus* with a low crown and a low bowl-shaped aboral cup, composed of three low, wider than long basals and five radials nearly as long as wide, and somewhat wider than the primanal; plates very convex and bulbous with typically three very coarse radiating ridges at the radial surface (Figs. 3.2.5.26, 3.2.6.20) and low tubercles at the basal surface; stem impression wide, impressed; arms heterotomously branching after the proximal branch, free strictly uniserial arms, short and small; two rami in each ray, zigzag arrangement of brachials; rami branching heterotomously with moderately long, somewhat narrower, bilateral and unbranched ramules; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials wide and U-shaped, compound, possessing (?)two pinnules each (bipinnulated) except on asymmetrical and pentagonal axillaries; column circular in cross section, with single pentalobate axial canal; tegmen and posterior interradial plate unknown.

3.2.7.3.6 Species *Megaradialocrinus exsculptus*

Megaradialocrinus exsculptus (GOLDFUSS, 1839) n. comb.[88]

Figs. 3.2.6.1-3

- *Hexacrinites exsculptus* (GOLDFUSS, 1839). BASSLER & MOODEY, 1943, p. 508. MIESEN, 1971, p. 37; figs. 51, 51a-d, *non* figs. 51e-g (= *M. aliculatus* n. sp.[89]). HAUSER, 1997, p. 145; pls. 47, figs. 5-6; 48, figs. 2-4, (?)5, 6; 52, figs. 2, *non* fig. 4 (= *M. aliculatus* n. sp.[90]), (?)5 [= *M*. aff. *aliculatus* n. sp.[91]], *non* fig. 6 [= lectotype of *M. ornatus* n. comb.[92] (*sic*!)]. HAUSER, 2001, pls. 6, fig. 2; 8, figs. 5-5a. WEBSTER, 2003 (*pars*), *Hexacrinites exsculptus*, internet edition of the Bibliography and Index of Palaeozoic crinoids. HAUSER, 2004, p. 30; fig. 30.
- *vidi Platycrinites exsculptus.* GOLDFUSS, 1839, p. 347; pl. 32, figs. 3a-c. BASSLER & MOODEY, 1943, p. 508.
- *Platycrinus exsculptus* (GOLDFUSS, 1839). BRONN, 1848, p. 993. DUJARDIN & HUPÉ, 1862, p. 155.
- *Hexacrinus exsculptus* (GOLDFUSS, 1839). SCHULTZE, 1866, pp. 77-78; pl. 9, figs. 2, 2b-c,

---

[88] = *Megaradialocrinus exsculptus* (GOLDFUSS, 1839) *sensu* ICZN

[89] = *M. aliculatus* BOHATÝ, in press *sensu* ICZN

[90] = *M. aliculatus* BOHATÝ, in press *sensu* ICZN

[91] = *M.* aff. *aliculatus* BOHATÝ, in press *sensu* ICZN

[92] = *M. ornatus* (GOLDFUSS, 1839) *sensu* ICZN

non figs. 2d-f (= *M. aliculatus* n. sp.[93]), 2g-(?)2h [= *M.* cf. *exsculptus* n. comb.[94]]. QUENSTEDT, 1885, p. 952; pl. 76, fig. 18. HOLZAPFEL, 1895, p. 302. PAECKELMANN, 1913, p. 335. BASSLER & MOODEY, 1943, p. 508.

- *non Hexacrinus exsculptus* GF. sp. STEINMANN, 1903, p 175; figs. 241A-B. STEINMANN, 1907, p. 195; figs. 276A-B. STEINMANN & DÖDERLEIN, 1890, p. 160; figs. 160A-B (= *M. aliculatus* n. sp.[95]).
- *Hexacrinites elongatus* GOLDF. MIESEN, 1971, p. 39; fig. 54h (= *M.* cf. *exsculptus* n. comb.[96]).
- *Hexacrinites* cf. *elongatus* (GOLDF., 1838). HAUSER, 1997, pl. 45, fig. 1.
- *Hexacrinites* sp. (*ornatus*?). MIESEN, 1971, p. 63, unnumbered figure below right (= *M.* cf. *exsculptus* n. comb.[97]).

Diagnosis.—A *Megaradialocrinus* with a low and slightly cone-shaped crown, composed of a large inverted coniform aboral cup (Figs. 3.2.6.1-3), widest lateral radius of the cup within the uppermost radial circlet; typically with long radials or rarely low and bowl-shaped; three basals, wider than long, the five radials nearly as long as wide; radials and the wider primanal are rarely smooth, typically with anastomising ridges and/or bulges, coarse ridges may parallel plate boundaries; impression of stem relatively wide and slightly impressed; tegmen high and inflated (Figs. 3.2.6.1-3), with a single, elongated and "rod-shaped" posterior interradial plate (see HAUSER 1997, pl. 48, fig. 3) below the subcentral anal opening; relatively slender arms with heterotomous branching after the proximal branch, free strictly uniserial arms, short and small; two rami in each ray, zigzag arrangement of brachials; rami branching heterotomously with moderately long, slender, bilateral and unbranched ramules; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials wide and U-shaped, compound, possessing (?)two pinnules each (bipinnulated) except on asymmetrical and pentagonal axillaries; plates brownish.

3.2.7.3.7 Species *Megaradialocrinus winteri*

Megaradialocrinus winteri n. sp.[98]

Figs. 3.2.6.21-26

(for synonymy and description see 3.2.7.4.2)

---

[93] = *M. aliculatus* BOHATÝ, in press *sensu* ICZN

[94] = *M.* cf. *exsculptus* (GOLDFUSS, 1839) *sensu* ICZN

[95] = *M. aliculatus* BOHATÝ, in press *sensu* ICZN

[96] = *M.* cf. *exsculptus* (GOLDFUSS, 1839) *sensu* ICZN

[97] = *M.* cf. *exsculptus* (GOLDFUSS, 1839) *sensu* ICZN

[98] = *Megaradialocrinus winteri* BOHATÝ, in press *sensu* ICZN

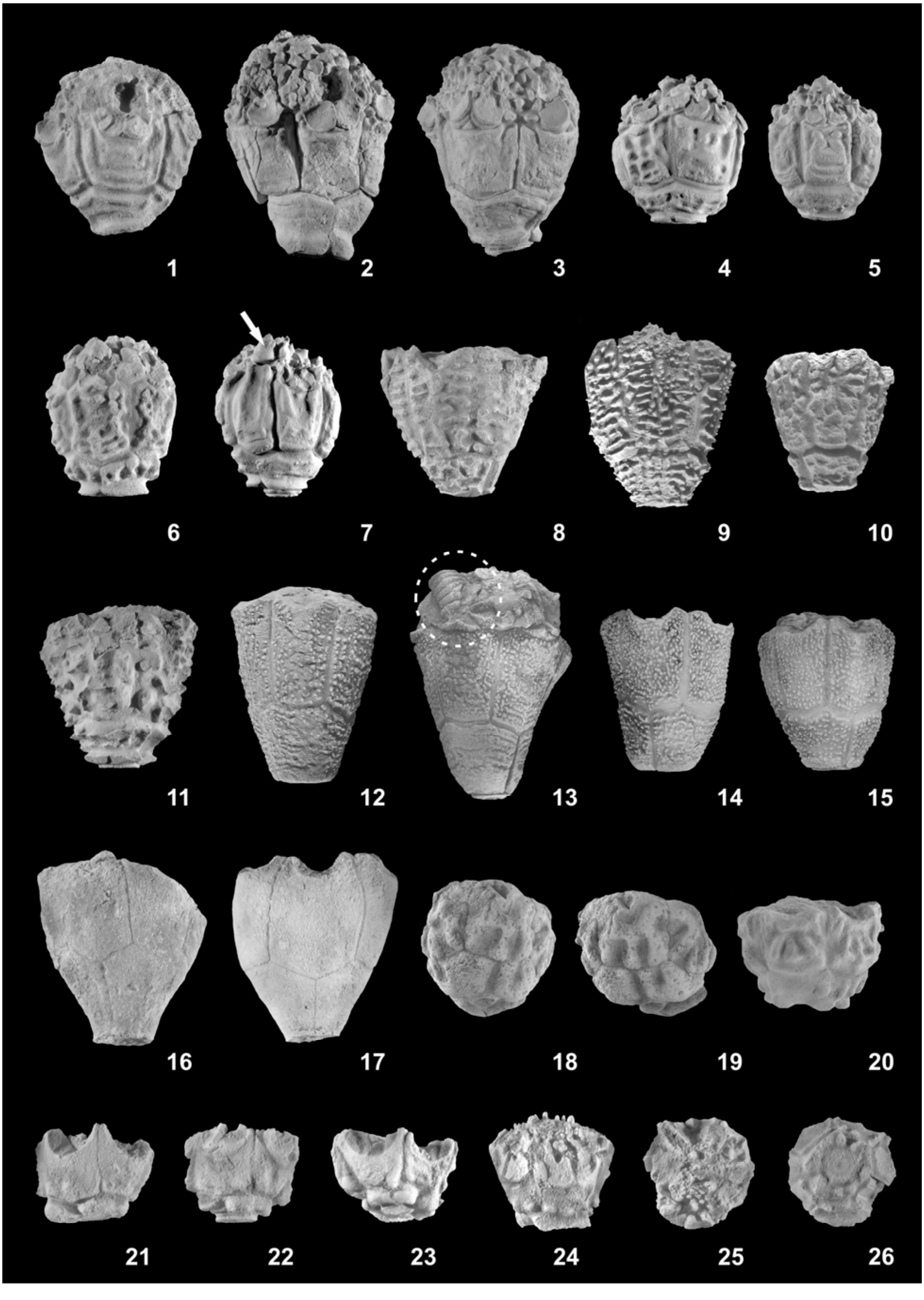


FIGURE 3.2.6 (legend p. 85)

Figure* 3.2.6 (see p. 84)**—*Megaradialocrinus* aboral cups from the Hustley Member (Loogh Formation, lowermost Lower Givetian) of the northeastern slope of the railway cut near the station of Gerolstein (Gerolstein Syncline, Eifel, Rhenish Massif) [2***, ***4-16***, ***21-26***], from the Eifelian/Givetian threshold of Kerpen (Hillesheim Syncline, Eifel) [***1***, ***17***], from the Hustley Member of Berlingen (Gerolstein Syncline) [***3***] and from the Baarley Member (Loogh Formation, lowermost Lower Givetian) of the "Mühlenwäldchen", SW-Gerolstein [***18-20***]. ***1-3***, *Megaradialocrinus exsculptus* (Goldfuss, 1839) n. comb. ***1***, No. GIK-1971, anterior view of A ray, typical low morphotype, x 1.2; ***2***, No. GIK-1972 (field-no. CREF33a-Hein-43), left anterolateral view of B ray, typical long morphotype, x 1.1; ***3***, No. GIK-1973 (field-no. CREF38-Hein-1), anterior view of A ray, typical long morphotype, x 1.1; ***4-7***, *Megaradialocrinus aliculatus* n. sp. ***4***, No. GIK-1974 (field-no. CREF33a-Hein-28), lateral view of BA interray, x 1.8; ***5***, **Holotype**, no. SMF-75473, anterior view of A ray, x 1.1; ***6***, No. GIK-1975 (field-no. CREF33a-Hein-29), right anterolateral view of E ray of the strongly ornamented aboral cup, x 1.6; ***7***, No. GIK-1976 (field-no. CREF33a-Hein-30), left posterior view of primanal with posterior interradial plate (arrow) and C ray, showing external bulges protruding toward the exterior, thus resulting in lowered plate centres, x 1.3; ***8-11***, *Megaradialocrinus anaglypticus* (Goldfuss, 1839) n. comb. ***8***, No. GIK-1977 (field-no. CREF33a-Hein-31), lateral view of EA interray, x 1.4; ***9***, No. GIK-1978 (field-no. CREF33a-Hein-32), right anterolateral view of E ray, x 1.2; ***10***, No. GIK-1979 (field-no. CREF33a-Hein-33), left posterior view of C ray, x 1.3; ***11***, No. GIK-1980 (field-no. CREF33a-Hein-34), lateral view of AE interray, x 2.0; ***12-15***, *Megaradialocrinus turritus* (Bohatý, 2006e) n. comb. ***12***, **Holotype**, no. MB.E.-2364, anterior view of A ray, x 1.2; ***13***, No. GIK-1981 (field-no. CREF33a-*turritus*-Hein-2), inverted coniform aboral cup, proximal part of uniserial arms preserved (encircled), left anterolateral view of EA interray, x 1.4; ***14***, No. GIK-1982 (field-no. CREF33a-*turritus*-Hein-3), aboral cup with well preserved ornamentation, left lateral view with E and D ray, x 1.3; ***15***, No. GIK-1983 (field-no. CREF33a-*turritus*-Hein-4), left anterolateral view of EA interray, x 1.6; ***16-17***, (?)*Megaradialocrinus piriformis* (Schultze, 1866) n. comb.; ***16***, No. GIK-1984 (field-no. CREF33a-Hein-35), lateral view of primanal and C ray, x 1.5; ***17***, No. GIK-1985, right anterolateral view of E ray, x 1.1; ***18-19***, *Megaradialocrinus hieroglyphicus* (Goldfuss, 1839) n. comb. **Holotype**, no. IPB-Goldfuss-1317, aboral view of stem impression and DE interray (***18***) and left anterolateral view of E ray (***19***) of the strongly weathered aboral cup, radials ornamented by radiating bulges, x 1.4; ***20***, No. CREF41-1 (col. Janke), *Megaradialocrinus ornatus* (Goldfuss, 1839) n. comb. with affinities to *M. hieroglyphicus* (Goldfuss, 1839) n. comb., anterior view of A ray, x 1.4; ***21-26***, *Megaradialocrinus winteri* n. sp.; ***21***, No. GIK-1986 (field-no. CREF33a-Hein-36) with lost primibrachials, lateral view of DE interray, x 1.8; ***22***, No. GIK-1987 (field-no. CREF33a-Hein-37) with preserved primibrachials, lateral view of DE interray, x 2.2; ***23***, **Holotype**, no. SMF-75474, lateral view of CB interray, x 1.5; ***24-26***, No. GIK-1988 (field-no. CREF33a-Hein-38) with preserved primibrachials and tegmen, anterior view of A ray (***24***); oral view (***25***); aboral view (***26***), x 2.1.

3.2.7.3.8 Species *Megaradialocrinus anaglypticus*

Megaradialocrinus anaglypticus (GOLDFUSS, 1839) n. comb.[99]

Figs. 3.2.6.8-11

- *Hexacrinites anaglypticus* (GOLDFUSS, 1839). BASSLER & MOODEY, 1943, p. 507. MIESEN, 1971, p. 33; figs. 44-44a, (?)44c, 45a, *non* fig. 44b (= *M. crispus* n. comb.[100]); *non* p. 35; figs. 45, 45b-c (= *M. crispus* n. comb.[101]); 60, unnumbered figure above left. MURRAY, 1990, p. 185; figs. 7.4.4A-B. HAUSER, 1997, pp. 139-141; pls. 40, figs. 1-5; 41, figs. 1-6; 42, figs. 1-2, *non* figs. 3-6 (= *M. crispus* n. comb.[102]). HAUSER, 2001, *non* p. 11; fig. 5, *non* figs. 4, 6 (= *M. crispus* n. comb.[103]); pls. 8, fig. 1; 25, figs. 2-2a. WEBSTER, 2003 (*pars*) *Hexacrinites anaglypticus,* internet edition of the Bibliography and Index of Palaeozoic crinoids.
- *vidi Platycrinites anaglypticus.* GOLDFUSS, 1839, p. 348; pl. 32, fig. 4. BASSLER & MOODEY, 1943, p. 507. SPRENG & PARKS, 1953, p. 594; figs. 1e, h. WEBSTER, 1977, p. 96. SMITH, 1985, p. 166; pl. 7.4.4. WEBSTER, 1988, p. 94.
- *Platycrinus anaglypticus* (GOLDFUSS, 1839). BRONN, 1848, p. 993. DUJARDIN & HUPÉ, 1862, p. 155.
- *Hexacrinus anaglypticus* (GOLDFUSS, 1839). SCHULTZE, 1866, pp. 72-74; pl. 8, figs. 1, 1a-b, 1h, *non* figs. 1c-g, 1i (= *M. crispus* n. comb.[104]). WILSON, 1916, p. 510; pl. 3, figs. 5-6. WANNER, 1943, p. 37; unnum. fig. p. 37. BASSLER & MOODEY, 1943, p. 507. WEBSTER, 1977, p. 96.
- *Hexacrinus anaglypticus* var. *granulosa.* SCHULTZE, 1866, p. 73; pl. 8, fig. 1h. BASSLER & MOODEY, 1943, p. 507.
- *Hexacrinites anaglypticus granulosa* (SCHULTZE, 1867). HAUSER, 1997, p. 139.
- *non Hexacrinites anaglypticus* aff. *granulosa* (SCHULTZE, 1867). HAUSER, 1997, p. 139; pl. 42, figs. 3-4 (= *M. crispus* n. comb.[105]).
- *Hexacrinites anaglypticus granulosus* (SCHULTZE, 1866). BASSLER & MOODEY, 1943, p. 507. HAUSER, 2001, p. 11; fig. 5. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*cum syn.*).

---

[99] = *Megaradialocrinus anaglypticus* (GOLDFUSS, 1839) *sensu* ICZN
[100] = *M. crispus* (QUENSTEDT, 1861) *sensu* ICZN
[101] = *M. crispus* (QUENSTEDT, 1861) *sensu* ICZN
[102] = *M. crispus* (QUENSTEDT, 1861) *sensu* ICZN
[103] = *M. crispus* (QUENSTEDT, 1861) *sensu* ICZN
[104] = *M. crispus* (QUENSTEDT, 1861) *sensu* ICZN
[105] = *M. crispus* (QUENSTEDT, 1861) *sensu* ICZN

Diagnosis.—A *Megaradialocrinus* with long, inverted coniform aboral cup (Figs. 3.2.6.8-11); basal circlet inverted coniform, composed of three slightly wider than long basals, with a smooth stem impression surrounded by tripartite basal flanges; radials five, long and somewhat wider than the primanal, surface of plates sculptured by mostly horizontal depressions or slightly meandering ridges and intermediary tubercles at the radial centres (Fig. 3.2.6.9); tegmen flat, composed of numerous plates, which are sculptured with low, generally irregularly arranged tubercles and/or spines; with a single posterior interradial plate below the subcentral anal opening; column circular in cross section, with single pentalobate axial canal; arms unknown.

3.2.7.3.9 Species *Megaradialocrinus turritus*

Megaradialocrinus turritus (BOHATÝ, 2006e) n. comb.[106]

Figs. 3.2.6.12-15

- *vidi Hexacrinites turritus.* BOHATÝ, 2006e, figs 2, 6.1-6.11 (*cum syn.*).
- *Hexacrinites triradiatus* (SCHULTZE, 1867). HAUSER, 1997, pls. 53, fig. 6 [= holotype of *M. turritus* (BOHATÝ, 2006e) n. comb.[107] (*vidi*)]; 54, figs. 1-2.
- *vidi Hexacrinites thomasbeckeri.* HAUSER, 2004, pl. 2, figs. 7-8.

Diagnosis.—Crown (BOHATÝ 2006e, p. 264; fig. 2) slender; aboral cup longer than wide, conical to “tower-shaped” (Figs. 3.2.6.12-15); basal circlet inverted coniform, composed of three slightly wider than long basals, with a smooth stem impression; radials five, long and somewhat wider than the primanal; plates sculptured with low, generally irregularly arranged tubercles, very infrequently (especially in juvenile aboral cups) the plates are sculptured with discontinuous low and irregularly arranged nodes to sinuous ridges and tubercles forming extremely faint lines parallel to plate edges on radials and/or lines parallel to the proximal sutures of radials; free strictly uniserial arms, two rami in each ray, nearly straight- to slightly zigzag; rami branching heterotomously with somewhat narrower, bilateral and unbranched ramules; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials three to four times wider than long, ornamented with

---

[106] = *Megaradialocrinus turritus* (BOHATÝ, 2006e) *sensu* ICZN

[107] = *M. turritus* (BOHATÝ, 2006e) *sensu* ICZN

fine granules (see 2006, p. 264; fig. 2), U-shaped and compound, possessing (?)two pinnules each (bipinnulated) except on asymmetrical and pentagonal axillaries; column circular in cross section, with single pentalobate axial canal and sculptured with regularly arranged tubercles; tegmen and posterior interradial plate unknown.

3.2.7.3.10 Species (?)*Megaradialocrinus piriformis*

(?)*Megaradialocrinus piriformis* (SCHULTZE, 1866) n. comb.[108]

Figs. 3.2.6.16-17

- *Hexacrinites piriformis* (SCHULTZE, 1867). BASSLER & MOODEY, 1943, p. 510. WEBSTER, 1973, p. 148. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*cum syn.*).
- *Hexacrinites piriformis* (SCHULTZE, 1866). HAUSER, 2001, p. 36; figs. 26; pl. 7, fig. 3.
- *Hexacrinus piriformis.* SCHULTZE, 1866, pp. 76-77. BASSLER & MOODEY, 1943, p. 510.
- *Hexacrinus pyriformis.* SCHULTZE, 1866, pl. 10, figs. 1, 1a-b, (?)1c.
- *Hexacrinites pyriformis* (SCHULTZE, 1867). MIESEN, 1971, p. 39; figs. 55, 55a-b, (?)55c. HAUSER, 1997, p. 161; pl. 52, fig. 8.

Diagnosis.—A large (?)*Megaradialocrinus* with a presumably long crown, and an elongated "pear-shaped" aboral cup (Figs. 3.2.6.16-17); basal circlet long and inverted coniform, composed of three basal plates nearly as long as wide; radial circlet composed of long radials and a somewhat narrower primanal, all slightly longer than wide, radial circlet inflated toward the lateral exterior; plates either smooth or typically microgranulated, sometimes slightly facetted parallel to the plate edges; stem impression moderately impressed; free strictly uniserial arms, two zigzagged rami in each ray; rami branching heterotomously with bilateral and unbranched ramules; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials U-shaped, compound, possessing (?)two pinnules each (bipinnulated) except on asymmetrical axillaries; column circular in cross section, with single pentalobate axial canal; tegmen and posterior interradial plate unknown.

---

[108] = (?)*Megaradialocrinus piriformis* (SCHULTZE, 1866) *sensu* ICZN

3.2.7.3.11 Species *Megaradialocrinus hieroglyphicus*

Megaradialocrinus hieroglyphicus (GOLDFUSS, 1839) n. comb.[109]

Figs. 3.2.6.18-19

- *Hexacrinites hieroglyphicus* (GOLDFUSS, 1839). HAUSER, 2004, pp. 27-31; figs. 24-25, 27-28; pl. 2, figs. 2a-b, 3; *non* p. 28; fig. 26 [= holotype of *M. marginatus* (SCHULTZE, 1866) n. comb.[110] (*sic*!)]. BOHATÝ & HERBIG, 2007, pp. 731-735; figs. 3A-C, 5A-H.
- *vidi Platycrinites hieroglyphicus.* GOLDFUSS, 1839, p. 344; pl. 31, figs. 9a-b. BRONN, 1848, p. 993. D'OEBIGUY, 1850, p. 103. DUJARDIN & HUPÉ, 1862, p. 152. BASSLER & MOODEY, 1943, p. 621. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids, *pars Platycrinites hieroglyphicus.*
- *non Hexacrinus hieroglyphicus* (GOLDFUSS, 1839). QUENSTEDT, 1876, pl. 109, fig. 68 [= *Hexacrinites pateraeformis* (SCHULTZE, 1866)].
- *Hexacrinites marginata* (SCHULTZE, 1866). HAUSER, 1997, pp. 152-153; pl. 50, figs. 7-8. (fig. 8 = oral view of fig. 7, not of fig. 6 as given in the explanation).
- *sic*! *vidi Hexacrinites* aff. *marginata* (SCHULTZE, 1866). HAUSER, 1997, pl. 53, fig. 4 [= holotype of *M. hieroglyphicus* (GOLDFUSS, 1839) n. comb.[111]].
- (?)*Hexacrinites ornatus* (G. A. GOLDFUSS, 1839). HAUSER, 2001, pl. 25, figs. (?)3-3a [= *M.* aff. *hieroglyphicus* (GOLDFUSS, 1839) n. comb.[112]].
- *sic*! *vidi Hexacrinites* (?)*ornatus* (GOLDFUSS, 1839). HAUSER, 1997, p. 213 [= holotype of *M. hieroglyphicus* (GOLDFUSS, 1839) n. comb.[113]].
- *sic*! *vidi Hexacrinites* sp. HAUSER, 2001, p. 183 [= holotype of *M. hieroglyphicus* (GOLDFUSS, 1839) n. comb.[114]].

Diagnosis.—A *Megaradialocrinus* with a massive aboral cup, composed of three wider than long basals, forming a low basal circlet and five radials nearly as long as wide, somewhat wider than the primanal; radials and primanal sculptured with four to six radiating ridges and rarely by variously formed minor ridges between, all plate sculpturing strongly protruding toward the exterior, especially in radials (Figs. 3.2.6.18-19); plate

---

[109] = *Megaradialocrinus hieroglyphicus* (GOLDFUSS, 1839) *sensu* ICZN

[110] = *M. marginatus* (SCHULTZE, 1866) *sensu* ICZN

[111] = *M. hieroglyphicus* (GOLDFUSS, 1839) *sensu* ICZN

[112] = *M.* aff. *hieroglyphicus* (GOLDFUSS, 1839) *sensu* ICZN

[113] = *M. hieroglyphicus* (GOLDFUSS, 1839) *sensu* ICZN

[114] = *M. hieroglyphicus* (GOLDFUSS, 1839) *sensu* ICZN

boundaries impressed, which cover most of the central part of the radials; tegmen moderately inflated; with a single posterior interradial plate below the subcentral anal opening; plates brown or rarely grey (BOHATÝ & HERBIG 2007); stem impression relatively small and surrounded by the wide basis of the aboral cup; column circular in cross section, with single pentalobate axial canal; arms unknown.

3.2.7.3.12 Species *Megaradialocrinus aliculatus*

Megaradialocrinus aliculatus n. sp.[115]

Figs. 3.2.6.4-7

(for synonymy and description see 3.2.7.4.1)

3.2.7.3.13 Species *Megaradialocrinus limbatus*

Megaradialocrinus limbatus (MÜLLER, 1856) n. comb.[116]

Figs. 3.2.7.1-4

- *Hexacrinites limbatus* (MÜLLER, 1856). BASSLER & MOODEY, 1943, p. 509. MIESEN, 1971, p. 37; figs. 50, 50a-c. UBAGHS in MOORE & TEICHERT, 1978, p. T474; fig. 279, no. 1d. WEBSTER, 1986, p. 170. HAUSER, 1997, pp. 149-150; pl. 50, figs. 1-3. HAUSER, 2001, pl. 28, fig. 4. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*cum syn.*).
- *Hexacrinus limbatus.* MÜLLER, 1856, p. 354; pls. 1, figs. 5-9; 2, fig. 1. SCHULTZE, 1866, p. 78; pl. 9, figs. 1, 1a-e. BASSLER & MOODEY, 1943, p. 509.
- *Hexacrinites* cf. *limbatus* (J. MUELLER, 1856). HAUSER, 2001, pl. 28, fig. 3.

Diagnosis.—A *Megaradialocrinus* with a long crown (compare to SCHULTZE 1866, pl. 9, fig. 1) and a short "pear-shaped" aboral cup (Figs. 3.2.7.1-4), composed of three basals, lower than radials, forming a low inverted coniform basis and five radials longer than wide and somewhat wider than the primanal, radial circlet inflated toward the lateral exterior; plates smooth or sometimes slightly facetted parallel to the plate edges; tegmen less convex,

---

[115] = *Megaradialocrinus aliculatus* BOHATÝ, in press *sensu* ICZN

[116] = *Megaradialocrinus limbatus* (MÜLLER, 1856) *sensu* ICZN

with a single, elongated and “rod-shaped” posterior interradial plate below the subcentral anal opening, with vertically arranged spines (most likely a defence against platyceratid gastropods, compare to Figs. 3.2.9.2-3) giving the plate a “cockscomb-shaped” surface (Figs. 3.2.7.1-2, 3.2.7.4; also see model, Fig. 3.2.9.3); impression of stem moderately concave, typically surrounded by ring-shaped flange (Fig. 3.2.7.1); free strictly uniserial arms, two rami in each ray, zigzag (SCHULTZE 1866, pl. 9, fig. 1; also see model, Fig. 3.2.8.2); rami branching heterotomously with narrower, bilateral and unbranched ramules; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials wide and U-shaped, compound, possessing (?)two pinnules each (bipinnulated) except on asymmetrical and pentagonal axillaries; stem circular in cross section, smooth latus, without cirri, perforated by a small, single axial canal with pentalobate cross section.

3.2.7.3.14 Species *Megaradialocrinus piriculaformis*

Megaradialocrinus piriculaformis n. sp.[117]
Figs. 3.2.7.5-7
(for synonymy and description see 3.2.7.4.3)

3.2.7.3.15 Species *Megaradialocrinus lobatus*

Megaradialocrinus lobatus (MÜLLER, 1856) n. comb.[118]
for lithography and photos see SCHULTZE (1866, pl. 10, figs. 6, 6a-c)
and HAUSER (2001, pl. 12, figs. 1-1a)

- *Hexacrinites lobatus* (MÜLLER, 1856). BASSLER & MOODEY, 1943, p. 509. MIESEN, 1971, p. 43; figs. 60, 60a-c. POLYARNARYA, 1986, p. 79; unnum. pl., figs. 1, 3. WEBSTER, 1993, p. 68. HAUSER, 1997, pp. 150-152. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*cum syn.*).
- *vidi Hexacrinus lobatus.* MÜLLER, 1857, p. 248; pl. 1, figs. 10-12. SCHULTZE, 1866, p. 84; pl. 10, figs. 6, 6a-c. QUENSTEDT, 1885, p. 953; pl. 76, fig. 21. BASSLER & MOODEY, 1943, p. 509.

---

[117] = *Megaradialocrinus piriculaformis* BOHATÝ, in press *sensu* ICZN
[118] = *Megaradialocrinus lobatus* (MÜLLER, 1856) *sensu* ICZN

- *Hexacrinites* cf. *lobatus* (MUELLER, 1856). HAUSER, 1997, pl. 50, figs. 5-6.
- *vidi Hexacrinites lobatus* (L. SCHULTZE). HAUSER, 2001, pl. 12, figs. 1-1a [= holotype of *M. lobatus* (MÜLLER, 1856) n. comb.[119]; authorship wrongly assigned to DR. LUDWIG SCHULTZE].

Diagnosis.—A relatively small *Megaradialocrinus* with low bowl-shaped aboral cup, composed of three wide basals surrounding the small stem impression with irregularly developed nodes that project proximally – “lobe-shaped” – from basal plates (SCHULTZE 1866, pl. 10, figs. 6-6a) and five radials wider than long and somewhat wider than primanal, radials and primanal sculptured at the proximal sutures by “lobe-shaped” sculpturing or blunt spines, which strongly protrude toward the lateral or aboral exterior; arm facets small and laterally salient; massive tegmen, composed of few massive, convex modified ambulacral plates, very convex orals, and a characteristic “funnel-shaped” spine at the central tegminal plate (most likely a defence against platyceratid gastropods) [see HAUSER 2001, pl. 12, figs. 1-1a], length of tegmen 50% of the complete length of aboral cup; with a single posterior interradial plate below the subcentral anal opening; stem circular in cross section, perforated by a small, single axial canal with pentalobate cross section; arms unknown.

3.2.7.3.16 Species *Megaradialocrinus callosus*

Megaradialocrinus callosus (SCHULTZE, 1866) n. comb.[120]

Fig. 3.2.7.9

- *Hexacrinites callosus* (SCHULTZE, 1867). BASSLER & MOODEY, 1943, p. 507. MIESEN, 1971, p. 39; figs. 52, 52a-e. HAUSER, 1997, pp. 143-144; *non* pl. 51, figs. 4-6 [= *H. websteri* HAUSER, 2001; also given as pl. 77, fig. 2, but there is no plate 77]. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*cum syn.*).
- *Hexacrinus callosus.* SCHULTZE, 1866, pp. 83-84; pl. 9, figs. 3, 3a-e. BASSLER & MOODEY, 1943, p. 507.
- *non Hexacrinites* cf. *callosus* (SCHULTZE, 1867). HAUSER, 1997, pl. 51, fig. 3. (= *H. websteri* HAUSER, 2001).

---

[119] = *M. lobatus* (MÜLLER, 1856) *sensu* ICZN

[120] = *Megaradialocrinus callosus* (SCHULTZE, 1866) *sensu* ICZN

- *Hexacrinites* aff. *callosus* (SCHULTZE, 1867). HAUSER, 1997, pl. 44, fig. 2.
- *vidi non Hexacrinites sp.* aff. *Hexacrinites callosus* (SCHULTZE, 1867). HAUSER, 1997, pl. 53, fig. 1 (= *Megaradialocrinus winteri* n. sp.[121]).

Diagnosis.—A relatively small *Megaradialocrinus* with a low bowl-shaped aboral cup, composed of massive plates: three very low basals, forming a low, wide "tyre-shaped" basal circlet (Fig. 3.2.7.9) and five massive and wide radials, which are somewhat wider than primanal and longer than basals; radials and primanal forming a quadrangular outline in oral view, radials and primanal typically smooth, rarely adorned with blunt tubercles mostly at the proximal sutures of radials; impression of stem moderately impressed; stem circular in cross section, perforated by a small, single axial canal with pentalobate cross section; arms, tegmen and posterior interradial plate unknown.

3.2.7.3.17 Species *Megaradialocrinus crispus*

Megaradialocrinus crispus (QUENSTEDT, 1861) n. comb.[122]

Figs. 3.2.7.10-12

- *Hexacrinites crispus* (QUENSTEDT, 1861). BOHATÝ, 2006c, figs. 1a-d, 2a-d, 3a-f. WEBSTER, 2003, internet edition of the Bibliography and Index of Palaeozoic crinoids (*pars*), *non* "*H. crispus*" *sensu* DUBATOLOVA (1964: p. 34; pl. 4, figs. 3-4) [= "*Hexacrinites prokopi*" n. nov. *sensu* BOHATÝ (2006c) = *M. prokopi* (BOHATÝ 2006c) n. comb.[123]].
- *vidi Hexacrinus crispus* QUENSTEDT, 1861, p. 327, unnum. woodcut. QUENSTEDT, 1876, p. 562; pl. 109, fig. 58. QUENSTEDT, 1885, p. 952; fig. 357. BASSLER & MOODEY, 1943, p. 507.
- *Hexacrinus anaglypticus* var. *stellaris.* SCHULTZE, 1866, pp. 72-74; pl. 8, figs. 1c-g. MIESEN, 1971, pls. 11, fig. 44b; 12, figs. 45b-c.
- *Hexacrinites anaglypticus stellaris* HAUSER, 2001, p. 11; fig. 6.
- *Hexacrinites anaglypticus* aff. *stellaris* (SCHULTZE, 1867). HAUSER, 1997, pp. 139-141; pl. 42, fig. 6.
- *Hexacrinus anaglypticus* var. *frondosa* (*Platycrinus frondosus* GOLDF. Mus. Bonn). SCHULTZE, 1866, pl. 8, fig. 1i. MIESEN, 1971, pl. 12, fig. 45.
- *vidi Hexacrinites anaglypticus* aff. *frondosa* (SCHULTZE, 1867). HAUSER, 1997, pp. 139-141; pl. 42, fig. 5.

---

[121] = *Megaradialocrinus winteri* BOHATÝ, in press *sensu* ICZN

[122] = *Megaradialocrinus crispus* (QUENSTEDT, 1861) *sensu* ICZN

[123] = *M. prokopi* (BOHATÝ 2006c) *sensu* ICZN

- *Hexacrinites anaglypticus frondosus* (SCHULTZE, 1867). HAUSER, 2001, p. 11; fig. 4.
- "*Hexacrinites frondosus* n. comb." *sensu* HAUSER, 2004, pp. 26-27; figs. 20-21.
- *vidi Hexacrinites anaglypticus* aff. *granulosa* (SCHULTZE, 1867). HAUSER, 1997, pp. 139-141; pl. 42, figs. 3-4.
- "*Hexacrinites ludwigschultzei*". HAUSER, 2004, pp. 33-35; figs. 34-36 [compare HAUSER, 2004, fig. 21 ("*H. frondosus*") with fig. 34 ("*H. ludwigschultzei*")].

Diagnosis.—Aboral cup wider than long, bowl-shaped, composed of three basals wider than long, forming a low and wide basal circlet and five radials nearly as long as wide, wider than the primanal and twice as long as the basals; all plates sculptured by irregular anastomosing ridges (QUENSTEDT 1861, p. 327; 1876, p. 562); structures either unoriented (Fig. 3.2.7.10) or slight to strong radiating ridges (QUENSTEDT 1876, pl. 109, fig. 58; SCHULTZE 1866, pl. 8, fig. 1i) [Figs. 3.2.7.11-12]; tegmen moderately inflated, composed of numerous plates, which are sculptured by short spines and tubercles and a characteristic, single posterior interradial plate below the subcentral anal opening (see model, Fig. 3.2.9.2), with a massive spine at the surface (most likely a defence against platyceratid gastropods, compare to Figs. 3.2.9.2-3); impression of stem wide and moderately concave; stem circular in cross section, perforated by a small, single axial canal with pentalobate cross section; arms unknown.

3.2.7.3.18 Species *Megaradialocrinus theissi*

Megaradialocrinus theissi n. sp.[124]
Figs. 3.2.7.13-17
(for synonymy and description see 3.2.7.4.4)

3.2.7.3.19 Species (?)*Megaradialocrinus bulbiformis*

(?)*Megaradialocrinus bulbiformis* n. sp.[125]
Figs. 3.2.7.8
(for synonymy and description see 3.2.7.4.5)

---

[124] = *Megaradialocrinus theissi* BOHATÝ, in press *sensu* ICZN

[125] = (?)*Megaradialocrinus bulbiformis* BOHATÝ, in press *sensu* ICZN

3.2.7.4 Description of new species

3.2.7.4.1 Species *Megaradialocrinus aliculatus*

Megaradialocrinus aliculatus n. sp.[126]

Figs. 3.2.6.4-7

- *Hexacrinites exsculptus* (Goldfuss, 1839). Miesen, 1971, p. 37; figs. 51e-g. Hauser, 1997, pl. 52, figs. 4-(?)5 [= *M*. aff. *aliculatus* n. sp.[127]]. Webster, 2003 (*pars*), *Hexacrinites exsculptus*, internet edition of the Bibliography and Index of Palaeozoic crinoids.
- *Hexacrinus exsculptus* (Goldfuss, 1839). Schultze, 1866, pl. 9, figs. 2d-f.
- *Hexacrinus exsculptus* Gf. sp. Steinmann, 1903, p. 175; figs. 241A-B. Steinmann, 1907, p. 195; figs. 276A-B. Steinmann & Döderlein, 1890, p. 160; figs. 160A-B.

Holotype.—Isolated aboral cup, no. SMF-75473, deposited in the *Forschungsinstitut und Naturmuseum Senckenberg*, Frankfurt/Main, Germany (Fig. 3.2.6.5).

Other material examined.—Aboral cups nos. GIK-1974 (field-no. CREF33a-Hein-28) [Fig. 3.2.6.4], GIK-1975 (field-no. CREF33a-Hein-29) [Fig. 3.2.6.6], GIK-1976 (field-no. CREF33a-Hein-30) [Fig. 3.2.6.7] and original of Schultze (1866, pl. 9, figs. 2d-f) [unfigured].

Derivatio nominis.—After the shape of the conical tegmen with the central spine, giving an alicula-shaped appearance (*alicula* = tapered Roman headdress).

Locus typicus.—Northeastern slope of the railway cut near the station of Gerolstein, Gerolstein Syncline, Eifel, (Rhenish Massif, northwestern Rhineland-Palatinate, westernmost Germany); topographic map (1:25.000) of the Landesvermessungsamt Rheinland-Pfalz: MTB 5706 Hillesheim r(25)477500/h(55)656375.

Stratum typicum.—Hustley Member [equivalent to the Rech Member (Hotz, Kräusel & Struve 1955, p. 117) within Gerolstein Syncline (*sensu* Winter 1965, p. 290)] of upper Loogh Formation, Lower Givetian (Middle Devonian; *hemiansatus* Conodont Biozone).

---

[126] = *Megaradialocrinus aliculatus* Bohatý, in press *sensu* ICZN

[127] = *M*. aff. *aliculatus* Bohatý, in press *sensu* ICZN

Distribution.—Eifel; stratum typicum of the Hillesheim Syncline (village Kerpen) and Gerolstein Syncline (Gerolstein, Pelm and Berlingen).

Diagnosis.—A *Megaradialocrinus* with globe-shaped aboral cup, composed of three wider than long basals, forming a low convex base and five typically slightly longer than wide radials, which are somewhat wider than the primanal; widest lateral radius within the equatorial region of the cup, tegmen long cone-shaped with central spine at the summit and a single, elongated and "rod-shaped" posterior interradial plate (Fig. 3.2.6.7) below the subcentral anal opening; free strictly uniserial arms, two rami in each ray, zigzag; rami branching heterotomously with long, bilateral, unbranched and long ramules, nearly as wide as rami; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials U-shaped, compound, possessing two [to (?)four] pinnules each except on axillaries; plates of unweathered skeleton dark grey to black; impression of stem wide and planar; stem circular in cross section, perforated by a small, single axial canal with pentalobate cross section.

Measurements of the holotype (max. length/width in mm).—Aboral cup (with preserved tegmen): 28.0/21.5; basals: 8.0/13.0; radials: 13.0/10.0; primanal: 15.0/8.0; diameter of stem impression: 11.5; diameter of stem facet: 5.5.

Description.—The globe-shaped aboral cup without preserved tegmen is slightly wider than long, with preserved tegmen longer than wide; longitudinal section elliptical to "egg-shaped" (Figs. 3.2.6.5, 3.2.6.7), widest lateral radius within the equatorial region of the aboral cup; basals wider than long, smooth or with horizontal ornament in the form of ring-shaped folds surrounding the wide planar stem impression (Fig. 3.2.6.6); radials longer than wide and convex toward the lateral exterior, typically sculptured by variously shaped ridges (Figs. 3.2.6.4, 3.2.6.6), which are mainly parallel to the proximal end of the radials, plate sutures impressed; the long tegmen is cone-shaped and characterised by a central spine at the distal end (most likely a defence against platyceratid gastropods) [Figs. 3.2.6.5, 3.2.6.7], the orals and modified ambulacral plates protrude with spine-shaped ends toward the oral exterior, giving the depth of plates an idealised "drop-shaped" morphology (Figs. 3.2.6.4-5, 3.2.6.7); with a single, elongated and "rod-shaped" posterior interradial plate (Fig. 3.2.6.7) below the subcentral anal opening; free strictly uniserial arms, two rami in each ray, zigzag; rami branching heterotomously with long, bilateral, unbranched and long ramules, nearly as wide as rami; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials low, wide and U-shaped, compound, possessing two [to (?)four] pinnules each except on axillaries; the plates of the unweathered skeleton are dark grey to black; other skeletal elements unknown.

Differentiation.—*Megaradialocrinus aliculatus* n. sp.[128] is similar to *M. ornatus* n. comb.[129] and *M. exsculptus* n. comb.[130] *M. ornatus* developed a smaller and shorter aboral cup with a lower and wider basal circlet. The new species developed low and globe-shaped aboral cups instead of long and conical cups as in *M. exsculptus*. The basals are lower than those of *M. exsculptus*. The widest lateral diameter of *M. aliculatus* is within the equatorial region of the aboral cup, whereas *M. exsculptus* has the widest region at the radial summit. The inverted cone-shaped tegmen of the new species is constructed by "drop-shaped" plates, forming inflated polygons, and a characteristic central spine at the distal top, which is not developed in the cupola-shaped tegmen of *M. exsculptus*. The unweathered crinoid plates are dark grey to black in contrast to the brownish plates of *M. exsculptus* [feature of certain taxonomic value, already described in cupressocrinitids, gasterocomids (BOHATÝ 2005a; 2006a-b) and hexacrinitids (BOHATÝ & HERBIG 2007)].

3.2.7.4.2 Species *Megaradialocrinus winteri*

Megaradialocrinus winteri n. sp.[131]
Figs. 3.2.6.21-26

- *vidi Hexacrinites* sp. aff. *Hexacrinites callosus* (SCHULTZE, 1867). HAUSER, 1997, pl. 53, fig. 1.

Holotype.—Isolated aboral cup, no. SMF-75474, deposited in the *Forschungsinstitut und Naturmuseum Senckenberg*, Frankfurt/Main, Germany (Fig. 3.2.6.23).

Other material examined.—Aboral cups nos. GIK-1986 (field-no. CREF33a-

---

[128] = *Megaradialocrinus aliculatus* BOHATÝ, in press *sensu* ICZN
[129] = *M. ornatus* (GOLDFUSS, 1839) *sensu* ICZN
[130] = *M. exsculptus* (GOLDFUSS, 1839) *sensu* ICZN
[131] = *Megaradialocrinus winteri* BOHATÝ, in press *sensu* ICZN

HEIN-36) [Fig. 3.2.6.21], GIK-1987 (field-no. CREF33a-HEIN-37) [Fig. 3.2.6.22], GIK-1988 (field-no. CREF33a-HEIN-38) [Figs 3.2.6.24-26], CREF33a-81 (col. PRESCHER) [infested by a platyceratid gastropod, unfigured] and one isolated aboral cup as well as approx. 150 isolated radial plates from the uppermost Baarley Member (Loogh Formation, lowermost Lower Givetian) of the "Berlinger Bach" (to the west of Berlingen, Gerolstein Syncline, Eifel, Germany) [without repository, unfigured].

Derivatio nominis.—In honour of PROF. DR. JOSEF WINTER (Bad Orb; Professor Emeritus at the Johann Wolfgang Goethe-University, Frankfurt/Main), whose stratigraphical studies represents the fundamental groundwork of the Gerolstein Syncline.

Locus typicus.—Northeastern slope of the railway cut near the station of Gerolstein, Gerolstein Syncline, Eifel, (Rhenish Massif, northwestern Rhineland-Palatinate, westernmost Germany); topographic map (1:25.000) of the Landesvermessungsamt Rheinland-Pfalz: MTB 5706 Hillesheim r(25)477500/h(55)656375.

Stratum typicum.—Hustley Member [equivalent to the Rech Member (HOTZ, KRÄUSEL & STRUVE 1955, p. 117) within Gerolstein Syncline (*sensu* WINTER 1965, p. 290)] of upper part of Loogh Formation, Lower Givetian (Middle Devonian; *hemiansatus* Conodont Biozone).

Distribution.—Eifel; Baarley and Hustley members of the lower and uppermost Loogh Formation (lowermost Lower Givetian) and Hustley Member of Gerolstein, Pelm and Berlingen (Gerolstein Syncline).

Diagnosis.—A small *Megaradialocrinus* with low, bowl-shaped aboral cup, composed of three basals much wider than long, forming a low, wide and idealised "cloverleaf-shaped" basal circlet (Figs. 3.2.6.23, 3.2.6.26) and five radials wider than long, which are deeply notched by the radial facets; tegmen moderately inflated, composed of small, spinose plates with fine central spines at the distal top; with a single posterior interradial plate below the subcentral anal opening; free strictly uniserial arms, two rami in each ray, zigzag; rami branching heterotomous with somewhat narrower, bilateral and unbranched ramules; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials wide and U-shaped, compound, possessing two pinnules each (bipinnulated) except on asymmetrical and pentagonal axillaries; impression of stem relatively wide; stem circular in cross section, perforated by a small, single axial canal with pentalobate cross section.

Measurements of the holotype (max. length/width in mm).—Aboral cup (without tegmen): 9.5/15.0; basals: 3.5/8.0; radials: 7.0/8.5; primanal: 8.0/6.5; diameter of stem impression: 10.0; diameter of stem facet: 4.0.

Description.—The small and low bowl-shaped aboral cup (Figs. 3.2.6.21-26) is wider than long without preserved tegmen, with tegmen nearly as long as wide; the very low and idealised “cloverleaf-shaped” basal circlet (Figs. 3.2.6.23, 3.2.6.26) is typically smooth or sculptured by two to three blunt tubercles; the radials are typically as long as wide or wider than long, with sculpturing at the proximal end of three blunt tubercles (Fig. 3.2.6.24) that protrude aborally, in some specimens the centre tubercle is extended aborally, overhanging the radial/basal suture by forming triangular lowermost radial flanges; radials without greatly reduced primibrachials (Figs. 3.2.6.22, 3.2.6.24) deeply notched to the radial centres (Figs. 3.2.6.21, 3.2.6.23); the peaked and coniform tegmen (Figs. 3.2.6.24-25) is constructed by small spinose plates, giving the depth of plates an idealised “elongated lozenged” to “arrowhead-shaped” morphology, and fine-spinose orals at the centre, which is dominated by a characteristic corona of fine central spines at the distal top; with a single posterior interradial plate below the subcentral anal opening; free strictly uniserial arms, two rami in each ray, zigzag (see model, Fig. 3.2.8.3); rami branching heterotomously with somewhat narrower, bilateral and unbranched ramules; two primibrachials, primibrachial 1 greatly reduced and covered by the axillary primibrachial 2, brachials wide and U-shaped, compound, possessing two pinnules each (bipinnulated) except on asymmetrical and pentagonal axillaries; other skeletal elements unknown.

Differentiation.—*Megaradialocrinus winteri* n. sp.[132] is similar to *M. brevis* n. comb.[133] and *M. lobatus* n. comb.[134] *M. brevis* developed convex tegminal plates instead of fine tuberculated plates with central spines at the top. The radials of *M. brevis* are not deeply notched as in *M. winteri*, and the insertions of the primibrachials are located closer to the tegmen, instead of central as in *M. winteri*. The horizontal outline of *M. brevis* is subcircular,

---

[132] = *Megaradialocrinus winteri* BOHATÝ, in press *sensu* ICZN

[133] = *M. brevis* (GOLDFUSS, 1839) *sensu* ICZN

[134] = *M. lobatus* (MÜLLER, 1857) *sensu* ICZN

whereas *M. winteri* is rather angular. Confusion of mistaking the new species with *M. lobatus* is only possible when the massive tegmen of the latter is not preserved. In this case, the aborally overhanging lobes constructed by the basal circlet of *M. lobatus* affords a clear differentiation.

3.2.7.4.3 Species *Megaradialocrinus piriculaformis*

Megaradialocrinus piriculaformis n. sp.[135]

Figs. 3.2.7.5-7

- *vidi* Crinoide sp. indet. D [(?)Jugendform von *Hexacrinites* sp.]. HAUSER, 1997, pl. 39, fig. 11.

Holotype.—Isolated aboral cup, no. SMF-75475, deposited in the *Forschungsinstitut und Naturmuseum Senckenberg*, Frankfurt/Main, Germany (Fig. 3.2.7.6).

Other material examined.—Aboral cups nos. GIK-1993 (field-no. CREF33a-HEIN-42) [Fig. 3.2.7.5] and GIK-1994 (field-no. CREF32-PRESCHER-24) [Fig. 3.2.7.7].

Derivatio nominis.—After the shape of the small, pear-shaped aboral cup (lat. = *piricula*).

Locus typicus.—Northeastern slope of the railway cut near the station of Gerolstein, Gerolstein Syncline, Eifel, (Rhenish Massif, northwestern Rhineland-Palatinate, westernmost Germany); topographic map (1:25.000) of the Landesvermessungsamt Rheinland-Pfalz: MTB 5706 Hillesheim r(25)477500/h(55)656375.

Stratum typicum.—Hustley Member [equivalent to the Rech Member (HOTZ, KRÄUSEL & STRUVE 1955, p. 117) within Gerolstein Syncline (*sensu* WINTER 1965, p. 290)] of upper Loogh Formation, Lower Givetian (Middle Devonian; *hemiansatus* Conodont Biozone).

Distribution.—So far restricted to the stratum typicum of the type locality.

---

[135] = *Megaradialocrinus piriculaformis* BOHATÝ, in press *sensu* ICZN

Diagnosis.—A very small *Megaradialocrinus* with long, “pear-” to “mushroom-shaped” aboral cup (Figs. 3.2.7.5-7), composed of a slender, cylindrical basal circlet with three wider than long basals and an extended radial circlet, with five as long as wide radials, which are somewhat wider than the primanal; plates smooth; impression of stem moderately concave; stem circular in cross section, perforated by a small, single axial canal with pentalobate cross section.

Measurements of the holotype (max. length/width in mm).—Aboral cup (without tegmen): 7.5/7.0 (incomplete); basals: 3.5/5.0; radials: 5.0/5.0; primanal: not preserved; diameter of stem impression: 3.5; diameter of stem facet: 2.5.

Description.—The very small aboral cup is long and “pear-” to “mushroom-shaped” (Figs. 3.2.7.5-7); juvenile cups are twice as long as wide and slender conical, adult cups without preserved tegmen are nearly as long as wide, with a slightly lower and widened basal circlet, composed of three wider than long basals; smooth basals either with (Figs. 3.2.7.5, 3.2.7.7) or without (Fig. 3.2.7.6) smooth flange surrounding the slender stem impression, which is moderately impressed; the suture of basals and radials is positioned at the midlength of the cup; five radials, typically as long as wide, smooth with small brachial facets; the stem is circular in cross section and perforated by a small, single axial canal with pentalobate cross section; other skeletal elements unknown.

Differentiation.—*Megaradialocrinus piriculaformis* n. sp.[136] is similar to *M. brevis* n. comb.[137] The knob-shaped radial circlet, the narrow stem impression and the length of the aboral cup clearly separate both hexacrinitids. Furthermore, the primanal of the new species does not extend above the radial circlet, as in *M. brevis*, and the brachial facets of *M. piriculaformis* are narrower than in *M. brevis*. Furthermore, the general morphology of the adult *piriculaformis* aboral cup bears resemblance with *Mycocrinus boletus* SCHULTZE, 1866.

3.2.7.4.4 Species *Megaradialocrinus theissi*

Megaradialocrinus theissi n. sp.[138]

Figs. 3.2.7.13-17

- *vidi Hexacrinites exsculptus* (GOLDF., 1838). HAUSER, 1997, pl. 52, fig. 7.

---

[136] = *Megaradialocrinus piriculaformis* BOHATÝ, in press *sensu* ICZN

[137] = *M. brevis* (GOLDFUSS, 1839) *sensu* ICZN

[138] = *Megaradialocrinus theissi* BOHATÝ, in press *sensu* ICZN

Holotype.—Isolated aboral cup, no. SMF-75476, deposited in the *Forschungsinstitut und Naturmuseum Senckenberg*, Frankfurt/Main, Germany (Figs. 3.2.7.13-16).

Other material examined.—Aboral cup no. GIK-1999 (field-no. CREF33a-PRESCHER-124) [Fig. 3.2.7.17].

Derivatio nominis.—In honour of DR. ANDREAS THEISS (Nackenheim), the discoverer and donator of the new species.

Locus typicus.—Northeastern slope of the railway cut near the station of Gerolstein, Gerolstein Syncline, Eifel, (Rhenish Massif, northwestern Rhineland-Palatinate, westernmost Germany); topographic map (1:25.000) of the Landesvermessungsamt Rheinland-Pfalz: MTB 5706 Hillesheim r(25)477500/h(55)656375.

Stratum typicum.—Hustley Member [equivalent to the Rech Member (HOTZ, KRÄUSEL & STRUVE 1955, p. 117) within Gerolstein Syncline (*sensu* WINTER 1965, p. 290)] of upper Loogh Formation, Lower Givetian (Middle Devonian; *hemiansatus* Conodont Biozone).

Distribution.—So far restricted to the stratum typicum of the type locality.

Diagnosis.—A *Megaradialocrinus* with nearly flat base, composed of three wider than long basals and five nearly as long as wide radial plates, which are somewhat wider than the primanal; all plates distinguished by irregular anastoming ridges and central depressions on radials; tegmen moderately inflated; single posterior interradial plate with a blunt spine at the surface below the subcentral anal opening; impression of stem moderately impressed; stem circular in cross section, perforated by a small, single axial canal with pentalobate cross section.

Measurements of the holotype (max. length/width in mm).—Aboral cup (with preserved tegmen): 13.0/13.0; basals: 2.5/7.0; radials: 7.0/7.0; primanal: 8.0/4.5; diameter of stem impression: 9.0; diameter of stem facet: 3.5.

Description.—Aboral cup with preserved tegminal plates slightly longer than wide; the thick plates caused a “chunky” and “robust” shape; cup (Figs. 3.2.7.13-17) constructed by three thick basal plates, widely flanging laterally, forming flat basal circlet; five thick radial plates, nearly as long as wide, with wide deep notches in the central part of plates (Figs. 3.2.7.15-17); one primanal, slightly narrower than the radials; all plates sculpturing composed of low, irregularly arranged and narrow ridges; sculpturing of primanal somewhat radiating; the sutures are deeply impressed; stem impression circular in cross section, even and penetrated by a small axial canal with a subcircular to very small pentagonal lumen; free arms (not preserved), two in each ray, two primibrachials, primibrachial 1 wider than long, greatly reduced and covered by the axillary primibrachial 2 (Fig. 3.2.7.16) which is nearly as long as wide; tegmen (Fig. 3.2.7.13) moderately inflated, with four large and two small orals, flat and smooth; all orals with large surfaces and separated by modified ambulacral plates at the centre of the tegmen and a characteristic posterior interradial plate (Fig. 3.2.7.15) below the subcentral anal opening, with a blunt spine at the surface (most likely a defence against platyceratid gastropods); marginal positioned anal opening surrounded by a rosette of small plates; the stem is circular in cross section and perforated by a small, single axial canal with pentalobate cross section; unweathered plates brownish; further skeletal elements unknown.

Differentiation.—Because of the depressions at the central part of the radials, the new *M. theissi* n. sp.[139] is similar to *M. marginatus* n. comb.[140], which developed longer basals and lacks plate ornamentation. The proportions of the aboral cup resemble *M. prokopi* (BOHATÝ, 2006c) n. comb.[141], *M. confragosus* n. comb.[142] and *M. invitabilis* n. comb.[143] [both (DUBATOLOVA, 1964), described from the Early Devonian of the Kuznetsk Basin (Russia)] as well as to (?)*M. macrotatus* (AUSTIN & AUSTIN, 1845) n. comb.[144] from the Middle Devonian of Wolborough (Great Britain). All species differ from *M. theissi* by the shape of the tegminal plates. Compared to the four taxa, *M. theissi* has thicker plates, more deeply impressed sutures and central depressions on the radials. Also, the basal circlet of *H. theissi* is lower and more circular.

---

[139] = *M. theissi* BOHATÝ, in press *sensu* ICZN

[140] = *M. marginatus* (SCHULTZE, 1866) *sensu* ICZN

[141] = *M. prokopi* (BOHATÝ, 2006c) *sensu* ICZN

[142] = *M. confragosus* (DUBATOLOVA, 1964) *sensu* ICZN

[143] = *M. invitabilis* (DUBATOLOVA, 1964) *sensu* ICZN

[144] = (?)*M. macrotatus* (AUSTIN & AUSTIN, 1845) *sensu* ICZN

FIGURE 3.2.7 (legend p. 105)

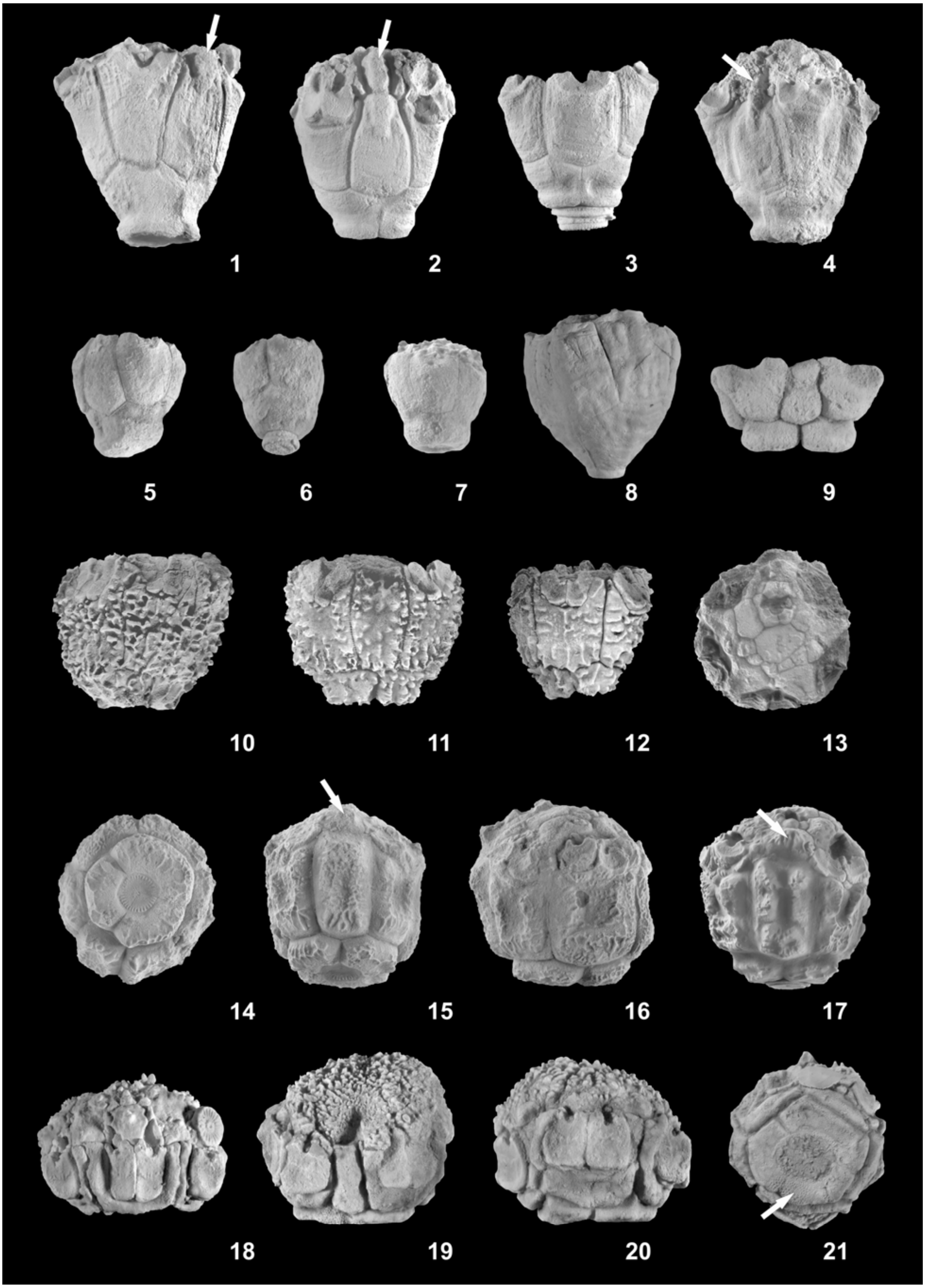


FIGURE 3.2.7 (see p. 104)—*Megaradialocrinus* aboral cups from the Hustley Member (Loogh Formation, lowermost Lower Givetian) of the northeastern slope of the railway cut near the station of Gerolstein (Gerolstein Syncline, Eifel, Rhenish Massif) [***1-3***, ***5-6***, ***8***, ***12-17***], from the Hustley Member of Berlingen [***4***] and Pelm [***7***] (Gerolstein Syncline), from the Baarley Member (Loogh Formation, lowermost Lower Givetian) of the "Mühlenwäldchen", SW-Gerolstein [***9-11***, ***19-21***] and from the lower Rech Member (upper Loogh Formation, Lower Givetian) of Berndorf (Hillesheim Syncline, Eifel) [***18***]. ***1-4***, *Megaradialocrinus limbatus* (MÜLLER, 1856) n. comb. ***1***, No. GIK-1989 (field-no. CREF33a-HEIN-39), right posterior view of D ray and primanal with "cockscomb-shaped" posterior interradial plate (arrow) of adult aboral cup, x 1.9; ***2***, No. GIK-1990 (field-no. CREF33a-HEIN-40), posterior view of primanal with "cockscomb-shaped" posterior interradial plate (arrow) of the aboral cup with preserved tegmen, x 1.8; ***3***, No. GIK-1991 (field-no. CREF33a-HEIN-41), juvenile aboral cup, right anterolateral view of E ray, x 2.9; ***4***, No. GIK-1992 (field-no. CREF38-HEIN-2), adult aboral cup with inflated tegmen and morphological affinities to *M. exsculptus* (GOLDFUSS, 1839) n. comb., lateral view of primanal with "cockscomb-shaped" posterior interradial plate (arrow) and C ray, x 1.5; ***5-7***, *Megaradialocrinus piriculaformis* n. sp. ***5***, No. GIK-1993 (field-no. CREF33a-HEIN-42), lateral view of C ray and primanal, x 3.9; ***6***, **Holotype**, no. SMF-75475, anterior view of A ray, x 2.7; ***7***, No. GIK-1994 (field-no. CREF32-PRESCHER-24), left posterior view of C ray, x 3.4; ***8***, No. SMF-75477, (?)*Megaradialocrinus bulbiformis* n. sp., **holotype**, left posterior view of primanal and C ray, x 1.6; ***9***, No. GIK-1995 (field-no. CREF41-BOHATÝ-2), *Megaradialocrinus callosus* (SCHULTZE, 1866) n. comb., posterior view of primanal, x 2.8; ***10-12***, *Megaradialocrinus crispus* (QUENSTEDT, 1861) n. comb. ***10***, No. GIK-1996 (field-no. CREF41-PRESCHER-5), showing irregularly arranged ornament, left anterolateral view of B ray, x 1.5; ***11***, No. GIK-1997 (field-no. CREF41-HEIN) with some aligned ornamentation, posterior view of primanal, x 1.6; ***12***, No. GIK-1998 (field-no. CREF33a-BOHATÝ-41), the plates are ornamented by aligned wrinkles, left anterolateral view of E ray, x 2.1; ***13-17***, *Megaradialocrinus theissi* n. sp. ***13-16***, No. SMF-75476, **holotype**, showing irregular anastoming ridges of all plates and central depressions on radials; ***13***, Oral view, x 2.3; ***14***, Aboral view, x 2.3; ***15***, Posterior view of primanal and posterior interradial plate (arrow), x 2.5; ***16***, Lateral view of CB interray, x 2.6; ***17***, No. GIK-1999 (field-no. CREF33a-PRESCHER-124), posterior view of primanal and posterior interradial plate (arrow), x 2.1; ***18-21***, *Megaradialocrinus globohirsutus* n. nov. ***18***, No. GIK-2000 (field-no. CREF37b-LEUNISSEN-0), partly preserved aboral cup with lost basal circlet, anterior view of A ray, x 2.1; ***19-21***, No. MB.E.-2362, **holotype**; **19**, Posterior view of primanal, posterior interradial plate missing; ***20***, Right anterolateral view of E ray, x 1.9; ***21***, Aboral view, the basal circlet is encrusted by a trepostome bryozoan (arrow), x 1.5.

3.2.7.4.5 Species (?)*Megaradialocrinus bulbiformis*

(?)*Megaradialocrinus bulbiformis* n. sp.[145]

Fig. 3.2.7.8

Holotype.—Isolated aboral cup, no. SMF-75477, deposited in the *Forschungsinstitut und Naturmuseum Senckenberg*, Frankfurt/Main, Germany (Fig. 3.2.7.8).

Derivatio nominis.—After the bulbous aboral cup of the new species.

Locus typicus.—Northeastern slope of the railway cut near the station of Gerolstein, Gerolstein Syncline, Eifel, (Rhenish Massif, northwestern Rhineland-Palatinate, westernmost Germany); topographic map (1:25.000) of the Landesvermessungsamt Rheinland-Pfalz: MTB 5706 Hillesheim r(25)477500/h(55)656375.

Stratum typicum.—Hustley Member [equivalent to the Rech Member (HOTZ, KRÄUSEL & STRUVE 1955, p. 117) within Gerolstein Syncline (*sensu* WINTER 1965, p. 290)] of upper part of Loogh Formation, Lower Givetian (Middle Devonian; *hemiansatus* Conodont Biozone).

Distribution.—One aboral cup from the stratum typicum of the locus typicus.

Diagnosis.—A (?)*Megaradialocrinus* with “bulbous” aboral cup, composed of three slightly wider than long basals, forming an inverted coniform basal circlet with narrow base and five longer than wide radials, which are somewhat wider than the primanal; stem impression shallow; stem circular in cross section, perforated by a small, single axial canal with pentalobate cross section.

Measurements of the holotype (max. length/width in mm).—Aboral cup (without tegmen): 19.0/19.0; basals: 10.0/13.0; radials: 10.0/8.0; primanal: 11.0/10.5; diameter of stem impression: 4.5; diameter of stem facet: 3.5.

---

[145] = (?)*Megaradialocrinus bulbiformis* BOHATÝ, in press *sensu* ICZN

Description.—The bulbous aboral cup (Fig. 3.2.7.8) without preserved tegmen is as wide as long, the basal circlet is narrow and rapidly expanding toward the radial/basal articulation as the widest diameter of the cup; the long basal circlet is inverted coniform, the three basals are wider than long and sculptured by low, irregularly arranged crinkles and short ridges; the five radials are longer than wide and also sculptured by low crinkles and short ridges; radial facets relatively small; three brachials preserved, primibrachial 1 greatly reduced and covered by the primibrachial 2 and the axillary primibrachial 3; stem impression small and shallow with a narrow stem facet, surrounded by a moderately developed basal flange; stem circular in cross section, perforated by a small, single axial canal with pentalobate cross section; other skeletal elements unknown.

Differentiation.—(?)*Megaradialocrinus bulbiformis* n. sp.[146] is similar to (?)*M. piriformis* (SCHULTZE, 1866) n. comb.[147] and *M. limbatus* (MÜLLER, 1856) n. comb.[148] but differs in having a smaller basal circlet and stem impression and different plate sculpturing: low crinkles and short ridges in (?)*M. bulbiformis vs.* smooth or microgranular, sometimes slightly faceted plates in (?)*M. piriformis* and smooth or slightly faceted plates in *M. limbatus*. Furthermore, the new species is similar to *M. conicus* CHEN & YAO, 1993, but the coarser sculpturing (?)*M. bulbiformis* and the characteristic, uneven plate boundaries of *M. conicus*, which are intermeshed with each other, separate both crinoids.

3.2.7.5 Renaming of the homonym “*Hexacrinites magnificus* HAUSER, 2007a”

3.2.7.5.1 Species *Megaradialocrinus globohirsutus*

Megaradialocrinus globohirsutus n. nov.[149]

Figs. 3.2.7.18-21

- *vidi Hexacrinites* sp. HAUSER, 1997, pl. 44, figs. 4-6.
- *vidi Hexacrinites magnificus* n. sp. HAUSER, 2006c, published on private web-page, (does

---

[146] = (?)*Megaradialocrinus bulbiformis* BOHATÝ, in press *sensu* ICZN

[147] = (?)*M. piriformis* (SCHULTZE, 1866) *sensu* ICZN

[148] = *M. limbatus* (MÜLLER, 1856) *sensu* ICZN

[149] = *Megaradialocrinus globohirsutus* BOHATÝ, in press *sensu* ICZN

not meet ICZN regulations for acceptable taxonomic names. Therefore, new name considered *nomen nudum* (pers. information, G. D. WEBSTER).

- *vidi Hexacrinites magnificus* n. sp. HAUSER, 2007a, pl. 13, figs. 4a-c = invalid homonym of *Hexacrinus magnificus* QUENSTEDT, 1866, p. 740; fig. 153; 1876, p. 565; pl. 109, figs. 67, 67D-U (ICZN article 10.6.).

Holotype.—Isolated aboral cup, no. MB.E.-2362, deposited in the *Museum für Naturkunde der Humboldt-Universität zu Berlin*, Germany (Figs. 3.2.7.19-21).

Other material examined.—Aboral cup no. GIK-2000 (field-no. CREF37-LEUNISSEN-0) with lost basalia (Fig. 3.2.7.18) and one unfigured aboral cup (col. S. BIALAS); both from the lower Rech Member (upper Loogh Formation, Lower Givetian) of Berndorf (Hillesheim Syncline, Eifel, Germany).

Derivatio nominis.—Combined, after the shape of the spheroidal aboral cup (lat. = *globosus*) and the fine acanthaceous tegmen (lat. = *hirsutus*).

Locus typicus.—“Mühlenwäldchen”, SW-Gerolstein, Gerolstein Syncline, Eifel (Rhenish Massif, northwestern Rhineland-Palatinate, Germany); topographic map (1:25.000) of the Landesvermessungsamt Rheinland-Pfalz: MTB 5705 Gerolstein r(25)464000/h(55)651000.

Stratum typicum.—Lower Baarley Member [equivalent to the uppermost Wotan Member (HOTZ, KRÄUSEL & STRUVE 1955) within Gerolstein Syncline (*sensu* WINTER 1965)] of middle Loogh Formation, Lower Givetian (Middle Devonian; *hemiansatus* Conodont Biozone).

Distribution.—So far restricted to the stratum typicum of the type locality.

Diagnosis.—A low and spherical *Megaradialocrinus* with an extremely flat and wide base, composed of three more than five times wider than long basals and five slightly wider than long radials, which are three times wider than the narrow primanal; arm facets wide, occupying the majority of the radials (Figs. 3.2.7.18-20); tegmen inflated, sculptured by numerous fine spines; single posterior interradial plate below the subcentral anal opening; stem impression wide and shallow; stem circular in cross section, perforated by a small, single axial canal with pentalobate cross section.

Measurements of the holotype (max. length/width in mm).—Aboral cup (with preserved tegmen): 16.5/21.0; basals: 2.0/11.0; radials: 7.0/9.0; primanal: 7.0/3.0; diameter of stem impression: 14.0; diameter of stem facet: 4.0.

Description.—Aboral cup with preserved tegminal plates wider than long, spherical; the thick plates caused a chunky and robust shape; cup (Figs. 3.2.7.19-21) constructed by three very flat basals, more than five times wider than long, form an extremely flat basal circlet (Fig. 3.2.7.21), plates sculpturing with irregularly arranged, low crinkles; five thick radial plates, slightly wider than long, with wide deep notches in the central part of plates, also sculptured by irregularly arranged, low crinkles; one primanal (Fig. 3.2.7.19), slender and three times narrower than the radials; stem impression (Fig. 3.2.7.21) circular in cross section, even and penetrated by a small axial canal with a very small pentagonal lumen; large arm facets (Figs. 3.2.7.18-20) protruding toward the lateral exterior, and positioned at the equatorial layer of the spheroidal aboral cup with preserved tegmen, taking two thirds of the radial area, "horseshoe-shaped"; tegmen (Figs. 3.2.7.18-20) inflated with fine spined orals and modified ambulacral plates, marginal positioned anal opening surrounded by the finest spines of the tegmen; single posterior interradial plate below the subcentral anal opening; further skeletal elements unknown.

Differentiation.—*M. globohirsutus* n. nov.[150] is similar to *M. callosus* n. comb.[151] but distinguishable by the shape of the basal circlet and by the thickness of the radials and basals (extremely flat basal circlet and thinner plates in *M. globohirsutus vs.* a "tyre-shaped" basal circlet with massive plates in *M. callosus*).

Remark.—Two basals and one brachial of the holotype are encrusted by a trepostome bryozoan. This postmortem encrustation was recently observed in cupressocrinitid skeletons (BOHATÝ 2009).

---

[150] = *M. globohirsutus* BOHATÝ, in press *sensu* ICZN

[151] = *M. callosus* (SCHULTZE, 1866) *sensu* ICZN

3.2.8 DISCUSSION

Statigraphically and geographically, hexacrinitids, in particular *Megaradialocrinus* and *Hexacrinites*, have to be designated as cosmopolitan camerate crinoids. Several species occur as rare components of the echinoderm association within some fossil localities; on the other hand, there are several localities that were dominated by either *Megaradialocrinus* or *Hexacrinites*. Especially the studied locality of the NESG, yields a very diverse *Megaradialocrinus* fauna. Therefore, the outcrop has to be classified as one of the world's most famous *Megaradialocrinus* localities. In contrast, members of *Hexacrinites* are rare. This observation corresponds with other localities within the Eifel synclines and applies to the stratigraphic range from the lowermost Eifelian up to the lowermost Lower Givetian, with a maximum distribution from the upper Middle Eifelian to the Eifelian/Givetian threshold. A further *Megaradialocrinus* maximum is established within the Frasnian of the Belgian/French Ardennes (compare to WEBSTER et al. 2007). In contrast, the Givetian *Hexacrinites* type locality of Wolborough (Great Britain), as well as the Givetian outcrops of the Lahn-Dill area (south-eastern Rhenish Massif, Germany), are distinguished by both genera.

M. adaensis n. comb.[152] is herein assigned to genus *Megaradialocrinus*; it is the oldest known species and, therefore, could possibly be the progenitor of the Devonian hexacrinitids.

The intergeneric differentiation recognised here is mainly based on the morphologies of the hexacrinitid aboral cups and arms. Studies of preserved arms clearly support differentiation with uniserial (*Megaradialocrinus*) and primary or secondary biserial arms (*Hexacrinites*). This separation is affirmed by the visible difference of constantly wide and bowl-shaped aboral cups with flat, mostly pentagonal or hexagonal tegminal plates (*Hexacrinites*) and conical to elongate cups with few moderately to very convex tegminal plates (*Megaradialocrinus*). Furthermore, the separation is affirmed by the presence of a single (*Megaradialocrinus*) or of two posterior interradial plates below the subcentral anal opening (see models, Figs. 3.2.9.1-4).

---

[152] = *M. adaensis* (STRIMPLE, 1952) *sensu* ICZN

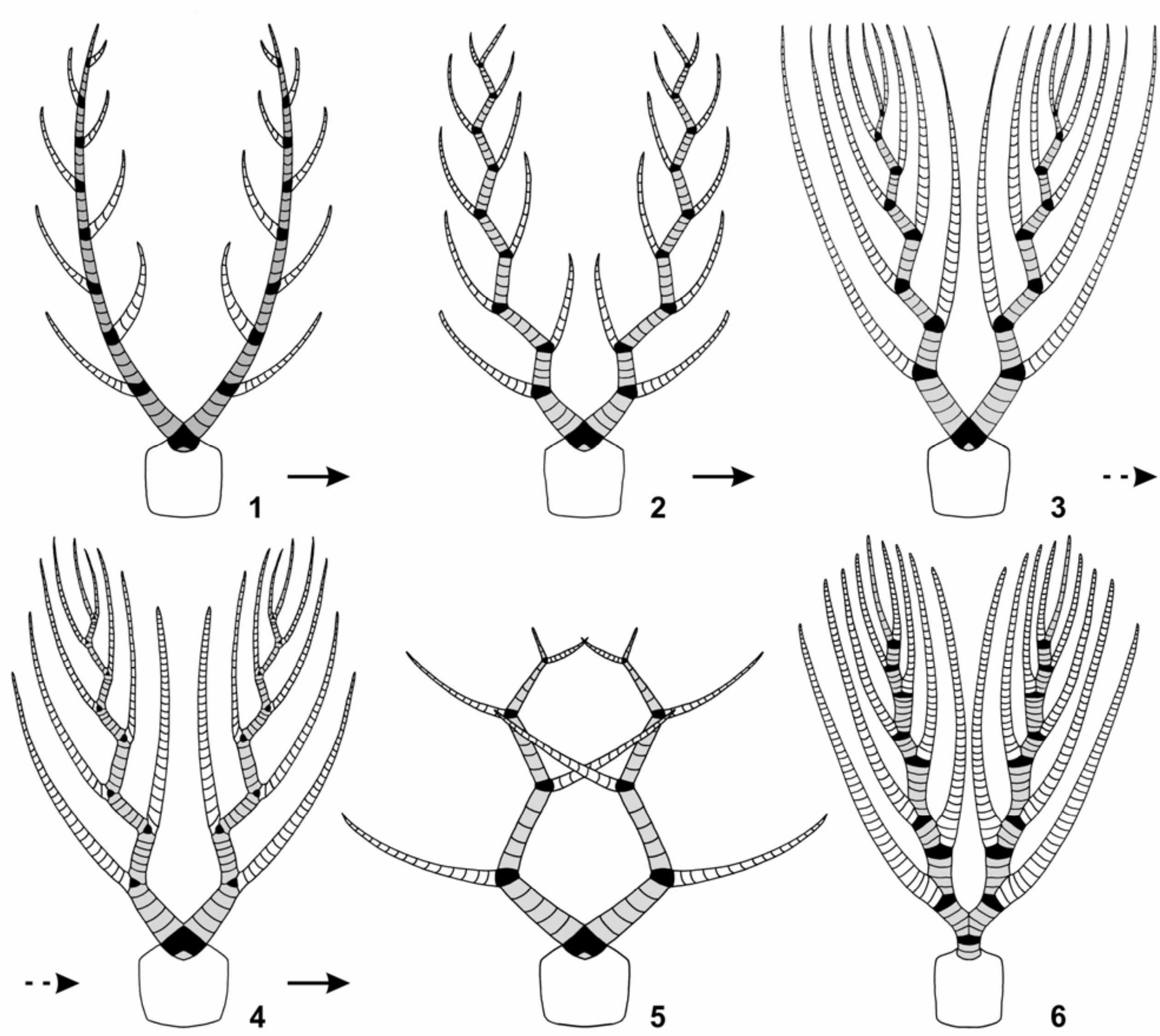


FIGURE 3.2.8—The five “morphological arm groups” of the bipinnulated *Megaradialocrinus* arms (pinnules not illustrated). ***1***, Straight-lined rami in each ray, the rami branch heterotomously with bilateral and unbranched, numerous and relatively short ramules (e.g. in *M. elongatus*); ***2***, The two straight rami are modified into slightly zigzagged rami (e.g. in *M. limbatus*); ***3***, Rami with a reduced number of longer ramules, the proximal ramules are nearly as long as the strongly zigzagged rami (e.g. in *M. brevis*); ***4***, A form with modified, triangular axillaries, which are surrounded by three hexagonal brachials (e.g. in *M. marginatus*); ***5***, Nearly orthogonal branching ramules (e.g. in *M. gibbosus*). Except of the number of primibrachials and the lateral partitions of several brachials, which are in contact with each other, this model shows similarity to the arm branching pattern of the Silurian-Eifelian monobathrid camerate genus *Bogotacrinus* SCHMIDT, 1937 (***6***) [modified from MCINTOSH 1987; Fig. 8e).

According to numerous observed transitional forms of the various aboral cup morphologies and the general variability of both genera, it is possible to differentiate certain “morphological aboral cup groups” that may belong to other genera outside of *Megaradialocrinus* and *Hexacrinites* (study in progress). For *Megaradialocrinus* these are (1.) an *aliculatus*-*marginatus* group with black coloured plates, massive and strongly sculptured plates and an inflated tegmen with very convex plates; (2.) a *ventricosus*-*nodifer* group with modified base (compare to SCHULTZE 1866, pl. 10, figs. 2, 3c-d); (3.) a *brevis*-*minor*-*unterthalensis*-*ornatus* group with low aboral cups, wide base and wide stem impression; (4.) a *conicus*-*piriformis*-*infundibulum*-*bulbiformis* group with an inverted coniform basal circlet with a narrow base and a long, wide radial circlet; (5.) a *macrotatus*-*confragosus*-*prokopi*-*invitabilis* group with moderately long aboral cups, wide base and massive, sculptured plates; (6.) a *turritus*-*rigel* group with “tower-shaped” aboral cups and granular sculpturing; and (7.) a *gibbosus*-*nitidus*-*persiaensis* group with ovoid and medium bowl-shaped aboral cups, with or without ornament. But the very gradual transitions between all these morphologies and, predominantly, the similar arms disallow a further differentiation at this time. Still unknown elements, like the arms and the tegmen of several rare species, which are so far only known from isolated aboral cups (even of the type species **M. conicus*), could possibly result in alternative taxonomic assignments. Therefore, the generic names of several species are currently combined with a question mark.

The few known Hexacrinitidae with preserved arms, herein assigned to genus *Megaradialocrinus*, allow the recognition of five “morphological arm groups”, i.e. of five branching modifications of the mostly bipinnulated arms (see models, Figs. 3.2.8.1-5). They indicate a phylogenetic lineage: (1.) the oldest form developed two straight-lined rami in each ray (Fig. 3.2.8.1); the rami branch heterotomously with bilateral and unbranched, numerous and relatively short ramules; (2.) in the second form, the two straight rami are modified into slightly zigzagged rami (Fig. 3.2.8.2); (3.) in a third step, the rami show a reduced number of longer ramules, the proximal ramules are nearly as long as the strongly zigzagged rami (Fig. 3.2.8.3); (4.) the fourth form modified the typically asymmetrical and pentagonal axillaries to symmetrical and triangular ones, which are surrounded by three hexagonal brachials (Fig. 3.2.8.4); (5.) the youngest form developed few nearly orthogonal branching ramules (Fig. 3.2.8.5).

It has to be noted that except for the number of primibrachials and the lateral partitions of several brachials, which are in contact with each other, this model has similarity with the arm branching pattern of the dicyclic, monobathrid camerate crinoid genus *Bogotacrinus* SCHMIDT, 1937 (Silurian-Eifelian) [see MCINTOSH 1987; Fig. 3.2.8.6], which is the only genera known to the author which shows such a comparable type of branching.

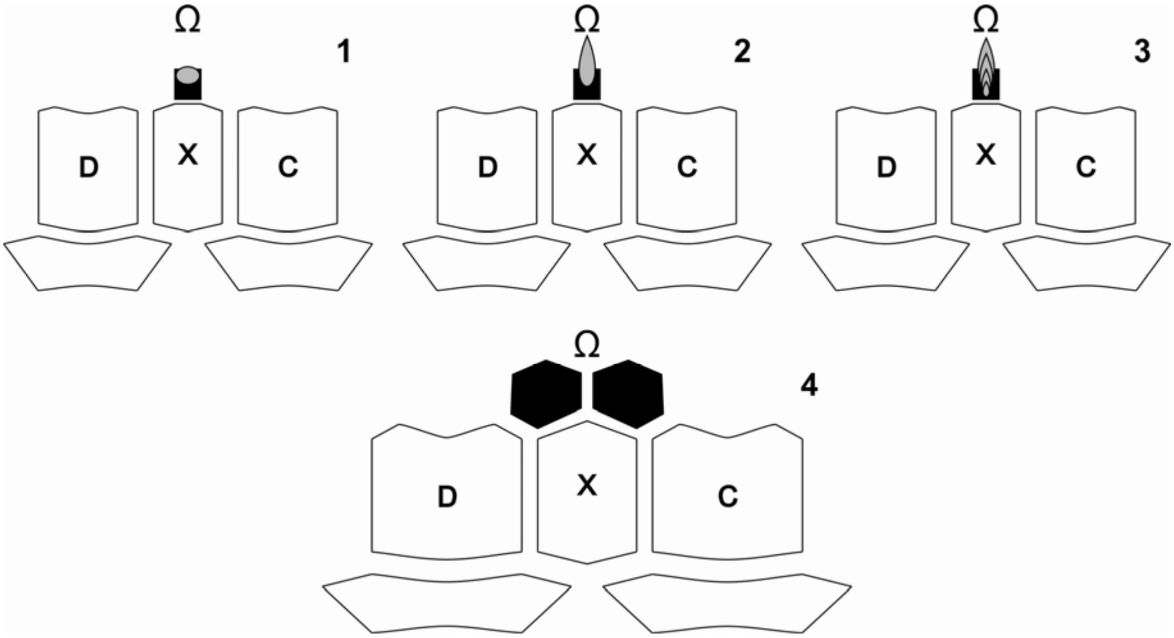


FIGURE 3.2.9—Sketches of the single posterior interradial plate modifications of genus *Megaradialocrinus* (***1-3***) and model of the two variously pentamerous to hexagonal shaped posterior interradial plates of genus *Hexacrinites* (***4***). ***1***, Posterior interradial plate with smooth and convex surface; ***2***, Posterior interradial plate with single spine (**grey**) [e.g. in *M. crispus*]; ***3***, Posterior interradial with a spate of “cockscomb-shaped” spines (**grey**) [e.g. in *M. limbatus*]. Figs. ***2-3*** possibly show a morphological defensive reaction in the form of developed endoskeletal-spines beyond the anal opening (**Ω**) that is most probably linked with the occurrence of platyceratid gastropods in the Eifelian/Givetian threshold of the Rhenish Massif.

Megaradialocrinids from the Upper Eifelian up to the Frasnian show variously developed spines on the posterior interradial plate and on the tegminal plates. These developments are rare in younger megaradialocrinids. Most probably, these elements were developed as defence against platyceratid gastropods, which settled either lateral near the anal opening or on top of the tegmen. Within the Eifel, the diversity and frequency of vagile benthic predators like platyceratid gastropods increases during Middle and Upper Eifelian (own, unpublished data). The necessity to advance the crown protection could possibly be linked to this ecological circumstance, indicating a predator driven endoskeletal evolution.

3.3 CHAPTER III. CRINOIDEA, DISPARIDA

REVISION OF THE DISPARID *STYLOCRINUS* FROM THE DEVONIAN OF EUROPE, ASIA AND AUSTRALIA

ABSTRACT—The discovery of new specimens and restudy of known collections result in revision of the diagnosis and the stratigraphic distribution of the disparid crinoid genus *Stylocrinus,* known from the Middle and Upper Devonian of Europe, Asia and Australia. The consistent development of three basal plates, the atomous arms with internally inclined edges adjoining laterally with adjacent brachials in an interlocking network, and an apparently rudimentary pinnulation is recognised. The high ecophenotypic plasticity of the common *S. tabulatus* negates the validity of several former subspecies and demonstrates the general morphologic variability of the aboral cup proportions. This contrasts with the low morphological spectrum of rarer stylocrinid species. With exclusion of "*S. elimatus*" (Silurian) from *Stylocrinus*, the genus is limited to the Devonian. A neotype is proposed for the lost holotype of *S. tabulatus*. *Stylocrinus prescheri* n. sp.[1] is described from the Eifelian to Givetian of Europe and Asia. The first evidence of the gastropod grazing trace fossil *Radulichnus* on a crinoid aboral cup (*S. tabulatus*), the postmortem incurred ossicular-boring of radial and basal plates, as well as the postmortem encrusting by a rugose coral are further observations on *Stylocrinus* aboral cups.

3.3.1 INTRODUCTION

The Devonian crinoid genus *Stylocrinus* SANDBERGER & SANDBERGER, 1856 is characterised by relatively simple crown construction with eight plates within the monocyclic aboral cup (three basals and five radials) followed by five atomous arms. Isolated aboral cups have been reported from Europe (e.g. GOLDFUSS 1839; MÜLLER in ZEILER & WIRTGEN 1855; SANDBERGER & SANDBERGER 1849-1856 and SCHULTZE 1866), Asia (REED 1908; DUBATOLOVA 1971), and Australia (JELL & JELL 1999). SCHULTZE (1866) and SANDBERGER

---

[1] = *Stylocrinus prescheri* BOHATÝ, in review *sensu* ICZN

& SANDBERGER (1849-1856) also described partly preserved crowns from Germany, where the genus is most abundant within the Eifelian and Givetian deposits of the Rhenish Massif (Eifel and Lahn-Dill vicinity). The Eifel Synclines contain the most famous localities of this low diverse but highly variable crinoid genus.

Since the nineteenth century, stylocrinids have been assigned to several genera, including "*Platycrinites*" (GOLDFUSS 1839), "*Hexacrinus*" (REED 1908), "*Symbathocrinus*" (MÜLLER in ZEILER & WIRTGEN 1855), or "*Scytalocrinus*" (WACHSMUTH & SPRINGER 1886). But the simple construction of the aboral cup allows an unquestioned identification defined by GOLDFUSS (1839, p. 345) and SANDBERGER & SANDBERGER (1856, pp. 399-400), with the exception of the arms, which were incorrectly described as "additional, elongated radials" by SANDBERGER & SANDBERGER. Following the revised diagnosis given herein, three species are recognised, *S. tabulatus* (GOLDFUSS, 1839), *S. granulatus* HAUSER, 1997 and *S. prescheri* n. sp.[2], based on differences in the skeletal features and plate sculpturing.

S. tabulatus has high ecophenotypic plasticity expressed as morphological variability of the aboral cup. The length and width proportions of ca. 1500 aboral cups have been analysed and interpreted. As a result, "*S. tabulatus altus*" and "*S. t. depressus*", both (MÜLLER in ZEILER & WIRTGEN, 1855), are rejected; therefore, the nominotypic subspecies "*S. tabulatus tabulatus*" is dissolved.

Rare crows (Figs. 3.3.1.1, 3.3.1.2-3, 3.3.1.5-6) and several isolated brachials (Figs. 3.3.4.1-14) represent an extraordinary construction of the atomous stylocrinid arms. They show internally inclined edges adjoining laterally with adjacent brachials in an interlocking network (Figs. 3.3.1.5-6), and an apparently rudimentary pinnulation (Figs. 3.3.4.3, 3.3.4.5), arising from inordinately distributed lateral notches, which are diagonally positioned to each other. This construction possibly affords feeding without totally opening the arms in an unprotected position.

Morphologic observations of stylocrinids require further research. One fossil aboral cup of *S. tabulatus* represents the first crinoid evidence of the radular grazing ichnogenus *Radulichnus* VOIGT, 1977 (Fig. 3.3.9). Isolated radial and basal plates have postmortem borings of unknown organisms (Figs. 3.3.8.1-9). Furthermore, other skeletal modifications, like an aboral cup with an additional fourth basal plate (Figs. 3.3.7.1-2) and the postmortem skeletal encrusting by a rugose coral (Fig. 3.3.10), are discussed.

---

[2] = *S. prescheri* BOHATÝ, in review *sensu* ICZN

3.3.2 MATERIAL AND METHODS

Type specimens are deposited in the *Forschungsinstitut und Naturmuseum Senckenberg*, Frankfurt am Main, Germany (SMF), the *Steinmann-Institut für Geologie, Mineralogie und Paläontologie der Rheinischen Friedrich-Wilhelms-Universität Bonn*, Germany (IPB) and the *Naturhistorische Landessammlung, Museum Wiesbaden*, Germany (MWNH). Additional specimens are stored in the collections of the *Institut für Geologie und Mineralogie der Universität zu Köln*, Germany (GIK) and the *Queensland Museum*, Queensland (QMF).

In addition to a detailed analysis of previously published data and original material, this study focuses on the endoskeletal morphology of the aboral cup and brachials, mainly observed in newly discovered crinoids from the Rhenish Massif. They were prepared using micro sand-streaming methods, as well as fine pneumatic probes, and studied *via* binocular and scanning electron microscope analyses (SEM). Photographs of NH_4Cl-whitened crinoids were arranged using digital image editing software.

Approximately 1500 aboral cups, one completely preserved and three partly preserved crowns, as well as one abnormal individual of *S. tabulatus* were analysed. Additionally, 35 aboral cups of *S. granulatus* and 25 aboral cups of *S. prescheri* n. sp.[3] were studied.

Higher classification of stylocrinids followed SIMMS & SEVASTOPULO (1993). Morphologic dimensions are given in length and width as defined by WEBSTER & JELL (1999).

The capitalisation of the Givetian subdivisions follows BECKER (2005; 2007).

3.3.3 GEOGRAPHICAL AND STRATIGRAPHICAL OCCURRENCES OF THE GENUS AND ASSIGNED SPECIES

3.3.3.1 Europe

Europe.—European *Stylocrinus* occurrences are mainly located within the Eifelian to Givetian deposits of the Rhenish Massif (Germany). The most prolific localities are in the Eifel Synclines and in the vicinity of Lahn-Dill.

---

[3] = *S. prescheri* BOHATÝ, in review *sensu* ICZN

Localities within the Eifel (Rhineland-Palatinate, Germany), especially the Middle Eifelian to lowermost Lower Givetian of the Hillesheim, Gerolstein and Prüm synclines yielded the highest recorded species diversity. While the generally common species *S. tabulatus* is geographically and stratigraphically widespread, the rarer species occurred locally within shorter time slices. *S. tabulatus* was recovered from the Nohn Formation (Lower Eifelian) to the Cürten Formation (Lower Givetian), whereas *S. granulatus* is limited to the Freilingen Formation (Eifelian) and *S. prescheri* n. sp.[4] occurred at the Eifelian/Givetian boundary.

Within the vicinity of Lahn-Dill, stylocrinids occur in deposits younger than the Eifel. *S. tabulatus* and, rarer, *S. prescheri* n. sp.[5] were found within the lowermost Middle Givetian "Roteisenstein" near Weilburg-Odersbach, NE of Limburg an der Lahn (Hesse, Germany).

3.3.3.2 Asia

Asia.—REED (1908) reported an aboral cup of "*Hexacrinus* aff. *pyriformis*" from the Devonian of the Northern Shan States (Burma). The figured aboral cup (1908, p. 40; pl. 5, fig. 13) can clearly be assigned to *S. tabulatus* and is recognised as the first report of the genus from Asia.

Stylocrinids are also known from the Asian part of Russia. As documented by DUBATOLOVA (1971), the genus occurs within the Eifelian deposits of NE Salair, near Gur'evsk (Kemerowo, Siberia, Russia; western part of the central Kusbass). The figured aboral cups can be assigned to *S. prescheri* (1971, pl. 1, figs. 5a-b) and *S. tabulatus* (1971, pls. 1, figs. 6a-b, 7a-b; 2, figs. 1a-c, 2a-b).

3.3.3.3 Australia

Australia.—JELL & JELL (1999) reported *S. tabulatus* aboral cups from the Frasnian part of the Sadler Limestone (lower Upper Devonian); this is the youngest report of the genus. The silicified aboral cup (1999, pp. 229-230; figs. 26A-D) was found SW of "Wade Knolls" in "Paddy's Valley" of Western Australia.

---

[4] = *S. prescheri* BOHATÝ, in review *sensu* ICZN

[5] = *S. prescheri* BOHATÝ, in review *sensu* ICZN

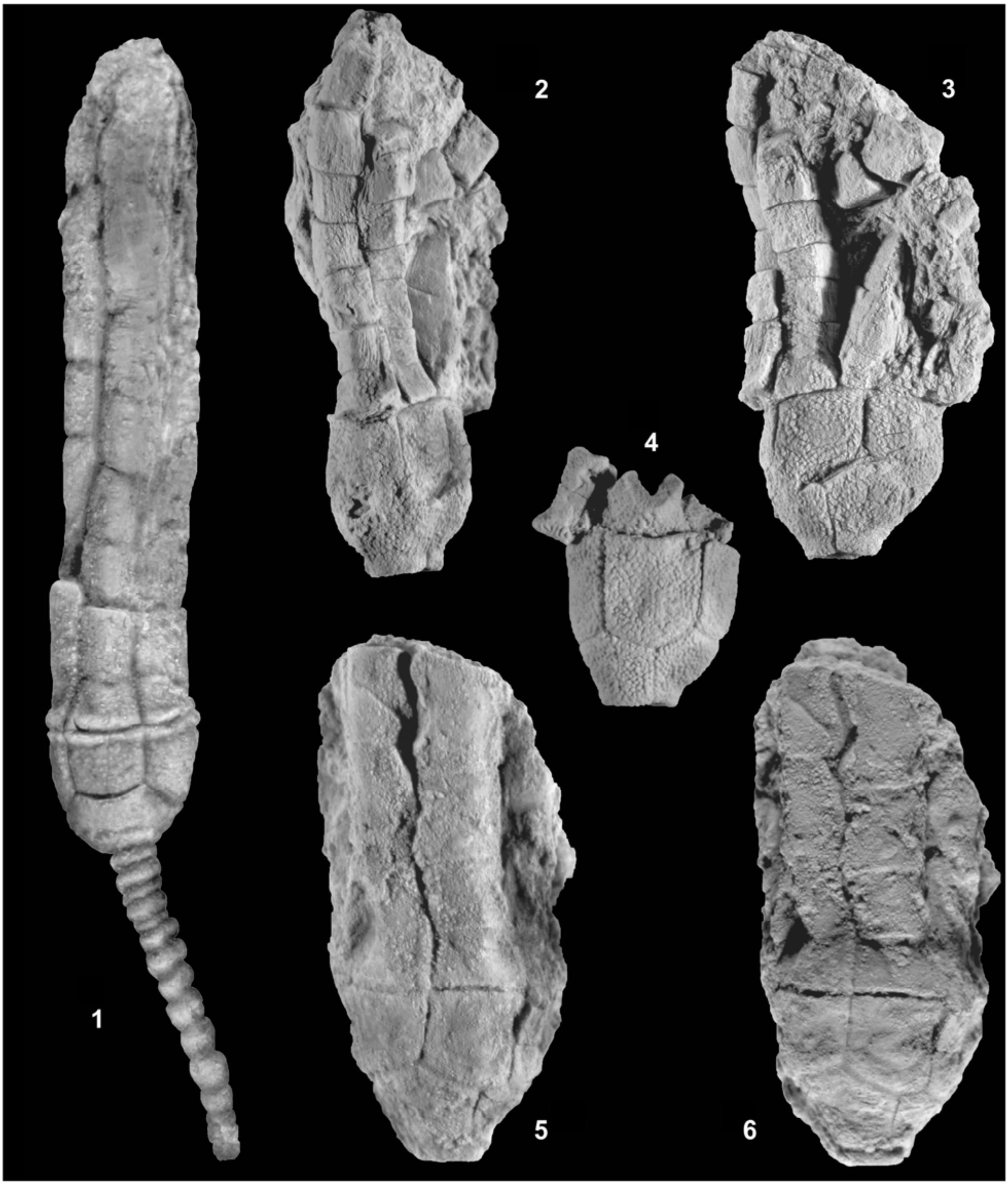


FIGURE 3.3.1.1-6—*Stylocrinus tabulatus* (GOLDFUSS, 1839), lateral views. ***1***, GIK-2001 (leg. LEUNISSEN), juvenile crown, part of stem preserved, x 6.2; ***2-3***, GIK-2003 (leg. PRESCHER), partly preserved crown, atomous arms showing internally inclined edges meeting laterally with adjacent brachials, x 4.3; ***4***, GIK-2004 (leg. SCHREUER), aboral cup with preserved proximal arms, x 4.5; ***5-6***, MWNH-306a, original of SANDBERGER & SANDBERGER (1856, pl. 35, fig. 12a), figured as "*Stylocrinus scaber*, GOLDF. sp.", partly preserved, juvenile crown, atomous arms showing internally inclined edges meeting laterally with adjacent brachials in an interlocking network, x 6.8.

3.3.4 SYSTEMATIC PALAEONTOLOGY

3.3.4.1 Crinoid systematic

3.3.4.1.1 Family Synbathocrinidae

Subclass Disparida MOORE & LAUDON, 1943
Superfamily Belemnocrinoidea MILLER, 1883
Family Synbathocrinidae MILLER, 1889

3.3.4.1.2 Genus *Stylocrinus*

Genus *Stylocrinus* SANDBERGER & SANDBERGER, 1856

Type species.—**Platycrinites tabulatus* GOLDFUSS, 1839.

Diagnosis.—Crown slender, long, and lanceolated (Fig. 3.3.1.1), with an unsculptured or typically pustulated surface (*S. tabulatus*, *S. prescheri* n. sp.[6]), or, rarely, sculptured by unoriented ridges, crinkles and tubercles (*S. granulatus*), sometimes moderately facetted parallel to the radial flanges (*S. tabulatus*, *S. prescheri* n. sp.[7]) [Figs. 3.3.2.6-7, 3.3.2.12, 3.3.2.20, 3.3.3.1-3, 3.3.3.17, 3.3.6.1-4]; stem narrow, circular in cross section, with one central, pentalobate axial canal (Figs. 3.3.2.7, 3.3.2.14, 3.3.5.1-2); monocyclic aboral cup with highly variable morphology (Figs. 3.3.2.1-40), typically bowl shaped, frequently transitions between cone, bowl and globe shape (*S. tabulatus*, *S. granulatus*), but inverted “pear-shaped” in *S. prescheri* n. sp.[8] (Figs. 3.3.6.1-16); aboral cup of *S. tabulatus* three times wider than long, as long as wide to three times longer than wide; aboral cup composed of three basals, forming a convex base, and five radials with plenary radial facets (Figs. 3.3.3.20-23, 3.3.6.6, 3.3.6.15-16) [see “Remarks” below] with a distinct transverse ridge; atomous arms (Fig. 3.3.1.1); the brachials are rectilinear in external view; strongly convex transversely, straight longitudinally; internally inclined edges adjoined laterally with adjacent brachials in an interlocking network (Figs. 3.3.1.5-6); inordinately distributed notches occur laterally, diagonally positioned to each other (Figs. 3.3.4.2-5, 3.3.4.8-9, 3.3.4.14), bearing obviously rudimental arm appendage (Figs. 3.3.4.3, 3.3.4.5).

---

[6] = *S. prescheri* BOHATÝ, in review *sensu* ICZN
[7] = *S. prescheri* BOHATÝ, in review *sensu* ICZN
[8] = *S. prescheri* BOHATÝ, in review *sensu* ICZN

Occurrence.—Middle to Upper Devonian. Eifelian: Asia (Salair, Kemerowo, Siberia, Russia). Eifelian-Givetian: Europe (Germany). Frasnian: Western Australia. Slightly modified from WEBSTER (2003).

The occurrence of *Stylocrinus* within the Silurian deposits of the United States (STRIMPLE 1963) is rejected based on the revised diagnosis herein (see “Remarks” below).

Remarks.—The plenary radial facets of the disparid *Stylocrinus* corresponds with the features defined for cladids by WEBSTER (2007, pp. 325-328).

The crinoid described by STRIMPLE (1963, pl. 1, figs. 6-8) as “*Stylocrinus elimatus*” (also see WEBSTER 1973, p. 247; 2003) does not belong to *Stylocrinus*. Presumably, “*S. elimatus*” belongs to the Pisocrinidae ANGELIN, 1878 (study in progress). In contrast to the *Stylocrinus* diagnosis of STRIMPLE (1963; also in MOORE et al. 1978, p. T560), the aboral cup of *Stylocrinus* possesses consistently three, not five, basal plates. This is a constant feature observed on each of the approximately 1500 aboral cups studied.

The recently published drawing of a *Stylocrinus* model (see HAUSER 2008, p. 25; fig. 48) is entirely incorrect. Wrongly, the model has (1.) a circular axial canal instead of a pentalobate one, (2.) five instead of three basals and (3.) the brachials lack the internally inclined edges adjoined laterally with adjacent brachials in an interlocking network (see “*Revised diagnosis*” below).

Because POLYARNAYA (1986) designated “*S. scaber*” as junior synonym of “*P.*” *tabulatus*, the type species of *Stylocrinus* SANDBERGER & SANDBERGER, 1856 is **Platycrinites tabulatus* GOLDFUSS, 1839 – not “**Stylocrinus scaber* SANDBERGER & SANDBERGER, 1856”, as given in MOORE et al. (1978, p. T560) and HAUSER (2008, p. 25).

3.3.4.1.3 Species *Stylocrinus tabulatus*

Stylocrinus tabulatus (GOLDFUSS, 1839)

Figs. 3.3.1.1-6, 3.3.2.1-40, 3.3.3.1-29, 3.3.4.1-14, 3.3.7.1-2, 3.3.8.1-9, 3.3.9, 3.3.10, 3.3.11(centre)

- *Platycrinites tabulatus* GOLDFUSS, 1839, p. 345. STEININGER, 1853, p. 37. QUENSTEDT, 1885, p. 952; pl. 76, fig. 17. BASSLER & MOODEY, 1943, p. 692. POLYARNAYA, 1986, p. 77. WEBSTER, 1993, p. 113. WEBSTER, 2003.

- *Platycrinus tabulatus* (GOLDFUSS, 1839). BRONN, 1848, p. 993. QUENSTEDT, 1852, p. 618; pl. 54, figs. 25a-c. QUENSTEDT, 1876, pp. 557-559. DUJARDIN & HUPÉ, 1862, p. 152. WEBSTER, 2003.
- *Platycrinus tabulatus* variatio *alta* (MÜLLER). QUENSTEDT, 1876, p. 558; pl. 109, fig. 47.
- *Platycrinus tabulatus* variatio *depressa* (MÜLLER). QUENSTEDT, 1876, p. 558; pl. 109, fig. 49.
- *Stylocrinus tabulatus* (GOLDFUSS, 1839). WACHSMUTH & SPRINGER, 1886, p. 171 (95). BASSLER & MOODEY, 1943, p. 692. MIESEN, 1971, p. 5; pl. 4, fig. 9g (undescribed), *non* fig. 9h (undescribed) [= *S. granulatus* HAUSER, 1997]. WEBSTER, 1993, p. 113. HAUSER, 1997, p. 96; pl. 70, fig. 5 (not pl. 70, figs. 1, 9 as given p. 96 *sic*!), *non* figs. 1-2 (= *Phimocrinus laevis* SCHULTZE, 1866). JELL & JELL, 1999, p. 229; fig. 26, nos. A-D. HAUSER, 2001, pp. 134-137; pl. 13, figs. 5-6. WEBSTER, 2003. *non* HAUSER, 2008, p. 26; fig. 49 (= *Stylocrinus prescheri* n. sp.[9]) [described as "*Stylocrinus tabulatus depressus* MÜLLER in ZEILER & WIRTGEN, 1855" in HAUSER, 2008, pl. 1, fig. 5 *sic*!].
- *Stylocrinus tabulatus* (MÜLLER). MIESEN, 1974, p. 77; fig. 1, *non* figs. 1a (= *S. granulatus* HAUSER, 1997), 1b [= (?)*S. prescheri* n. sp.[10]].
- *Stylocrinus tabulatus tabulatus* (GOLDFUSS, 1839). DUBATOLOVA, 1971, p. 19; pl. 1, figs. 6-8, *non* fig. 5 (= *S. prescheri* n. sp.[11]), *non* fig. 9 (= Crinoidea indet.). WEBSTER, 1977, p. 162. WEBSTER, 2003.
- *Symbathocrinus tabulatus* (GOLDFUSS, 1839). MÜLLER in ZEILER & WIRTGEN, 1855, p. 19; pl. 4, figs. 4-5. SCHULTZE, 1866, pp. 27-28; pl. 3, fig. 4h, *non* figs. 4c [= (?)*S. prescheri* n. sp.[12]], 4d, g (= Crinoidea indet.), 4e-f (= *Eohalysiocrinus* sp.), 4i (= *S. granulatus* HAUSER, 1997). HOLZAPFEL, 1895, p. 300. BASSLER & MOODEY, 1943, p. 692. WEBSTER, 2003.
- *Stylocrinus scaber* SANDBERGER & SANDBERGER, 1856, p. 400; pl. 35, fig. 12. QUENSTEDT, 1876, p. 558; pl. 109, fig. 50. BASSLER & MOODEY, 1943, p. 692 (*Platycrinites scaber* GOLDFUSS, ms). MOORE et al., 1978, p. T561; fig. 353, nos. 2a-c. POLYARNAYA, 1986, p. 77. WEBSTER, 1986, p. 293. WEBSTER, 1993, p. 113. WEBSTER, 2003. HAUSER, 2008, p. 25; fig. 46.
- *Symbathocrinus tabulatus* var. *alta* MÜLLER in ZEILER & WIRTGEN, 1855, p. 19; pl. 6, fig. 5. SCHULTZE, 1866, p. 27; pl. 3, figs. 4, 4a-b. BASSLER & MOODEY, 1943, p. 692. POLYARNAYA, 1986, p. 77. WEBSTER, 1993, p. 113. WEBSTER, 2003.
- *Stylocrinus tabulatus* var. *alta* (MÜLLER). MIESEN, 1971, pl. 3, figs. 9, 9a-b, *non* pl. 4, fig. 9c [= (?)*S. prescheri* n. sp.[13]]. MIESEN, 1974, pl. 76, figs. 4, 4a-b.

---

[9] = *S. prescheri* BOHATÝ, in review *sensu* ICZN

[10] = (?)*S. prescheri* BOHATÝ, in review *sensu* ICZN

[11] = *S. prescheri* BOHATÝ, in review *sensu* ICZN

[12] = (?)*S. prescheri* BOHATÝ, in review *sensu* ICZN

[13] = (?)*S. prescheri* BOHATÝ, in review *sensu* ICZN

- *Stylocrinus tabulatus alta* (MÜLLER, 1855). HAUSER, 1997, pp. 96, 98; pls. 70, figs. 6-7; 71, fig. 1. WEBSTER, 2003.
- *Stylocrinus tabulatus altus* (MÜLLER, 1855). BASSLER & MOODEY, 1943, p. 692. POLYARNAYA, 1986, p. 77; unnum. pl., fig. 3; fig. 1. WEBSTER, 1993, p. 113. HAUSER, 2001, p. 135. WEBSTER, 2003.
- *Scytalocrinus tabulatus* var. *alta* (MÜLLER, 1855). WACHSMUTH & SPRINGER, 1886, p. 171 (95). BASSLER & MOODEY, 1943, p. 692. WEBSTER, 2003.
- *Symbathocrinus tabulatus* var. *depressa* MÜLLER in ZEILER & WIRTGEN, 1855, p. 19; pl. 6, fig. 4. SCHULTZE, 1866, pp. 28-29; pl. 3, figs. 5, 5a-b. BASSLER & MOODEY, 1943, p. 692. POLYARNAYA, 1986, p. 78. WEBSTER, 1993, p. 113. WEBSTER, 2003.
- *Stylocrinus tabulatus* var. *depressa* (MÜLLER, 1855). WACHSMUTH & SPRINGER, 1886, p. 171 (95) [*pars*]. BASSLER & MOODEY, 1943, p. 692. MIESEN, 1974, pl. 77, figs. 2 (unnumbered), 2a-b. POLYARNAYA, 1986, p. 78. WEBSTER, 1993, p. 113. WEBSTER, 2003.
- *Stylocrinus* var. *depressa*. MIESEN, 1971, pl. 4, figs. 10, 10a-b.
- *Stylocrinus tabulatus depressa* (MÜLLER, 1855). HAUSER, 1997, p. 97; pl. 71, figs. 2, 8. HAUSER, 2001, p. 136. WEBSTER, 2003.
- *Stylocrinus tabulatus depressus* (MÜLLER, 1855). BASSLER & MOODEY, 1943, p. 692 (*pars*). DUBATOLOVA, 1971, p. 21; *non* pl. 1, figs. 10-11 (= Crinoidea indet.); pl. 2, figs. 1-2. WEBSTER, 1977, p. 162. POLYARNAYA, 1986, p. 78; fig. 2; unnum. pl., fig. 2. WEBSTER, 1993, p. 113. HAUSER, 2001, pp. 135-137; pl. 25, fig. 4. WEBSTER, 2003. *non* HAUSER, 2008, pl. 1, fig. 5 (= *S. prescheri* n. sp.[14]) [described as "*Stylocrinus tabulatus*" in HAUSER, 2008, p. 26; fig. 49 *sic*!].
- *Hexacrinus* aff. *pyriformis* (SCHULTZE). REED, 1908, p. 40; pl. 5, fig. 13.

Occurrence.—As for genus.

Proposed neotype.—Aboral cup, no IPB-BOHATÝ-10 (Fig. 3.3.2.27).

Revised diagnosis.—Crown slender, long and lanceolated, with an unsculptured or typically pustulate or fine granulate surface, sometimes moderately faceted parallel to the radial flanges; stem narrow, circular in cross section, with one central, pentalobate axial canal; aboral cup with highly variable morphology regarding length and width proportions (Figs. 3.3.2.1-40), typically bowl shaped, frequently transitions between

---

[14] = *S. prescheri* BOHATÝ, in review *sensu* ICZN

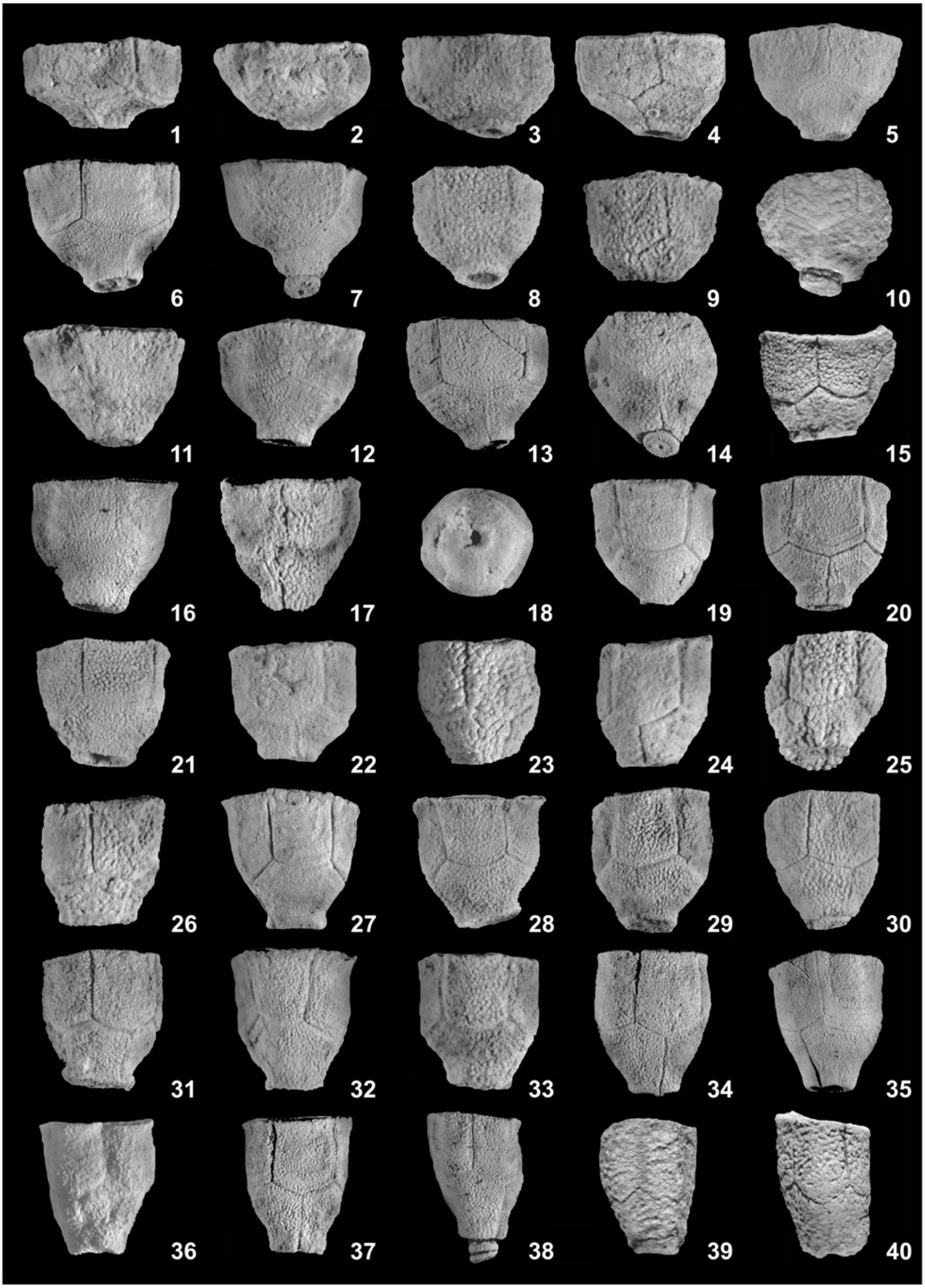
cone, bowl and globe shape; aboral cup three times wider than long, as long as wide to three times longer than wide, widest lateral radius of aboral cup at the radial facets; aboral cup composed of three basals, forming a convex base, and five radials with plenary radial facets with distinct transverse ridges; atomous arms; the brachials are rectilinear in external view; strongly convex transversely, straight longitudinally; internally inclined edges adjoin laterally with adjacent brachials in an interlocking network (Figs. 3.3.1.5-6); inordinately distributed notches occur laterally, diagonally positioned to each other (Figs. 3.3.4.2-5, 3.3.4.8-9, 3.3.4.14), bearing obvious rudimental arm appendages (Figs. 3.3.4.3, 3.3.4.5).

Type locality and stratigraphy.—Neither the type locality within the Eifel, nor the stratigraphy is given in the original description (GOLDFUSS 1939, p. 345). Therefore, data applies to the proposed neotype (Fig. 3.3.2.27):

New type locality.—Slope of the former planned roadwork extension of federal road “B51”, south of Brühlborn, northeast of Rommersheim (Prüm Syncline, Eifel, Rhenish Massif, Germany); UTM 50°12’24.88’’N/6°27’38.58’’E. Stratigraphy: Nims Member of the lower Grauberg Subformation, upper part of the Junkerberg Formation, upper Middle Eifelian (Middle Devonian); *kockelianus* Conodont Biozone.

Discussion.—The highly ecophenotypic plasticity and the resulting morphological variability of *S. tabulatus* aboral cups resulted in the subspecific differentiation by MÜLLER in ZEILER & WIRTGEN (1855). Due to the few known examples, “*Symbathocrinus tabulatus* var. *alta*” and “*S. t.* var. *depressa*” were established for short and long aboral cups. Analysis of approximately 1500 aboral cups demonstrates gradual transitions of length and width proportions. Therefore, both subspecies are combined with *S. tabulatus*, whereby the nominal subspecies “*S. tabulatus tabulatus*” is dissolved. JELL & JELL (1999, p. 229) assigned their stylocrinids [with length = width intermediate between *altus* (length > width) and *depressus* (width > length)] to the broader species concept. Disregarding the nominal subspecies *S. t. tabulatus*, the attempt of HAUSER (2001, p. 135) to interpret all with length > width as in *S. tabulatus*, and all the remainder as “*S. t. depressus*” is, therefore, irrelevant. This conclusion is affirmed by the identical brachials, the concordant plenary radial facets of all *S. tabulatus* morphotypes, and the same stem facet. Likewise the development of plate sculpturing and the irregularly arranged lateral depressions of the brachials may vary both in short and long aboral cups. However, it should be noted, that several *S. tabulatus*

***FIGURE* 3.3.2. (legend p. 125)**



localities yield a relatively constant spectrum of either short or long aboral cups, whereas other places, like the new type locality, has the broad spectrum of gradual transitions. Likewise, the dimensions are regionally different. Very abundant localities are dominated by smaller individuals.

Especially in the upper Middle Eifelian in the vicinity of Gondelsheim (Prüm Syncline, Eifel, Rhenish Massif, Germany; UTM 50°13’58.95’’N/6°29’44.73’’E and eastward to 50°13’58.85’’N/6°29’52.50’’E), rarer findings of large specimens are characteristic.

The atomous brachial construction, with interlocked lateral depressions, may support a sturdy resting or avoidance posture, which possibly affords heightened tolerance against hydrodynamic influences or predatory attacks. The lateral gearing of atomous arms is also known in Australian cupressocrinitids (compare to JELL et al. 1988, p. 394; fig. 26H).

The strongly convex brachials have distributed notches, which occur laterally, diagonally positioned to each other (Figs. 3.3.4.2-5, 3.3.4.8-9, 3.3.4.14). These notches bear an obvious rudimentary arm appendage (Figs. 3.3.4.3, 3.3.4.5) that possibly could extend in a semiclosed arm-crown position and may have allowed feeding in a protected posture.

FIGURE 3.3.2.1-40 (see p. 124)—*Stylocrinus tabulatus* (GOLDFUSS, 1839), the transitions between the different morphologies of the aboral cup and variations of plate sculpturing (***1-17***, ***19-40***, lateral; ***18***, aboral view). ***1***, GIK-2007, x 3.8; ***2***, GIK-2008, x 5.4; ***3***, GIK-2087, x 4.7; ***4***, GIK-2089, x 4.0; ***5***, GIK-2060, x 3.2; ***6***, GIK-2076, x 3.2; ***7***, GIK-2090 (leg. SCHREUER), one stem-ossicle preserved, x 3.6; ***8***, GIK-2068, x 3.7; ***9***, GIK-2092, x 6.7; ***10***, MWNH-306e, one stem-ossicle preserved, x 3.5; ***11***, GIK-2009, x 4.4; ***12***, GIK-2067, x 2.7; ***13***, GIK-2006, x 2.0; ***14***, GIK-2058 (leg. HEIN), one stem-ossicle preserved, x 2.6; ***15***, GIK-2091 (leg. HEIN), x 3.4; ***16***, GIK-2077, x 2.8; ***17***, GIK-2010, x 3.4; ***18-19***, GIK-2002 (leg. LEUNISSEN), aboral cup with a-typical narrow basis, x 4.0; ***20***, GIK-2059, x 3.6; ***21***, GIK-2093 (leg. SCHREUER), x 3.5; ***22***, GIK-2094 (leg. SCHREUER), x 3.5; ***23***, GIK-2063 (leg. SCHREUER), x 3.5; ***24***, GIK-2064 (leg. SCHREUER), x 3.3; ***25***, GIK-2065 (leg. SCHREUER), x 3.8; ***26***, GIK-2095, x 3.8; ***27***, Proposed **neotype**, IPB-BOHATÝ-10, x 3.1; ***28***, GIK-2096 (leg. SCHREUER), x 3.4; ***29***, GIK-2098, x 2.9; ***30***, GIK-2097 (leg. SCHREUER), x 4.2; ***31***, GIK-2099 (leg. SCHREUER), x 3.1; ***32***, GIK-2100 (leg. SCHREUER), x 3.1; ***33***, GIK-2061, x 4.0; ***34***, GIK-2070, x 2.4; ***35***, GIK-2071, x 2.1; ***36***, GIK-2066 (leg. SCHREUER), x 2.8; ***37***, GIK-2101 (leg. SCHREUER), x 2.9; ***38***, GIK-2062 (leg. HEIN), part of stem preserved, x 2.7; ***39***, MWNH-306f, x 4.5; ***40***, GIK-2088 (leg. HEIN), x 2.9.

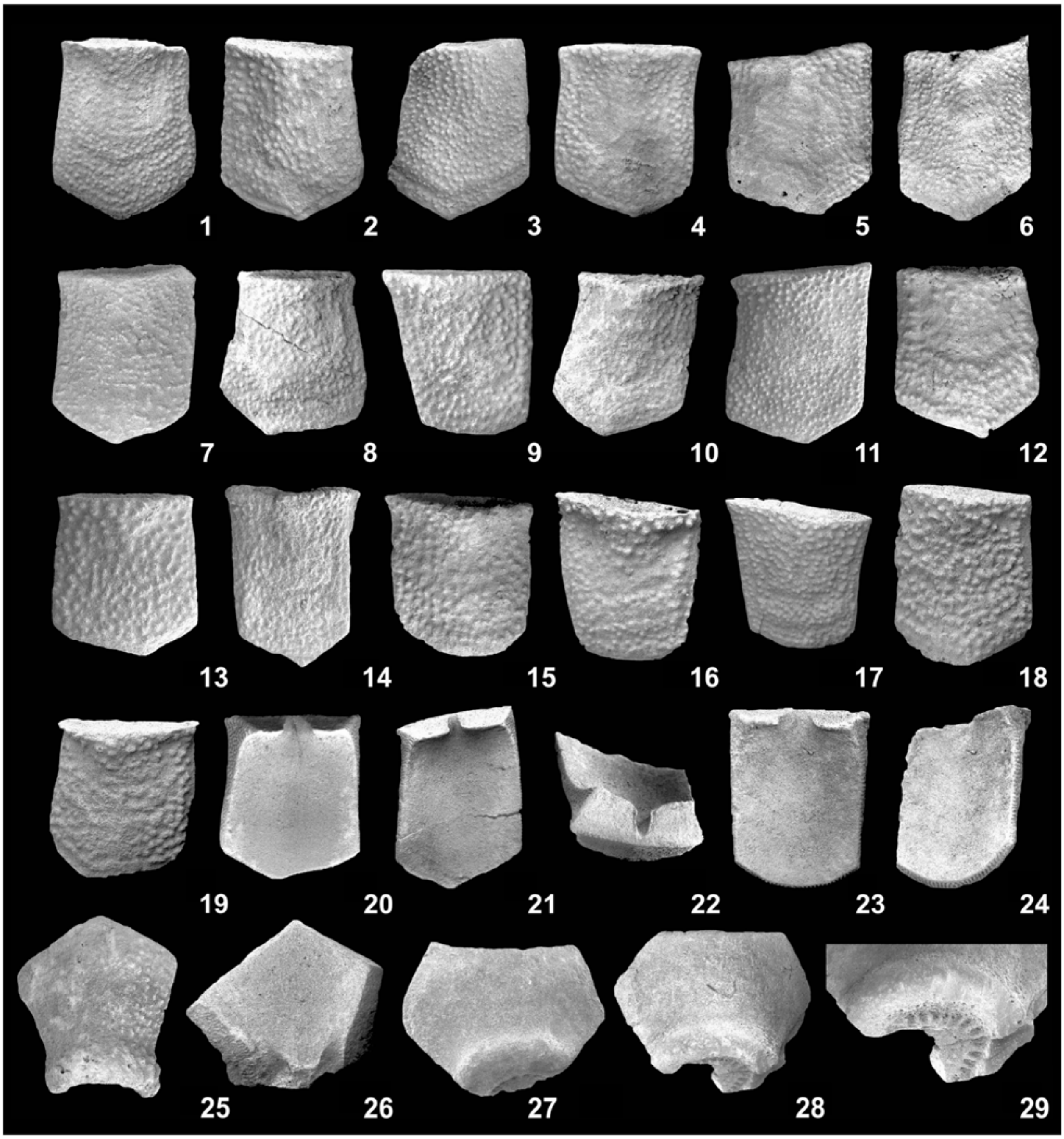


FIGURE 3.3.3.1-29—*Stylocrinus tabulatus* (GOLDFUSS, 1839), isolated radials (***1-24***) and basals (***25-29***) in lateral (***1-21***, ***23-28***) and facetal views (***22***, ***29***). ***1***, GIK-2024, x 6.1; ***2***, GIK-2025, x 7.1; ***3***, GIK-2026, x 5.3; ***4***, GIK-2027, x 5.6; ***5***, GIK-2028, x 6.3; ***6***, GIK-2029, x 5.4; ***7***, GIK-2030, x 8.2; ***8***, GIK-2031, x 6.1; ***9***, GIK-2032, x 7.6; ***10***, GIK-2033, x 6.0; ***11***, GIK-2034, x 5.6; ***12***, GIK-2035, x 8.0; ***13***, GIK-2036, x 8.7; ***14***, GIK-2037, x 5.6; ***15***, GIK-2038, x 8.6; ***16***, GIK-2039, x 8.1; ***17***, GIK-2040, x 5.2; ***18***, GIK-2041, x 8.3; ***19***, GIK-2042, x 8.4; ***20***, GIK-2043, interior view, x 6.4; ***21-22***, GIK-2044, interior side and view of plenary radial facets, x 6.1/6.8; ***23-24***, GIK-2045, interior view, x 6.7/6.2; ***25***, GIK-2046, also figured in Fig. 3.3.8.4, x 7.5; ***26***, GIK-2047, interior view, x 7.2; ***27***, GIK-2048, x 7.6; ***28-29***, GIK-2049, x 6.4/10.4.

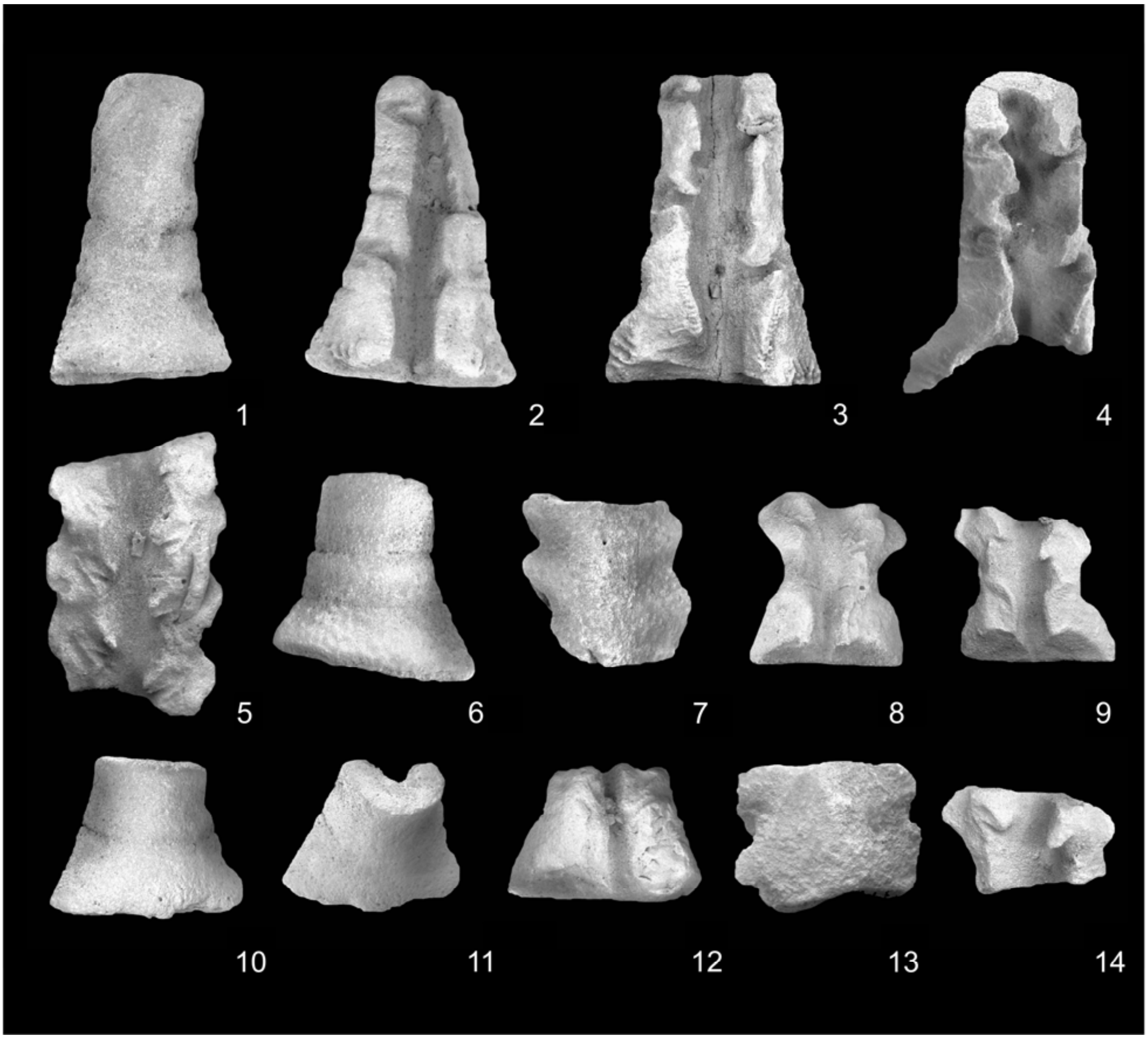


FIGURE 3.3.4.1-14—*Stylocrinus tabulatus* (GOLDFUSS, 1839), isolated brachials. ***1***, GIK-2018, lateral view, x 8.2; ***2***, GIK-2019, interior view showing inordinately distributed lateral notches (possibly for rudimental pinnulation?), which are diagonally positioned to each other, x 9.4; ***3-4***, GIK-2020, interior and facetal view, lateral notches and possibly one preserved rudimental pinnule(?) [upper right], x 7.4/7.7; ***5***, GIK-2012, interior view with well preserved lateral notches and one rudimental pinnule(?) [right centre], x 7.8; ***6***, GIK-2021, lateral view, x 7.6; ***7***, GIK-2013, lateral view of a plate with well developed lateral notches, x 8.0; ***8***, GIK-2014, interior view of proximal brachials with well developed lateral notches, x 6.1; ***9***, GIK-2015, interior view of proximal brachials with well developed lateral notches, x 5.7; ***10-11***, No. GIK-2022, lateral and lateral-facetal view of proximal plates, x 6.8/6.5; ***12***, GIK-2023, interior view of a weathered proximal plate, x 6.8; ***13***, GIK-2016, lateral view of a plate with well developed lateral notches, x 7.7; ***14***, GIK-2017, interior view, x 7.0.

3.3.4.1.4 Species *Stylocrinus granulatus*

Stylocrinus granulatus HAUSER, 1997
Figs. 3.3.5.1-4, 3.3.11(right)

- *Stylocrinus granulatus* HAUSER, 1997, pp. 98-99; pl. 71, figs. 3-4. HAUSER, 2001, p. 193.
- *sic*! *Stylocrinus granulosa* HAUSER, 1997, pp. 14, 98-99.
- *sic*! *Stylocrinus granulosus*. HAUSER, 2001, pp. 137, 151.
- *Symbathocrinus tabulatus* (GOLDFUSS). SCHULTZE, 1866, pl. 3, fig. 4i.
- *Stylocrinus tabulatus* (GOLDFUSS, 1839). MIESEN, 1971, pl. 4, fig. 9h (undescribed).
- *Stylocrinus tabulatus* (MÜLLER). MIESEN, 1974, p. 77; fig. 1a.

Holotype.—Aboral cup, no. MB.E.-2580 (not MB.E.-2581 as wrongly given in HAUSER 1997, p. 98; pers. information, C. NEUMANN, Berlin).

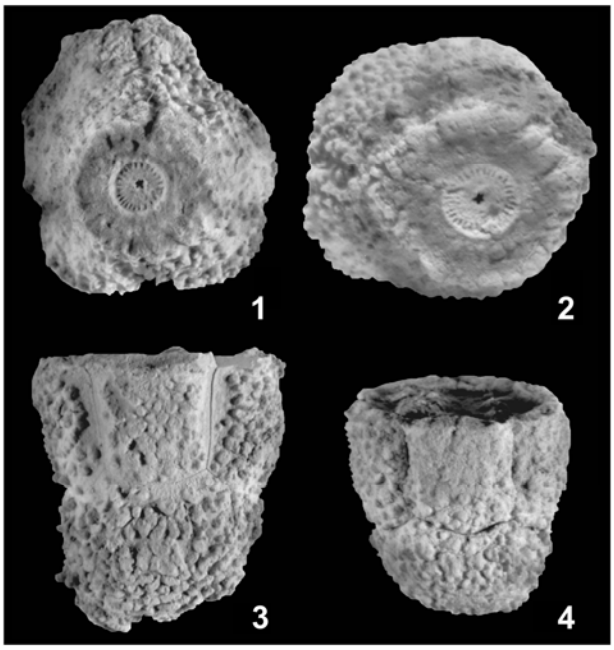


FIGURE* *3.3.5.1-4—*Stylocrinus granulatus* HAUSER, 1997, isolated aboral cups in aboral (***1-2***) and lateral view (***3-4***). ***1***, GIK-2074, showing pentalobate columnal axial canal and typical wide base, x 4.6; ***2***, GIK-2073, showing pentalobate columnal axial canal and typical wide base, x 5.4; ***3***, GIK-2072, plate sculpturing well preserved, x 4.3; ***4***; GIK-2075, x 3.7.

Type locality and stratigraphy.—“Auf den Eichen”, northeast of Nollenbach (Hillesheim Syncline, Eifel, Rhenish Massif, Germany); UTM 50°19’45.81’’N/6°44’38.33’’E. Stratigraphy: Bohnert Member of the upper part of the Freilingen Formation, Upper Eifelian (Middle Devonian); *kockelianus*/*ensensis* Conodont Biozone.

Diagnosis.—A *Stylocrinus* with a medium length cone shaped and monocyclic aboral cup with subhorizontal to slightly depressed and wide base with narrow stem impression (Figs. 3.3.5.1-4), all in all “flowerpot-like” (Fig. 3.3.5.4); aboral cup composed of three basals and five radials with plenary radial facets; plate boundaries notched; plates sculptured with rough, unaligned sculpturing (meandering crinkles and/or tubercles); widest lateral radius of aboral cup at the radial facet; stem narrow, circular in cross section, with one central, pentalobate axial canal. Arms, complete stem and holdfast unknown.

Occurrence.—In addition to the type locality, this species is recovered from the same stratigraphic interval of the abandoned Weinberg Quarry near Kerpen (Hillesheim Syncline, Eifel, Rhenish Massif, Germany); UTM 50°18’54.47’’N/6°42’53.63’’E.

Discussion.—This rare *Stylocrinus* is characterised by rough plate sculpturing and the wide base (Figs. 3.3.5.1-2). The new localities yield a relatively low diversity of aboral cup morphologies in comparison with the common *S. tabulatus*, which is rarely associated with relatively small individuals. *S. granulatus* is a very constant form with the shortest stratigraphical range of all known stylocrinids. The ecologically highly adapted species established after a regional event at the threshold of the Junkerberg and Freilingen formations of the upper Middle to Upper Eifelian (“*otomari* Event” *sensu* STRUVE et al. 1997 – a transgression that resulted in sedimentary changes within the Eifel region). The occurrence of *S. granulatus* is strictly limited to the Bohnert Member (upper part of the Freilingen Formation, Upper Eifelian), apparently unable to avoid rapid sedimentary changes in the superposed Ahbach Formation (Eifelian/Givetian).

3.3.4.1.5 Species *Stylocrinus prescheri*

Stylocrinus prescheri n. sp.[15]
Figs. 3.3.6.1-16, 3.3.11(left)

- (?)*Symbathocrinus tabulatus* (MÜLLER). SCHULTZE, 1866, pl. 3, fig. 4c.
- *Stylocrinus tabulatus tabulatus* (GOLDF.). DUBATOLOVA, 1971, pl. 1, figs. 5a-5.
- (?)*Stylocrinus tabulatus* (MÜLLER). MIESEN, 1974, p. 77; fig. 1b.

---

[15] = *Stylocrinus prescheri* BOHATÝ, in review *sensu* ICZN

- (?)*Stylocrinus tabulatus* var. *alta* (MÜLLER). MIESEN, 1971, pl. 4, fig. 9c.
- *sic*! *Stylocrinus tabulatus* (GOLDFUSS, 1839). HAUSER, 2008, p. 26; fig. 49 [also figured on pl. 1, fig. 5, described as "*Stylocrinus tabulatus depressus* MÜLLER in ZEILER & WIRTGEN, 1855"].
- *sic*! *Stylocrinus tabulatus depressus* (GOLDFUSS, 1839). HAUSER, 2008, pl. 1, fig. 5 [also figured on p. 26, fig. 49, described as *Stylocrinus tabulatus* GOLDFUSS, 1839].

Etymology.—In honour of Mr. HARALD PRESCHER (Kerpen-Horrem, Germany), the discoverer of the fossil layer at the type locality, who encouraged many aspects of my research.

Holotype.—Aboral cup, no. SMF-75408 (Fig. 3.3.6.8).

Type locality.—Slope of the former planned roadwork extension of federal road "B51", south of Brühlborn, northeast of Rommersheim (Prüm Syncline, Eifel, Rhenish Massif, Germany); UTM 50°12'27.14''N/6°27'37.45''E. The locality corresponds with the locus typicus of the cladid crinoid *Bactrocrinites porrectus* BOHATÝ, 2005b, pp. 403, 406-407.

Stratigraphy.—Olifant Member of the lower part of the Müllert Subformation, Ahbach Formation (lowermost Lower Givetian, Middle Devonian); *hemiansatus* Conodont Biozone.

Diagnosis.—A *Stylocrinus* with an inverted "pear-shaped" aboral cup (Figs. 3.3.6.1-2), wider than long, composed of three basals, forming a convex base, and five radials with plenary radial facets, radials peltiform, with widest diameter at the lower edges, narrowing distally; the widest lateral radius of the aboral cup is close to the radial/basal boundary; radial circlet constricted (Figs. 3.3.6.5-6); stem narrow, circular in cross section, with one central, pentalobate axial canal. Arms, complete stem and root unknown.

Measurements of the holotype (max. length/width in mm).—Aboral cup: 9.0/13.0; basals: 5.3/9.0; radials: 5.5/6.0; diameter of stem impression: 5.0; diameter of stem facet: 2.5.

Description.—The aboral cup is inverted “pear-shaped” (Figs. 3.3.6.1-2), wider than long and has its widest lateral radius close to the radial/basal boundary. The stem impression is surrounded by a moderate concavity (Figs. 3.3.6.12), which is surrounded by the lower rims of the three unequal basals, which formed a wide and convex base. All basals are sculptured by irregularly or slightly aligned coarser granules (Figs. 3.3.6.3, 3.3.6.9). The proximal part of the aboral cup is nearly as long as the radial circlet. Radials peltiform, with the widest diameter at the basal/radial boundary, constricted distally and also sculptured by mostly irregular arranged granules, or sculpturing arcuately arranged, parallel to the lower flange of the radials. The radials of adult aboral cups have arcuate sculpturing below the plenary radial facets; distal to a projecting stage (Fig. 3.3.6.1). Stem narrow, circular in cross section and penetrated by a single, small and pentalobate axial canal.

Differential diagnosis.—The inverted “pear-shaped” aboral cup clearly separates *S. prescheri* n. sp.[16] from all morphotypes of *S. tabulatus* and *S. granulatus*.

A simplified model of the characteristic aboral cup morphologies, differentiating the new species from *S. tabulatus* and *S. granulatus*, is given in Fig. 3.3.11.

Occurrence.—Middle Devonian. Eifelian (Mamontovsk’i Member, Pesterevsk’i Limestone): NE Salair, near Gur’evsk (Kemerowo, Siberia, Russia; western part of the central Kusbass, Asia). Upper Eifelian (lower part of the Ahbach Formation) to lowermost Lower Givetian [upper part of the Ahbach Formation to (?)Loogh Formation]: Prüm (Brühlborn/Rommersheim vicinity) and Hillesheim synclines (Ahütte) [both Eifel, Rhenish Massif, Germany]. Lowermost Upper Givetian (“Roteisenstein”): “Grube Lahnstein” near Weilburg-Odersbach, NE of Limburg an der Lahn (Rhenish Massif, Lahn-Dill Syncline, Germany).

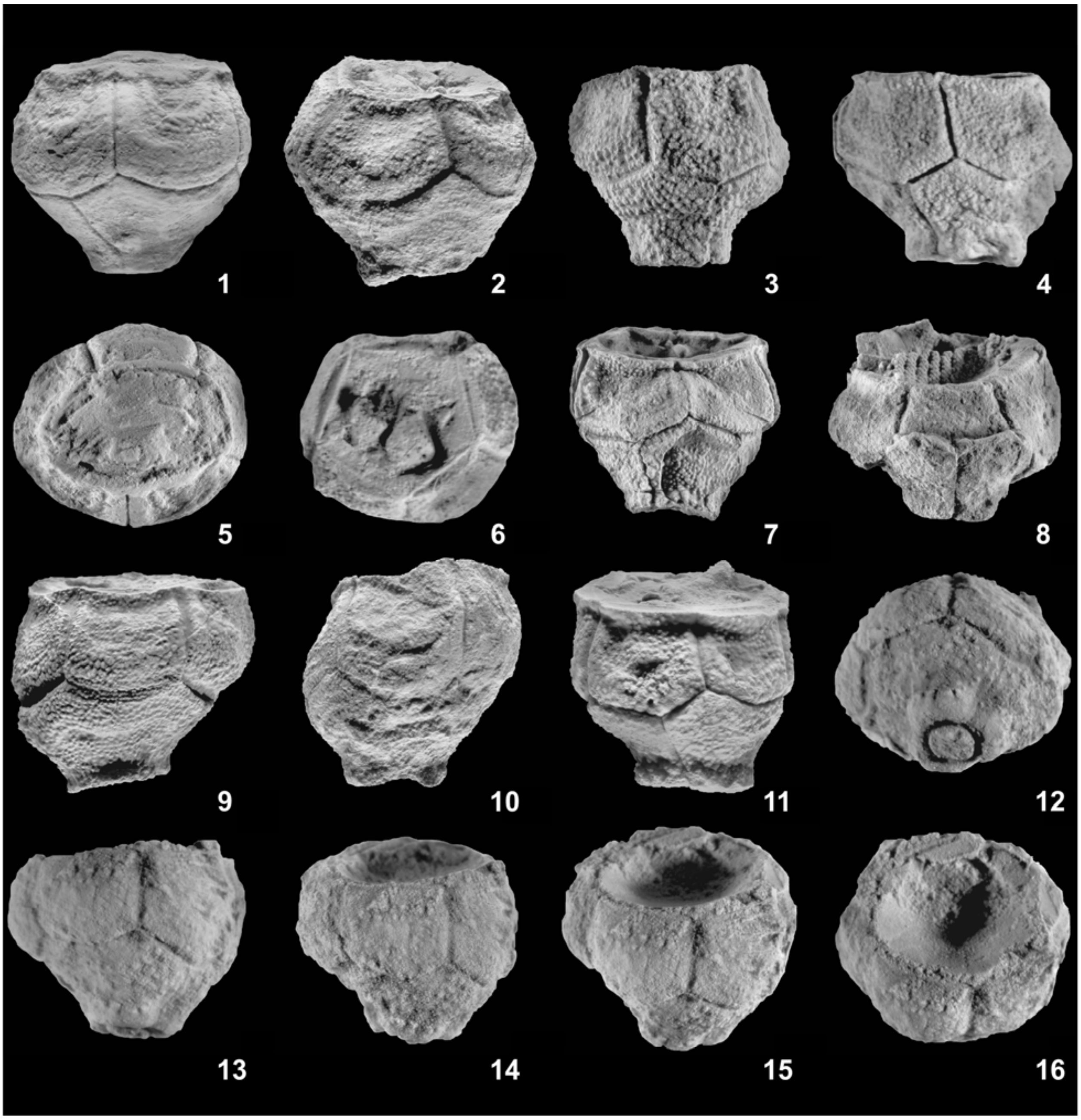
Discussion.—At all known *S. prescheri* localities, this rare stylocrinid is associated with *S. tabulatus*; an association of *S. prescheri* n. sp.[17] and *S. granulatus* was not observed.

Within the Eifel Synclines, the new species is restricted to the Eifelian/Givetian boundary. The few localities within the Rhenish Massif yield a relatively low diversity of aboral cup morphologies in comparison with the more common *S. tabulatus*.

---

[16] = *S. prescheri* BOHATÝ, in review *sensu* ICZN

[17] = *S. prescheri* BOHATÝ, in review *sensu* ICZN



F*IGURE *3.3.6.1-16*—*Stylocrinus prescheri n. sp., isolated aboral cups. ***1***, GIK-2084 (leg. PRESCHER), lateral view of a very typical aboral cup, x 3.3; ***2***, GIK-2078, lateral view, x 3.6; ***3***, GIK-2080 (leg. LEUNISSEN), lateral view of a strongly sculptured aboral cup, x 3.5; ***4***, GIK-2081 (leg. SCHREUER), lateral view, x 4.6; ***5***, Same as 1, oral view, x 3.3; ***6***, GIK-2079 (leg. SCHREUER), oral view of a juvenile aboral cup, x 5.7; ***7***, GIK-2082 (leg. PRESCHER), lateral view, x 2.7; ***8***, **Holotype**, SMF-75408, lateral view of slightly compressed aboral cup, x 2.8; ***9***, GIK-2085 (leg. PRESCHER), lateral view, x 3.4; ***10***, GIK-2083 (leg. PRESCHER), lateral view, x 3.9; ***11***, GIK-2086 (leg. PRESCHER), lateral view, x 5.0; ***12-16***, MWNH-306b, unfigured original of SANDBERGER & SANDBERGER (1856), x 4.9 (***12***, aboral; ***13***, lateral; ***14-15***, lateral-oral and ***16***, oral view).

3.3.5 PRE- AND POSTMORTEM SKELETAL MODIFICATIONS OF *STYLOCRINUS*

3.3.5.1 Premortem modifications

Premortem modifications.—In spite of the very large number of aboral cups, and in contrast to camerate or especially to cladid crinoids, premortem skeletal modifications of the disparid *Stylocrinus* are extremely rare and observed on only two of approximately 1500 individuals.

The aboral cup no. GIK-2005 developed an anomalous, additional basal plate (Figs. 3.3.7.1-2). This kind of pathology was recently classified in cupressocrinitids as "growth anomaly without recognisable external influences" and were probably characterising ‘‘genetic abnormalities" (BOHATÝ 2009, p. 53).

The aboral cup no. GIK-2002 has an uncommon base with a narrow stem-insertion (Figs. 3.3.2.18-19), which possibly is attributed to a skeletal (?)regeneration of the base.

Skeletal anomalies in Devonian crinoids have recently been described in the cladid cupressocrinitids, gasterocomoids and bactrocrinids (BOHATÝ 2001; 2005a-b; 2006a-b; BOHATÝ & HERBIG in review), and in the camerate hexacrinitids (BOHATÝ 2001; 2006d-e; in press). An extensive discussion about pre- and postmortem skeletal modifications of the cupressocrinitid skeletons is given in BOHATÝ (2009).

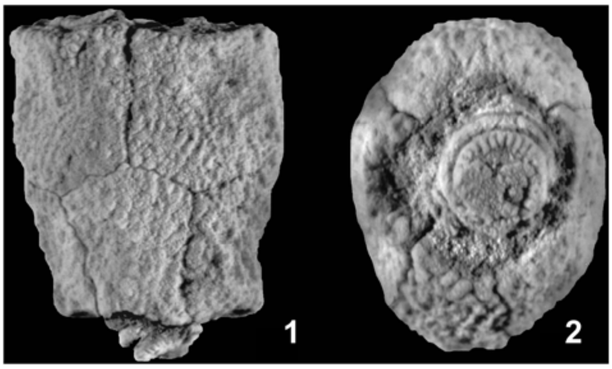
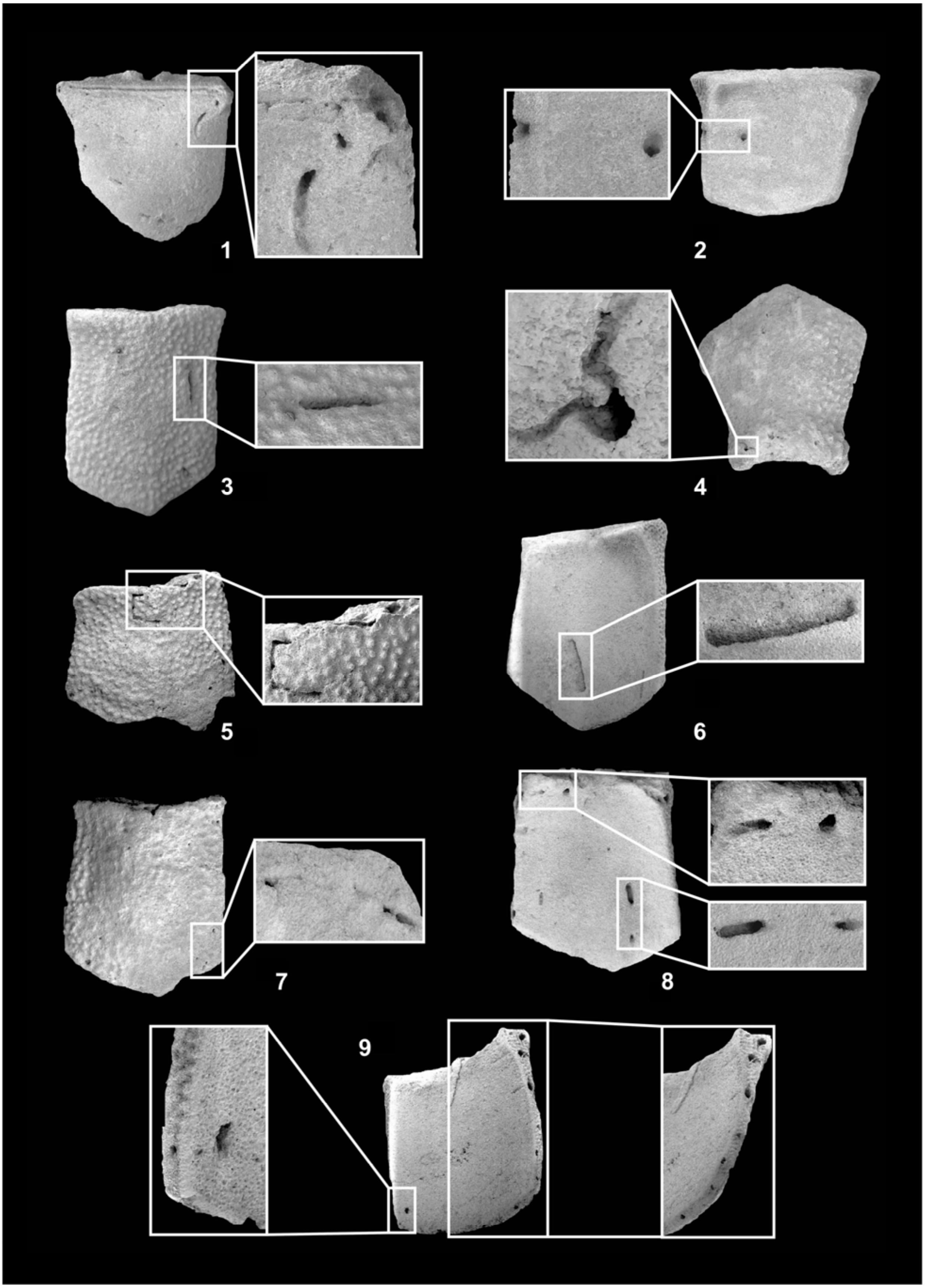


FIGURE 3.3.7.1-2—*Stylocrinus tabulatus* (GOLDFUSS, 1839), abnormal aboral cup, GIK-2005 (leg. SCHREUER), with four basal plates. ***1***, lateral view; ***2***, aboral view, x 5.0.

3.3.5.2 Postmortem modifications

Postmortem modifications.—Postmortem skeletal modifications in the form of ossicular borings are common in stylocrinids. Almost 60% of the studied skeletons were penetrated by two types of borings. Figs. 3.3.8.1-3, 3.3.8.6-9 shows rectilinear or less

***FIGURE* 3.3.8 (legend p. 135)**



meandering, endolithic borings of unknown affinity. Most likely, they occur after the disarticulation of the aboral cup, because the origin of most of these traces is at the radial or basal plate margins. Figs. 3.3.8.4-5 shows radial and basal plates which were affected by surficial meandering borings of an unknown organism (possibly a boring Bryozoa or a Porifera). These types are rarer in comparison with the endolithic traces. Different pre- and postmortem borings occurred as single and multi-borings observed in cupressocrinitid skeletons described by BOHATÝ (2009). They differ from the stylocrinid traces, which are related to the undescribed borings on the isolated radials of *Edriocrinus* sp. (PROKOP & PETR, 1995, pl. 1, figs. 1-16). The ossicles, especially the radials, of both species have very similar morphologies.

One aboral cup of *S. tabulatus* represents the first non-platyceratid gastropod trace fossil observed on a crinoid skeleton and was identified as the radular grazing trace fossil ichnogenus *Radulichnus* VOIGT, 1977 (Fig. 3.3.9), recently detected on Eifelian Brachiopods from the Rhenish Massif (GRIGO, in review). These traces are attributed to the activity of polyplacophorid and patellid gastropods (VOIGT 1977), but their affinity remains unclear.

One isolated *S. tabulatus* aboral cup was overgrown postmortem by a rugose coral, which attached to the plenary radial facets from oral direction with its root like basal extensions (no. GIK-2011; Fig. 3.3.10). The non-overgrown ossicles (radials and basals) remained articulated during the growth of the coral and, therefore, were probably enclosed by the sediment of the assumed soft-bottom. Also during the weathering processes of the coralite, the crinoid remained in good condition, while the former enclosing sediment was eroded.

FIGURE 3.3.8.1-9 (see p. 134)**—Stylocrinus tabulatus* (GOLDFUSS, 1839), postmortem borings on isolated radials (1-3***, ***5-9***) and on one basal plate (***4***). ***1***, GIK-2050, lateral view with one endolithic boring trace (enlarged), x 7.5; ***2***, GIK-2051, interior view with one endolithic boring trace (enlarged), x 9.3; ***3***, GIK-2052, lateral view with one external(?) boring (enlarged) [compare to Fig. *6*], x 7.4; ***4***, GIK-2046, also figured in Fig. 3.3.3.25, lateral view with one meandering boring trace (enlarged), x 9.1; ***5***, GIK-2053, lateral view of a fractured ossicle with one endolithic boring trace (enlarged), x 7.7; ***6***, GIK-2054, interior view with one external(?) boring trace (enlarged) [compare to Fig. *3*], x 9.1; ***7***, GIK-2055, lateral view with one endolithic boring trace (enlarged), x 6.5; ***8***, GIK-2056, lateral view of a fractured ossicle with two endolithic boring traces (enlarged), x 9.2; ***9***, GIK-2057, interior and facetal views of an ossicle with numerous endolithic borings (enlarged) at the ossicular facets, x 8.3.

***FIGURE* 3.3.9**—*Stylocrinus tabulatus* (GOLDFUSS, 1839), isolated, strongly weathered aboral cup GIK-2069, representing the first crinoid-evidence of the radular grazing trace fossil ichnogenus *Radulichnus* VOIGT, 1977 on two radials (framed), x 9.5.

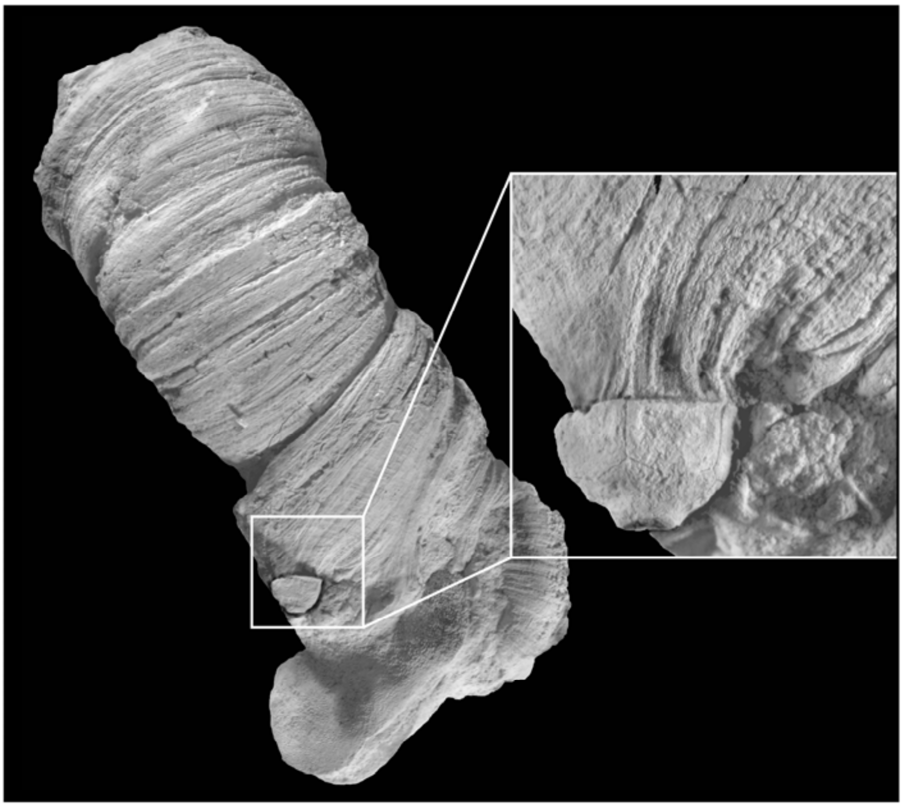


***FIGURE* 3.3.10**—*Stylocrinus tabulatus* (GOLDFUSS, 1839), isolated aboral cup, GIK-2011, x 1.1/4.0. The aboral cup was postmortem overgrown by a rugose coral. The base of the rugose also encrusted a tabulate coral.

3.3.6 DISCUSSION

To give a résumé of the present study it has to be noted that the common taxa are distinguished by a high morphological variability of the aboral cup length/width proportions and plate sculpturing. The rarer species, *S. granulatus* and the new *S. prescheri*, are less variable regarding these morphological features. Also, former authors differentiated *S. tabulatus* into three subspecies (*S. t. tabulatus, S. t. altus* and *S. t. depressus*), the analysis of approximately 1500 aboral cups in varying between short and long aboral cups clearly demonstrate that the intraspecific morphological variability of the type species is a matter of its ecophenotypic plasticity.

Within the Eifel, the stratigraphic distribution of the rarer taxa is confined to the Freilingen and Ahbach formations (Upper Eifelian), whereas *S. tabulatus* is known from the Lower, Middle and Upper Eifelian to the lowermost part of the Lower Givetian. The lowermost Upper Givetian *S. tabulatus* and *S. prescheri* findings in the Lahn Syncline are the youngest European occurrences. But the stylocrinids from Western Australia demonstrate that the genus is at least known from the lowermost part of the Lower Eifelian (Middle Devonian) to the Frasnian (Upper Devonian).

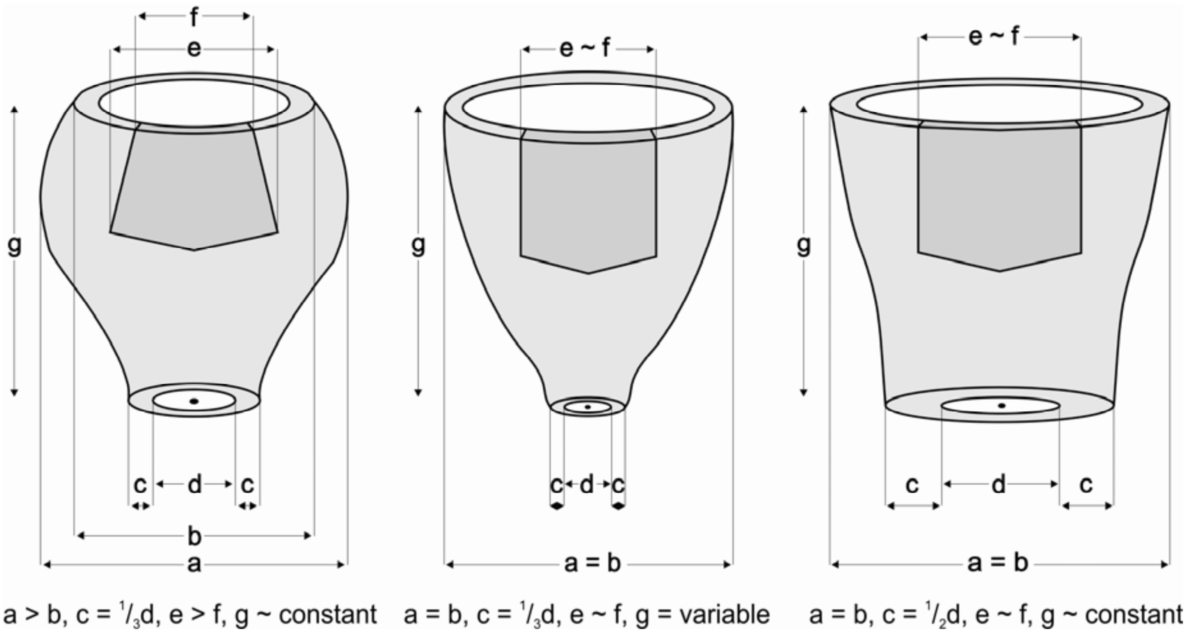


FIGURE 3.3.11—Idealised sketches of the most characteristic morphological features, distinguishing *Stylocrinus prescheri* n. sp. (left), *S. tabulatus* (Goldfuss, 1839) [centre] and *S. granulatus* HAUSER, 1997 (right).

S. granulatus has the shortest stratigraphical range of all known stylocrinids. The ecologically highly adapted species established after the "*otomari* Event" at the boundary of the Junkerberg and Freilingen formations (Upper Eifelian) and became extinct by the first change of the post-event facies with the beginning of the superposed Ahbach Formation (Eifelian/Givetian boundary).

Several localities within the Eifel are distinguished by mass occurrences of *S. tabulatus*, as it was recognised within the Junkerberg Formation (Eifelian) of Schwirzheim and Rommersheim (Prüm Syncline, Eifel, Rhenish Massif, Germany). But the findings are nearly completely restricted to isolated aboral cups. Postmortal, the aboral cups were relatively robust in contrast to the mostly disarticulated brachials. Therefore, crowns are unique occurrences. The postmortal stability of the aboral cup is also confirmed by the overgrowth of an adult rugose coral, using the aboral cup as hard ground during its growth, without disarticulation of the stylocrinid.

Considering the huge number of stylocrinid aboral cups, it is also remarkable that, contrary to cladid and camerate crinoids from the Eifel, only two abnormal individuals were recovered.

3.3.7 APPENDIX

3.3.7.1 The fossil localities and stratigraphy of the studied crinoids

GIK-2001, Locality: Agricultural area, to the west of Schwirzheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM unknown. Stratigraphy: Hönselberg Member, upper part of the Heinzelt Subformation, Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2002, Locality: Schwirzheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM unknown. Stratigraphy: Hönselberg Member, upper part of the Heinzelt Subformation, Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2003, Locality: "Hartelstein", NE-Schwirzheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM unknown. Stratigraphy: Hönselberg Member, upper part of the Heinzelt Subformation, Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2004, Locality: Brühlborn (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM unknown. Stratigraphy: Klausbach Member, lowermost part of the Heinzelt Subformation, lowermost part of the Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2005, Locality: Rommersheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM unknown. Stratigraphy: Klausbach Member, lowermost part of the Heinzelt Subformation, lowermost part of the Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2006, Locality: SW-“Hönselberg”, to the east of Loogh, south of Niederehe (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), UTM 50°18’09.55’’N/6°44’51.65’’E. Stratigraphy: Eilenberg Member, lower part of the Freilingen Formation (Upper Eifelian, Middle Devonian).

GIK-2007 to GIK-2010, Locality: Pelm, to the east of Gerolstein (Gerolstein Syncline, Eifel, Rhenish Massif, Germany), UTM unknown. Stratigraphy: Loogh Formation (Lower Givetian, Middle Devonian).

GIK-2011 to GIK-2017, Locality: W-housing subdivision “Unterm Sportplatz” of village Schwirzheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM 50°13’50.53’’N/6°31’08.72’’E. Stratigraphy: Hönselberg Member, upper part of the Heinzelt Subformation, Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2018 to GIK-2057, – same as locality 16.

GIK-2058, Locality: 600m SE of Ahrdorf (Ahrdorf Syncline, Eifel, Rhenish Massif, Germany), UTM unknown. Stratigraphy: Eilenberg Member, lower part of the Freilingen Formation (Upper Eifelian, Middle Devonian).

GIK-2059 to GIK-2060, Locality: SW-housing subdivision of village Gondelsheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM 50°13’58.85’’N/6°29’52.50’’E. Stratigraphy: Nims Member, lower part of the Grauberg Subformation, upper part of the Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2061, Locality: E-Niederehe (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), UTM 50°18’46.72’’N/6°46’13.74’’E. Stratigraphy: Klausbach Member, lowermost part of the Heinzelt Subformation, lowermost part of the Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2062, Locality: W-industrial area, SE of Weinsheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM 50°13’32.14’’N/6°28’42.97’’E. Stratigraphy: Upper part of the Rech Member, upper part of the Loogh Formation (Lower Givetian, Middle Devonian).

GIK-2063 to GIK-2066, Locality: SW-housing subdivision “Im Leimenpeschen” of village Schwirzheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM 50°13’47.54’’N/6°31’17.35’’E. Stratigraphy: Hönselberg Member, upper part of the Heinzelt Subformation, Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2067 to GIK-2068, Locality: W-Gondelsheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM 50°14’03.31’’N/6°29’50.47’’E. Stratigraphy: Klausbach Member, lowermost part of the Heinzelt Subformation, lowermost part of the Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2069 to GIK-2071, Locality: “Mühlenwäldchen”, SW-Gerolstein (Gerolstein Syncline, Eifel, Rhenish Massif, Germany), UTM 50°13’16.14’’N/6°39’01.00’’E. Stratigraphy: Baarley Member, lower part of the Loogh Formation (lowermost Lower Givetian, Middle Devonian).

GIK-2072 to GIK-2074, Locality: Abandoned “Weinberg Quarry”, NW of Kerpen (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), UTM 50°18’54.47’’N/6°42’53.63’’E. Stratigraphy: Bohnert Member, upper part of the Freilingen Formation (Upper Eifelian, Middle Devonian).

GIK-2075, Locality: “Auf den Eichen”, NE of Nollenbach (Hillesheim Syncline, Eifel, Rhenish Massif, Germany), UTM 50°19’45.81’’N/6°44’38.33’’E. Stratigraphy: Bohnert Member, upper part of the Freilingen Formation (Upper Eifelian, Middle Devonian).

GIK-2076 to GIK-2077, Locality: Agricultural area, to the west of Gondelsheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM 50°13’58.95’’N/6°29’44.73’’E. Stratigraphy: Nims Member, lower part of the Grauberg Subformation, upper part of the Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

GIK-2078 to GIK-2086, Locality: Slope of the former planed roadwork extension of federal road “B51”, south of Brühlborn, northeast of Rommersheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM 50°12’27.14’’N/6°27’37.45’’E. Stratigraphy: Olifant Member, lower part of the Müllert Subformation, Ahbach Formation (lowermost Lower Givetian, Middle Devonian).

GIK-2087 to GIK-2101, Locality: Slope of the former planned roadwork extension of federal road “B51”, south of Brühlborn, northeast of Rommersheim (Prüm Syncline, Eifel, Rhenish Massif, Germany), UTM 50°12’24.88’’N/6°27’38.58’’E. Stratigraphy: Nims Member, lower part of the Grauberg Subformation, upper part of the Junkerberg Formation (upper Middle Eifelian, Middle Devonian).

MWNH-306a to MWNH-306b; MWNH-306e to MWNH-306f, Locality: Weilburg-Odersbach, NE of Limburg an der Lahn (Lahn-Dill Syncline, Rhenish Massif, Germany), UTM unknown. Stratigraphy: Lowermost part of the Middle Givetian (Middle Devonian) “Roteisenstein”.

SMF-75408, – same as locality 20.

3.4 CHAPTER IV. CRINOIDEA, FLEXIBILIA

NEW MODE OF LIFE INTERPRETATION AND REVISION OF THE IDIOSYNCRATIC LECANOCRINID GENUS *AMMONICRINUS* (CRINOIDEA, FLEXIBILIA)

ABSTRACT—The mode of life of the idiosyncratic lecanocrinid *Ammonicrinus* (Flexibilia) is newly interpreted based on new material from the Middle Devonian of the Rhenish Massif (Eifel and Bergisches Land, Germany). Several species are defined as spined soft-bottom dwellers, feeding in still water through active ligament pumping of the stem via mutable connective tissues. These species show echinoid-like tubercles on the attachment and on the column, which bear movable spines. The intraspecific variability of the column is discussed for three facies-controlled morphotypes, herein classified as standard “exposed-” or “encased roller-type” and the rare “settler-type”. New specimens show floating transitions between different plate sculpturing and between those individuals with none or one to several columnals with herein termed “lateral columnal enclosure extensions” on the proximal-most, barrel-like dististele and the following mesistele, which is solely distinguished by these extensions. Based on this interpretation, *A. kongieli* is evaluated as a subjective junior synonym of *A. sulcatus*. The latter species is first recognised within the Eifel (Germany). “*A. wachtbergensis*”, from the Upper Eifelian of the Eifel, is declared a subjective junior synonym of *A. doliiformis*. The first complete specimen of *A. kredreoletensis* is described from the Lower Eifelian of Vireux-Molhain (southern Ardennes, France). Two new species are described: *Ammonicrinus jankei* n. sp.[1] and *A. leunissi* n. sp.[2] A functional morphologic trend of perfecting the crown-encasing by continuous modification of the lateral columnal enclosure extensions of the mesistele from the Eifelian to the Givetian, indicates a vagile benthic predator-driven evolution of ammonicrinids within the Eifel. The first known postmortem encrusting epizoans on ammonicrinid endoskeletons are reported.

3.4.1 INTRODUCTION

The idiosyncratic and rarely known Devonian *Ammonicrinus*, a lecanocrinid flexible crinoid, was described by SPRINGER (1926b) and afterwards discussed in comparatively few publications [KRAUSE 1927; EHRENBERG 1930; WOLBURG 1938a, b;

---

[1] = *Ammonicrinus jankei* BOHATÝ, submitted *sensu* ICZN

[2] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

Wanner 1943, 1954; Ubaghs 1952; Yakovlev & Ivanov 1956; Kongiel 1958; Piotrowski 1977; Moore 1978; Haude 1981; Głuchowski 1993; Hotchkiss et al. 1999; Le Menn & Jaouen 2003; Hauser 2005b; Hauser et al. 2009 and Prokop 2009 (see "Remarks" below)], mainly from the Devonian deposits of Germany (Rhenish Massif) and Poland (Holy Cross Mountains). *Ammonicrinus* is distinguished by the synarthrial articulation on columnals with fulcra aligned and unequal ligmentary areas on either side of each fulcrum, which produced a planispirally coiled proximal column presumably serving a protective function. With the exception of two other Palaeozoic genera, *Myelodactylus* Hall, 1852 and *Camptocrinus* Wachsmuth & Springer, 1897, the enrolled *Ammonicrinus* (Figs. 3.4.5, 3.4.7.1, 3.4.8) does not correspond to the erect model of most stalked crinoids, which were attached to the substrate by a diversely designed holdfast followed by an upright stem to elevate the food-gathering system, represented by the arms, above the sea-floor (e.g. Hess et al. 1999).

The extremely modified stem of *Ammonicrinus* served more specialised functions. Besides the attachment, the modified stem provided protection and, presumably, the functional morphology of the stem was a possible nutrient water flow generator. These modifications lead to the most atypical evolutional model among crinoids by drastically changing a "normal" crinoid crown into a "plate-encased" individual (Figs. 3.4.3.8, 3.4.4.1). Accordingly, the genus is easily defined by the development of the spheroidal crown hidden in an enrolled stem, which was, according to new data, either lying on soft-bottoms with long mesi- and dististele, attached with its holdfast to hard objects like brachiopod valves (Figs. 3.4.2.2, 3.4.2.5), corals or bryozoans (Figs. 3.4.5, 3.4.7.1-2; Pl. 3.4.1, Figs. 12-13; Pl. 3.4.2, Fig. 13), or settled completely on hard objects (e.g. brachiopods, see Fig. 3.4.8; Pl. 3.4.1, Fig. 14) by strongly reducing the dististele. The stem is distinguished by the abrupt xenomorphic change between the distal barrel-shaped (dististele) and the middle and proximal columnals with lateral columnal enclosure extensions (mesistele, proxistele).

In the following, the "Lateral Columnal Enclosure Extensions" are abbreviated as "LCEE".

Remarks: The privately published papers of Hauser (2005b) and Hauser et al. (2009) discussing *Ammonicrinus* contained errors. Striking in this context is his reconstruction of "*A. wanneri*" from isolated mesistele columnals from different individuals as a "circular sphere" (2005b, p. 34; pp. 38-39, figs. 5a-b). They are given no further consideration herein.

The isolated columnals described as "*A. bulbosus* sp. n. (col.)" by Prokop (2009, p. 162) are very similar to that isolated Lower Devonian ossicle, illustrated by Hotchkiss et al. (1999, p. 331, fig. 2.21). These elements could not be distinguished from juvenile ossicles of *A. sulcatus* (compare to Figs. 3.4.9.13-16 of this work) and are in urgent need of further research based on more complete material that have to evidence the validity of "*A. bulbosus*". Therefore, this species could not further be considered herein.

3.4.2 MODE OF LIFE – STATE OF THE ART

The first report (SPRINGER 1926b) of *Ammonicrinus* dealt with crowns, enrolled in mesi- and proxistele and several isolated columnals of the mesistele (Figs. 3.4.1.1-6). *Ammonicrinus* was recognised and classified as a true crinoid fossil from the Middle Devonian of the Prüm Syncline, in the vicinity of Locality 3 (Eifel, Rhenish Massif, Rhineland Palatinate, Germany). Because the dististele and the attachment were not preserved, SPRINGER's interpretation of this remarkable new genus was mainly based on comparison with other enrolled forms, like *Myelodactylus* or *Camptocrinus* (1926b, p. 24). SPRINGER assigned his new genus to the Camerata and to the "Hexacrinidae" with its genus *Arthroacantha* WILLIAMS, 1883 (1926b, p. 24).

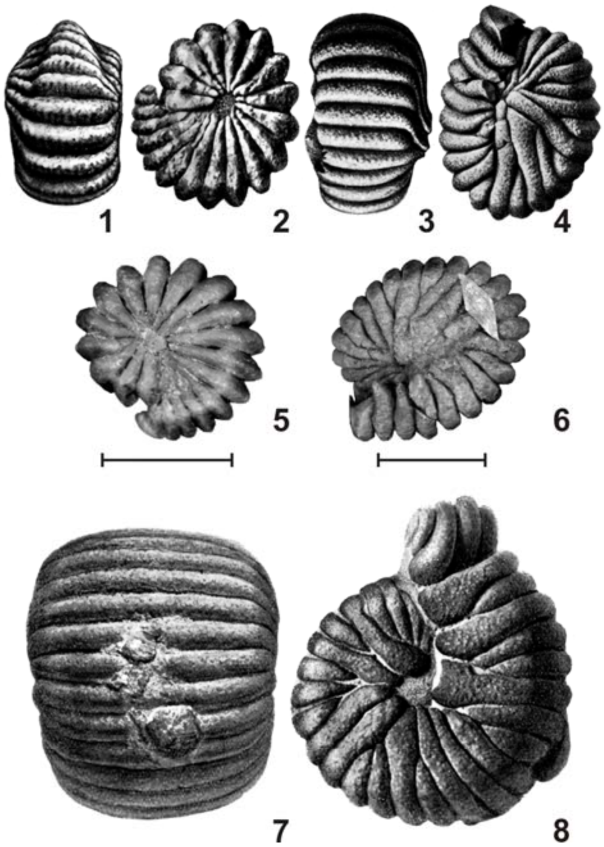


FIGURE 3.4.1—The first *Ammonicrinus* figures of SPRINGER (1926b) and KRAUSE (1927). ***1-2***, *A. wanneri* (taken from 1926b, pl. 6, figs. 4b, 4a); ***3-4***, "*A. wanneri*" (= *A. leunissi* n. sp.) [1926b, pl. 6, figs. 5b, 5], Figs. *1-4* not to scale; **5**, photograph of the holotype of *A. wanneri* (no. USNM-S2115); lateral view of coiled mesistele; connection between mesi- and dististele, dististele and attachment missing (see fracture surface at distal mesistele); ***6***, photograph of the SPRINGER original of "*A. wanneri*" (no. USNM-S2115, also; = *A. leunissi* n. sp.), lateral view of coiled mesistele; connection between mesi- and dististele, dististele and attachment missing (see fracture surface at distal mesistele); ***7-8***, "*A. wanneri*" (= *A. doliiformis*) [1927, pl. VIII, figs. 4, 2], Figs. *7-8* not to scale. [Scale bars = 1 cm]

It is herein recognised that SPRINGER figured three different species; (1) *A. wanneri* (1926b, pl. 6, figs. 4-4b; refigured in Figs. 3.4.1.1-2, 3.4.1.5 of the present work), (2) a species with a wider diameter of the coiled stem, herein described as *A. leunissi* n. sp.[3] (1926b, pl. 6, figs. 5-5b; refigured in Figs. 3.4.1.3-4, 3.4.1.6 of the present work) and (3) two isolated columnals from the mesistele of *A.* cf. *sulcatus* (1926b, pl. 6, fig. 6).

Also, the second note of an *Ammonicrinus* specimen (KRAUSE 1927) was based on an enrolled crown, covered by the mesi- and proxistele. It was classified as "*A. wanneri*", although the fossil differs from SPRINGER's type material by its coiled, wide, barrel-shaped proxi- and mesistele (Figs. 3.4.1.7-8; Pl. 3.4.2, Figs. 15-18). KRAUSE (1927, p. 454) interpreted the then known individuals as crinoids with free, unstalked and possibly planktonic adult life habits.

The interpretation of a planktonic adult life style has to be rejected based on more complete specimens of the wider *Ammonicrinus* described by KRAUSE (1927) as "*A. wanneri*" from the Upper Eifelian of Sötenich (Sötenich Syncline, Eifel; locality 5) in 1927. Another species, *A. doliiformis* WOLBURG, 1938a, from the Selscheider Formation of locality 11, was found attached to brachiopod valves via an attachment disc, which, furthermore, has an attached dististele. This dististele is similar to a "normal" crinoid stem (Figs. 3.4.2.1-2, 3.4.2.5).

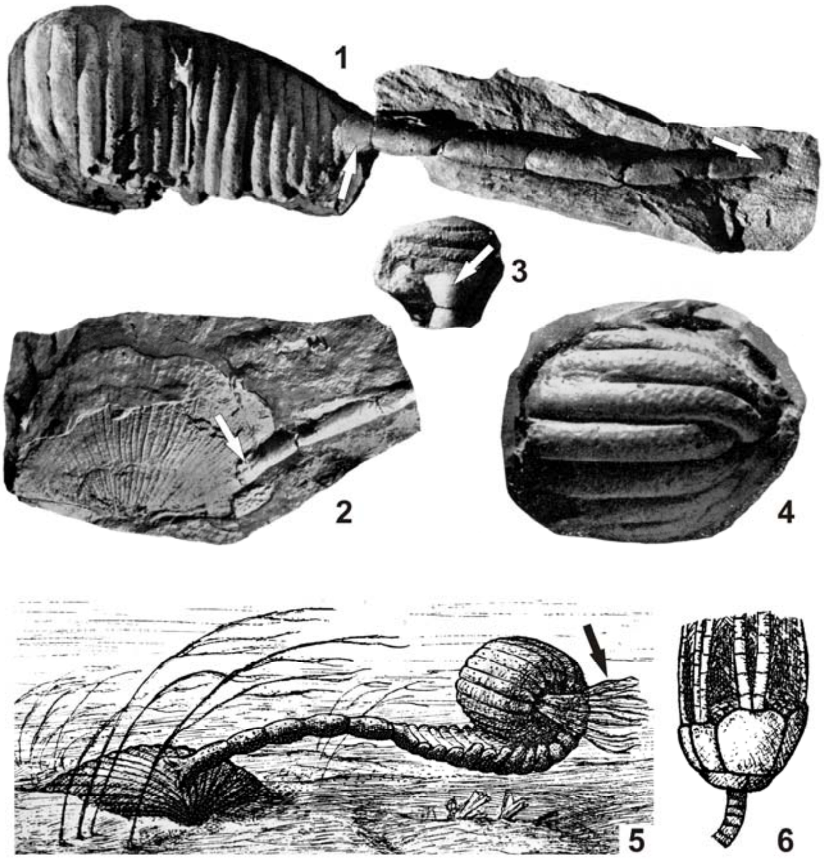
Based on his discoveries, WOLBURG (1938a, p. 238) correctly negated the presumed planktonic mode of life and classified *Ammonicrinus* as a bottom-dweller that lived attached to hard objects. His reconstruction of *A. doliiformis* had the crown protruding toward the lateral-exterior, whereas the crinoid is lying exposed toward the assumed water current (Fig. 3.4.2.5).

FIGURE 3.4.2 (see p. 145)—Casts of *Ammonicrinus doliiformis* WOLBURG, 1938a (not to scale). ***1***, Nearly complete specimen, attached to a brachiopod valve (right arrow), showing the characteristic triangular connection between mesi- and dististele (left arrow) and slightly compressed mesistele (1938a, pl. 17, fig. 1); ***2***, detail view of the attachment disc (arrow), encrusting the brachiopod (taken from 1938a, pl. 18, fig. 8); ***3***, detail view of the triangular connection between mesi- and dististele (arrow) [1938a, pl. 17, fig. 6a]; ***4***, coiled, slightly compressed mesistele (1938a, pl. 17, fig. 4); ***5***, former assumed reconstruction of life mode, figured with a crown that protrudes toward the lateral-exterior (arrow) [1938a, p. 240, fig. 5]; ***6***, former assumed reconstruction of the crown (1938a, p. 233, fig. 4).

---

[3] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

Figure 3.4.2 (legend p. 144)



By carefully excavating a preserved crown of "*A. wanneri*" from locality 8 (= *A. jankei* n. sp.[4]) Ubaghs (1952) demonstrated that the crown remained enclosed within the proximal-most part of the mesistele and the proxistele and did not protrude toward the lateral exterior while feeding (Figs. 3.4.3.4, 3.4.3.8-9). As interpreted here this solely applies to the younger ammonicrinids; but the oldest species, *A. kredreoletensis*, is not covered entirely by the LCEE; that possibly implies feeding in the current. Ubaghs also recognised the true plate diagram of the crown (Fig. 3.4.3.7) and recognised *Ammonicrinus* as a lecanocrinid Flexibilia (1952, p. 204).

It is confirmed herein that his second radianal plate (1952, p. 205, fig. 1), or "supplementary plate" of Wanner (1954), is based on an anomaly, as already assumed by the latter author (1954, p. 235).

---

[4] = *A. jankei* Bohatý, submitted *sensu* ICZN

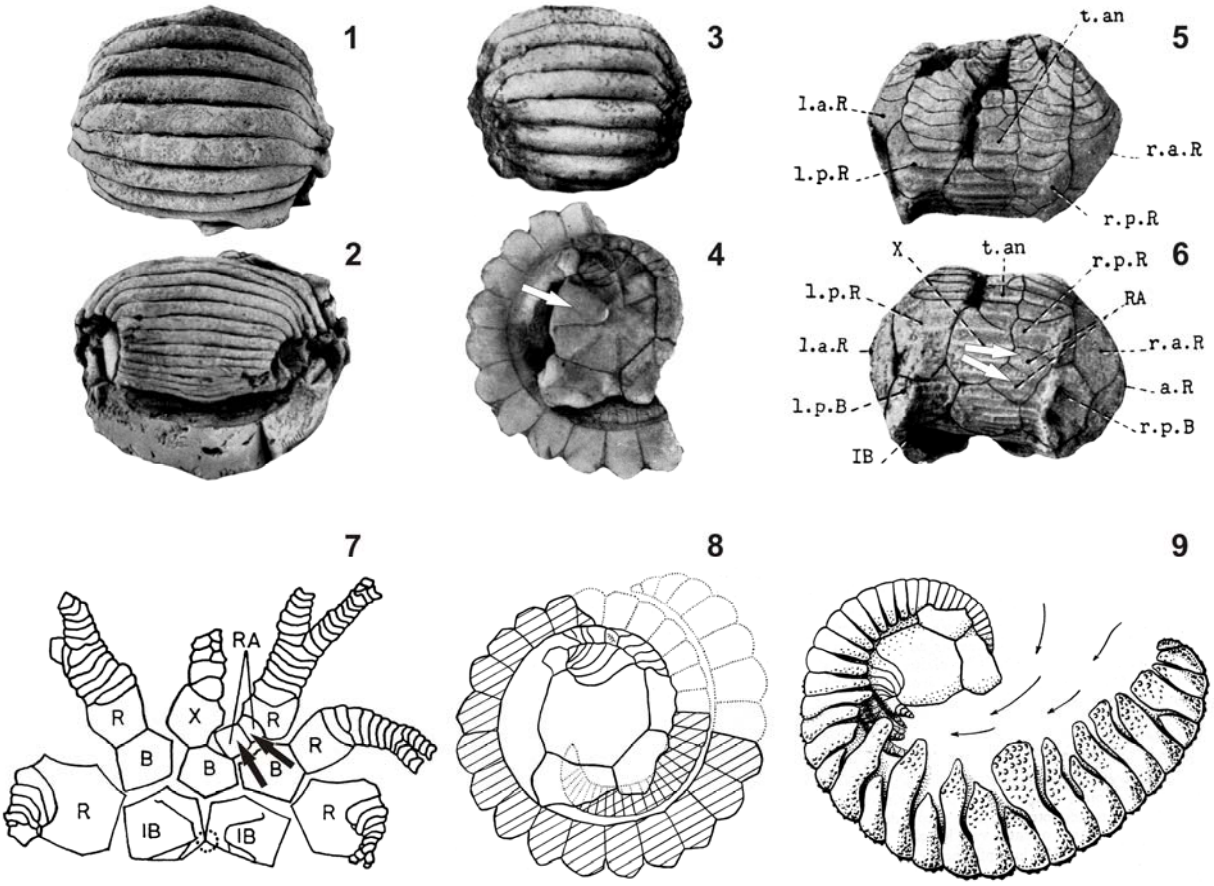


FIGURE 3.4.3—First illustration of the actual plate diagram and definition of genus *Ammonicrinus* as lecanocrinidid Flexibilia by UBAGHS (1952) [not to scale]. ***1-2***, *A. doliiformis* (no. SMF-XXIII-165a), view of coiled mesistele (***1***) and of exposed proxistele (***2***) [taken from 1952, pl. 3, figs. 1, 3]; ***3-9***, Anomalous crown of "*A. wanneri*" (= holotype of *A. jankei* n. sp., no. SMF-XXIII-167a) coiled by the mesistele; view of the coiled mesistele (***3***) [1952, pl. 1, fig. 3]; partly excavated crown, showing radiating ridges on radials and one slightly lobe-like enlarged appendage (***4***) that possibly could support the lateral water respectively faecal-ejection (arrow) [1952, pl. 1, fig. 4]; excavated crown, the second "radianal plate" respectively "supplementary plate" (see arrows) is based on an anomaly (***5-6***) [1952, pl. 2, figs. 3, 2]; plate diagram (***7***), showing the two anomalous plates (arrows) [slightly modified after 1952, p. 205, fig. 1]; schematic drawing of the coiled specimen (***8***) and of the assumed living feeding position (***9***) [1952, p. 110, fig. 2; p. 223, fig. 5].

Combining the concepts of UBAGHS with the most complete specimens from WOLBURG, PIOTROWSKI (1977, p. 208, fig. 2; p. 209, fig. 3) provides the best interpretation of the mode of life of *Ammonicrinus* (Figs. 3.4.4.1-2). He (1977, p. 208) assumed that the high specialisation of the stem provided a firm support in soft-bottom sediments and protection from water borne sediments. PIOTROWSKI also assumed that the crown was screened by an external cover so that the food could be supplied into it only by currents parallel to the bottom. "*The water carrying food was introduced into the central part of the stem through a furrow formed by distal parts of external cover and the outflow proceeded through umbilical openings. During feeding the arms were presumably resting on stem plates. The contortion of crown in relation to symmetry plane of stem could facilitate water circulation inside the external cover as water current was directed by contorted crown to umbilical opening*" (1977, p. 209). PIOTROWSKI compared *Ammonicrinus* with the mode of life of other crinoids (e.g. calceocrinids MEEK & WORTHEN, 1869), which were adapted to filter food out of a horizontal bottom-water currents (1977, p. 209).

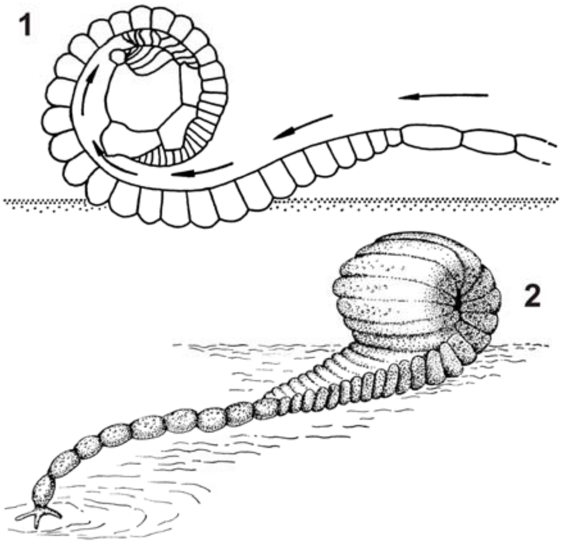


FIGURE 3.4.4—Schematic illustrations of *Ammonicrinus sulcatus* after PIOTROWSKI (1977) [not to scale]. ***1***, Lateral cross section through the feeding crinoid (taken from 1977, p. 209, fig. 3); ***2***, former reconstruction of life time position (1977, p. 208, fig. 2).

Carbonate microfacies analysis within several *Ammonicrinus*-localities of the Eifel (especially from locality 6) and the hydrodynamic interpretation of fragile but perfectly preserved bryozoans (see ERNST 2008), lead to the recognition of nearly still water close to the soft-bottoms, yielding a lack of the horizontal water current, assumed by PIOTROWSKI. Based on this recognition, the exigencies of a feeding method that supplemented PIOTROWSKI's interpretation in detail, is proposed; a method that presupposes a self produced water flow.

3.4.3 PROPOSED LIFE INTERPRETATION – *AMMONICRINUS* AS A SPINED SOFT-BOTTOM DWELLER FEEDING THROUGH ACTIVE "LIGAMENT PUMPING"

The morphology of *Ammonicrinus* suggests a reclined life position displaying certain affinities to the disparid calceocrinids (see above). The calceocrinids combined a stem that lay on the sea-floor with an attachment disc, but had a free, non-hidden crown. The enrolled *Ammonicrinus* preferred settling within muddy habitats, a fact that must have made it particularly vulnerable to burial and clogging of the ambulacra by turbidity. As assumed for calceocrinids, *Ammonicrinus* could have disengaged the crown from accumulated sediment by opening it, but because of enrollment, the cleaning-mechanism needed to be effectively modified.

The associated, diverse and abundant crinoid fauna displays well-developed tiering. *Ammonicrinus* escaped from food competition by settling and feeding directly on the soft-bottom. This life mode required a highly modified anatomical design compared to "normal" crinoids; the most important ecological constraint were:

1. The direct contact with partly predaceous faunal elements of the vagile benthos.

2. Heightened tolerance against infiltration of turbidity – or an effective mechanism of actively out-pumping contaminants.

3. Nutriment filtering within still water, which possibly requires a self-generated water flow.

New data, based on the first discoveries of completely preserved ammonicrinid specimens from the uppermost Eifelian (Middle Devonian) of the Eifel (Rhenish Massif), including numerous crowns, enrolled in the proximal parts of the stem, demonstrate not only the variability in the proportions, but also different ossicule sculpturing. The recently discovered and obliquely preserved ammonicrinids from two localities within the Hillesheim and Prüm synclines (localities 3, 6) provide the first complete skeletons with preserved movable spines (Figs. 3.4.5, 3.4.7.1-2, 3.4.8; Pl. 3.4.1, Figs. 9-10, 14). These skeletal elements were attached to the ammonicrinid holdfast and stem via echinoid-like spine-tubercles, as have been observed on several Palaeozoic crinoids such as *Arthroacantha* WILLIAMS, 1883. Several complete ammonicrinid skeletons, embedded in fine homogenous argillaceous limestones, were prepared using fine micro sand-streaming methods. Uncoiled individuals and numerous enrolled ammonicrinids were observed with preserved spines. A protective function against predatory influences like platyceratid gastropods, arthropods or the epizonal encrustation of bryozoans, tabulate corals, chaetitids or microconchids (see Fig. 3.4.10) is possible.

Also the body-stabilisation in an effective living position is a conceivable morphological function of this newly discovered morphological feature. Concordant to this theory, the longest spines are laterally positioned, directed toward the soft-bottom and could stabilise the individual in a lateral direction or, also, could help keep the body from sinking into the soft substrate.

The most studied and completely preserved ammonicrinids from the German Devonian were found essentially in the living position. The total skeletal surface is covered by spine-tubercles, previously considered as tubercled plate sculpturing (e.g. SPRINGER 1926b; PIOTROWSKI 1977). Whereupon the holdfast only bears few spines, an increasing density of spines is directly linked to the importance of safeguarding crinoid elements. Therefore, the highest density of spines is focused at the enclosed spheroidal crown, hidden in the enrolled stem. The involute proximal columnals also developed spine-tubercles, obviously losing the spines throughout the ontogenetic stages. The spines are clearly movable because several spined individuals were found with completely preserved mesisteles (e.g. Pl. 3.4.1, Fig. 1), indicating an extremely flexible connection between tubercles and spines. In all directions the spines are extended toward the exterior, while the laterally positioned spines are the longest and, in contrast, the elements in the centre of the columnals are the finest and shortest of the individual.

It is important to note that the development of these spines is directly controlled by the ecological environment and combined with a herein recognised intraspecific variability of the ammonicrinid column (length and number of the barrel-shaped columnals of the dististele, with or without additional LCEE and an attachment disc or various formed radiating cirri). Therefore, the development of spines is not solely usable for taxonomical differentiation between the species, because it is recognised in several ammonicrinids, e.g. in *A. sulcatus* and *A. leunissi* n. sp.[5] from the Eifel (localities 1-3, 6) as well as in *A. doliiformis* from the Eifel, the Bergisches Land and the Sauerland (localities 5, 10-11). Even within one species, the number of spines differs. Furthermore, the feature either composes the only, evenly distributed “ossicular adornment”, (compate to Figs. 3.4.9.5-6) or the spine-tubercles are unequally spaced on additional, “real plate sculpturings”, like unshaped nodes (compate to Figs. 3.4.9.1-4).

---

[5] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

Two interpretations derive from the observation of the new skeletal feature of the spined endoskeleton:

1. Exterior protection: Distribution of the spines on the skeleton indicates that attacks from vagile benthic predators had to be more effectively repelled than those from swimming predators. This is affirmed by the macrofossil record, explicitly documented by numerous discoveries of platyceratid gastropod conchs, whereas remains of nectic predators (placoderms, cephalopods) are rarely found. Moreover, in-vivo encrustation by epizoans was effectively prevented. In contrast, the ossicles of associated stalked crinoids are variously bored and pre- and postmortem infested by diverse organisms.

2. Interior protection: The spinose pattern also efficiently protected the crown, which could be exposed by partial opening of the enrolled proximal stem. Fine spines served as a skeletal micromesh. Nutrient particles transported with a water flow could pass – either passively infiltrated or actively absorbed, whereas the penetration of potential predators or larger sediment particles was prevented from entering the vital crown elements.

As a soft-bottom dweller within non-turbulent muddy habitats, two further aspects need to be interpreted:

1. The heightened tolerance against sedimentary material, respectively the circumvention of infiltering non-nutriment material.

2. The question of the feeding mode under still water conditions.

Except of the oldest known ammonicrinid, *A. kredreoletensis*, which has a laterally uncovered cup implying a non-enrolled feeding position in the current (Fig. 3.4.6), the younger ammonicrinids (*A. doliiformis*, *A. jankei* n. sp.[6], *A. leunissi* n. sp.[7], *A. sulcatus* and *A. wanneri*) presumably lived enrolled on the muddy sea-floor. Therefore, the infiltration of sedimentary material had to be particularly antagonistic. Active, slow out-pumping of contaminants, possibly in conjunction with excretory products is assumed, based on the new anatomical observations. Vice versa, also the ingestion of nutrient particles within still water

---

[6] = *A. jankei* BOHATÝ, submitted *sensu* ICZN

[7] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

calls for the generation of a biologically generated water flow and suggests the theory of an active, slow pumping mechanism. Alternating water pressure was generated in the interior of the enrolled proximal stem by rhythmic, bellow-like partial opening and closing of the base of the central mass. Active suction during opening created an ingesting water flow. It was funnelled in the "canal", formed by the unspined interior of the proximal columnals, whose U-shaped flanks were constructed by the LCEE. Active ejection during closure resulted from overpressure. To minimise faecal recycling, the water ejection may have occurred laterally, feasibly at both lateral centres, which have "openings" ("umbilical openings" sensu PIOTROWSKI 1977, p. 209) [Fig. 3.4.5].

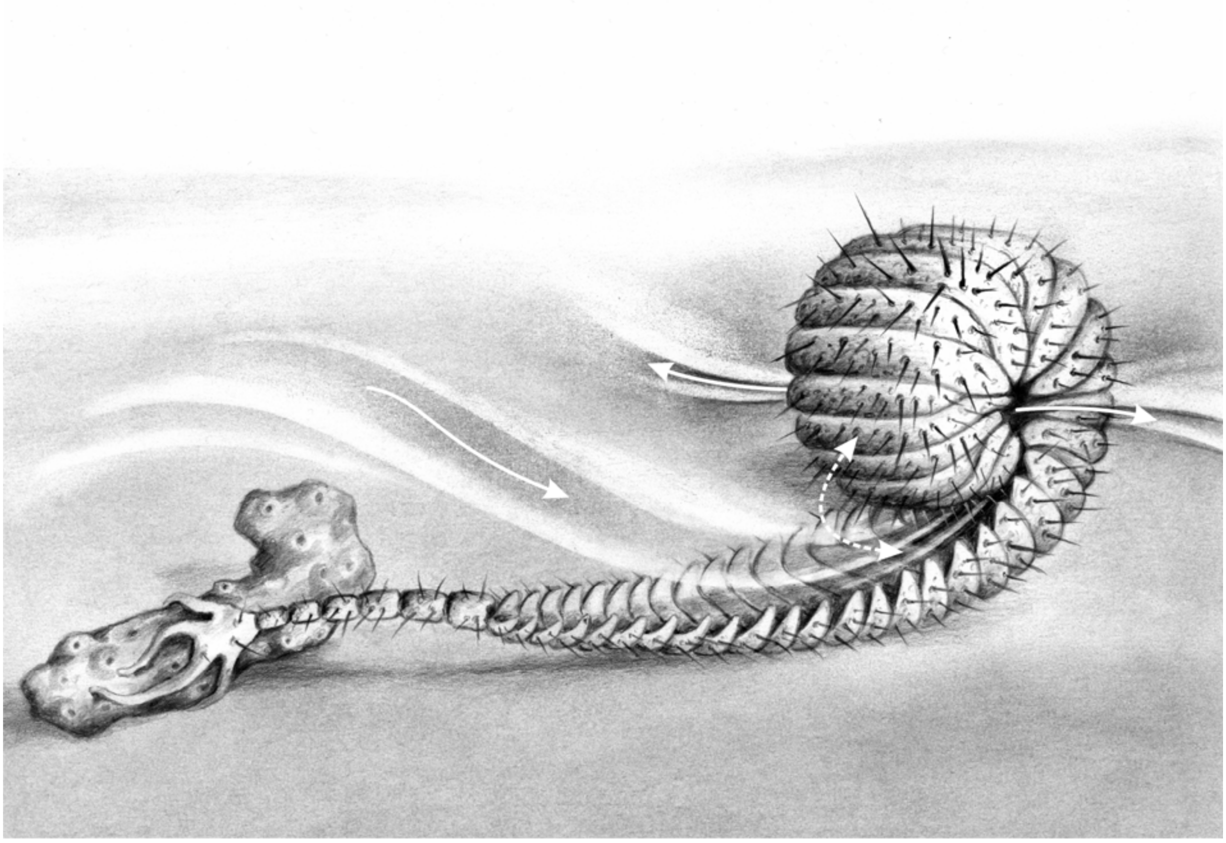


FIGURE 3.4.5—Reconstruction of a feeding "encased runner-type" of *A. leunissi* n. sp. (not to scale), attached to a tabulate coral (model); the spined specimen dwelled enrolled on the muddy sea-floor; alternating water pressure was obviously generated in the interior of the enrolled proximal stem globe by non-muscular, MCT-controlled, rhythmic, bellow-like partial opening and closing of the oblate sphere at its bottom (dashed arrow); active suction during opening created an ingesting water flow (see arrow on the left), which was funnelled in a "canal", formed by the unspined interior of the columnals of the mesistele, whose U-shaped LCEE additionally formed a protection against immersive sediment; active ejection during closure resulted from overpressure; to minimise faecal recycling, the water ejection occurred supposably laterally, feasibly at both lateral centres, which accordingly show "openings" (see arrows on the right).

The key to the non-muscular pumping activity of the middle and proximal stem could possibly be delivered by the development of effective mutable connective tissues (MCT) at the articulations of the ossicles. However, this had to be done slowly (pers. information, W. I. AUSICH). MCT (see WILKIE 1984) has the special ability to convert from stiff to soft in an instant, under ionic balance control. It is well recognised within modern crinoid arms and cirri (BIRENHEIDE & MOTOKAWA 1994; BIRENHEIDE 1995; 1996; BIRENHEIDE et al. 2000; MOTOKAWA et al. 2004) and was also reported within crinoid stalks (WILKIE et al. 1993; 2004). Recently, HOLLIS & AUSICH (2008) described unusual column postures suggesting a highly flexibility of the stem of the Middle Devonian to Lower Mississippian crinoid genus *Gilbertsocrinus* PHILLIPS, 1836. The authors expected passive locking and unlocking of the mutable collagenous tissue and discussed the possibility of a "slow, weak contractile ability of the *Gilbertsocrinus* stalk" (2008, p. 138).

3.4.4. THE SUBSTRATE-CONTROLLED MORPHOLOGICAL VARIABILITY OF THE DISTISTELE (DISTAL COLUMN AND HOLDFAST)

The best and nearly completely preserved *Ammonicrinus*-specimens from the Rhenish Massif came from the Eifel synclines (localities 3, 6). These specimens and additional ammonicrinids from the Sauerland (locality 11; see WOLBURG 1938a and Figs. 3.4.2.1-6 of the present work) and the Bergisches Land (locality 10) have substrate-controlled morphological variability of the dististele (distal column and holdfast). Together with the material from locality 12, three "morphological groups" are recognised:

1. The "exposed roller-type". These specimens predominantly have the general skeletal morphology, as illustrated in Fig. 3.4.6. This form is herein classified as an exposed roller-type and is recognised only in the oldest studied ammonicrinid, *A. kredreoletensis*. This type is characterised by a laterally unprotected crown that possibly implies feeding in the current. The new recovered material indicates that the stem of *A. kredreoletensis* tapers as it approaches the crown, not in quite as many columnals perhaps, but similar to that of camptocrinids, and their crown elevated up from the substrate. Their elevation is not much but puts them above the sediment and into a possible low velocity current for feeding (pers. information, G. D. WEBSTER). Likewise, own unpublished myelodactylids from the Eifelian strata of the Eifel Synclines show a similar mode of life and are also attached to hard objects, like brachiopods (study in progress).

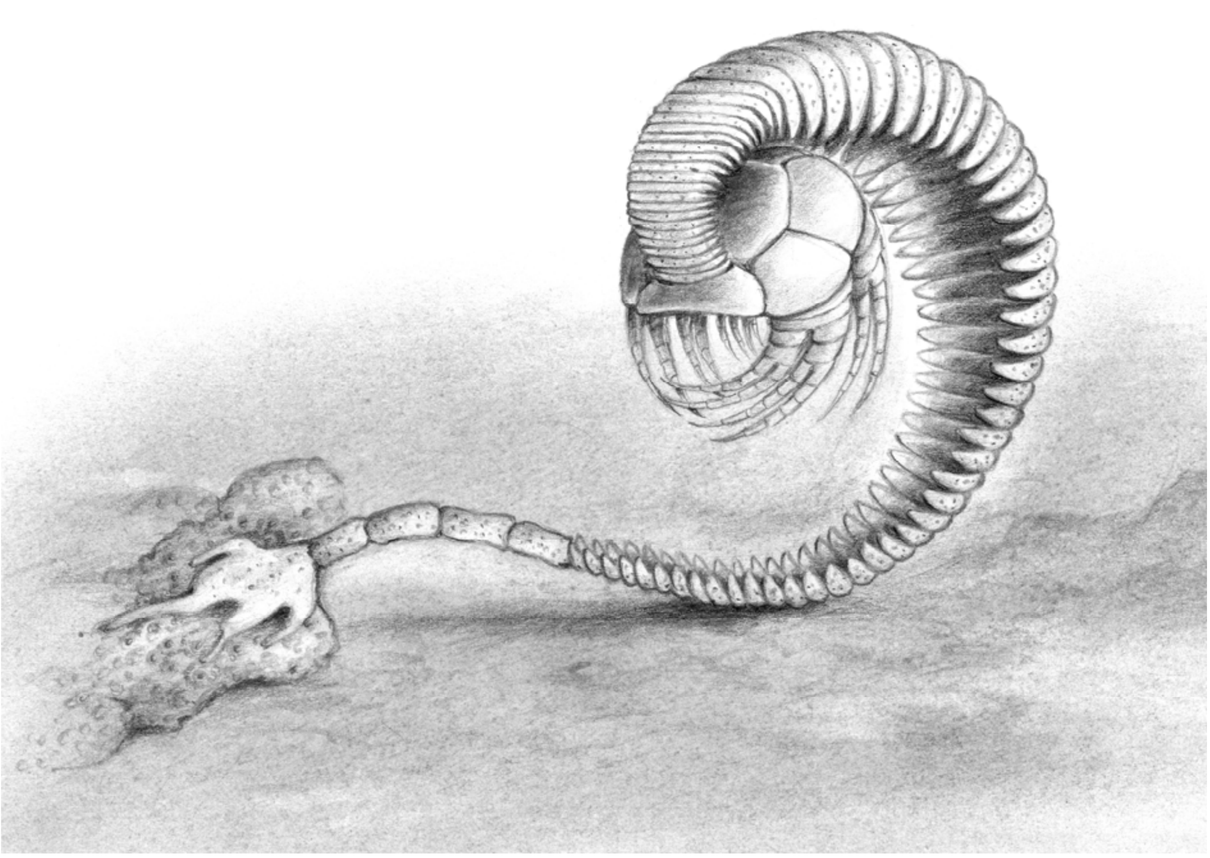


FIGURE 3.4.6—Reconstruction of a feeding "exposed runner-type" of *A. kredreoletensis* (not to scale), attached to a tabulate coral (model). The crown is laterally not covered by the LCEE and implies feeding in the current. The stem tapers as it approaches the crown, which was obviously elevated up from the substrate into a low velocity current for feeding.

2. The "encased roller-type". These specimens predominantly show the general skeletal morphology, as illustrated in Figs. 3.4.5, 3.4.7.1. This standard form is herein classified as encased roller-type and is recognised in all known ammonicrinids, except of *A. kredreoletensis*. The specimens are more or less enrolled; the LCEE of the proxistele and mesistele are followed by several barrel-like columnals of the dististele. The proxi- and mesistele skeleton laid on the soft-bottom, whereas the holdfast attached to hard objects, such as brachiopod valves (Figs. 3.4.2.2, 3.4.2.5), tabulate corals (Figs. 3.4.5, 3.4.7.1-2) or bryozoans (Pl. 3.4.1, Figs. 12-13; Pl. 3.4.2, Fig. 13). The hard object of attachment affects either the development of an attachment disc (Figs. 3.4.2.2, 3.4.2.5) or variously formed radiating cirri (see Figs. 3.4.5, 3.4.7.1-2; Pl. 3.4.1, Fig. 12). Both modes of attachment were observed in one species.

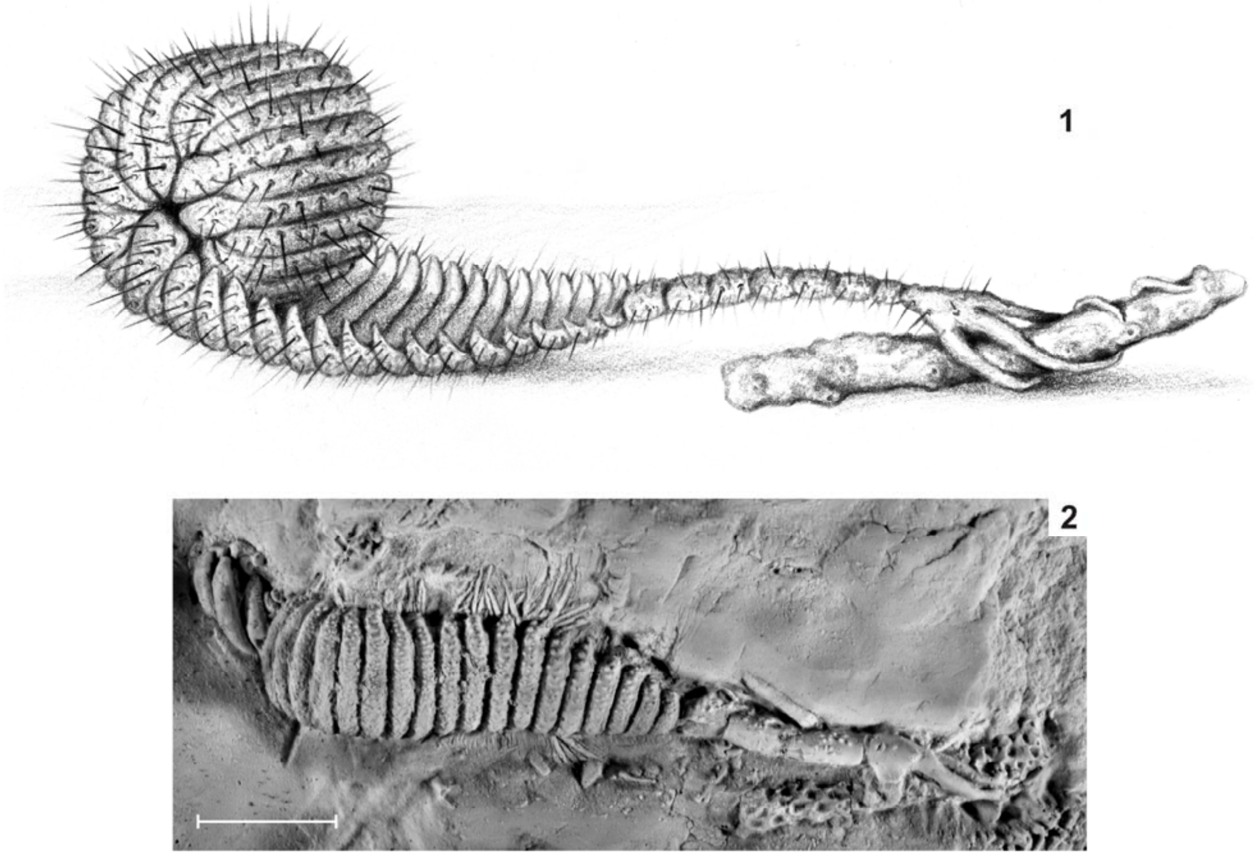


FIGURE 3.4.7—1, Reconstruction of an "encased runner-type" of *A. leunissi* n. sp. (not to scale), attached to a tabulate coral (model); the spined specimen dwelled enrolled on the muddy sea-floor; ***2***, the original (no. GIK-2102) from locality 6, showing slightly compressed proximal mesistele (scale bar = 1 cm).

3. The "settler-type". In addition to the predominant roller-types, rare discoveries of ammonicrinids with a reduced column length and columnal number of the dististele require further classification. They were mainly attached to empty brachiopod valves that laid on a soft-bottom. These ammonicrinids did not live partly enrolled on the sea-floor with the column, as recognised in the roller-types. The proximal part of the crinoid larval stage settled on top of the hard object (Fig. 3.4.8; Pl. 3.4.1, Fig. 14). This form is herein classified as the rare settler-type and is recognised in *A. leunissi* n. sp.[8], *A. sulcatus* and *A. wanneri*. Elevated above the ground, this mode of life potentially allowed the animal to profit from a low water flow above the nearly still water condition at the bottom but below the "normal" tiering levels into which associated, "regular" crinoid groups [e.g. *Abbreviatocrinites inflatus* (SCHULTZE, 1866); *A. sampelayoi* (ALMELA & REVILLA, 1950); *Arthroacantha* sp.] lifted their crowns for feeding. A question is why did not every

---

[8] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

Ammonicrinus profit from this (1) savings of skeletal material and (2) hydrodynamically advantageous feeding position above the muddy sea-floor. Perhaps, this is do to the instability of the soft-bottom and the continuous input of fine sediment. Most brachiopod valves partially sink in or, respectively, became buried postmortem by sediment.

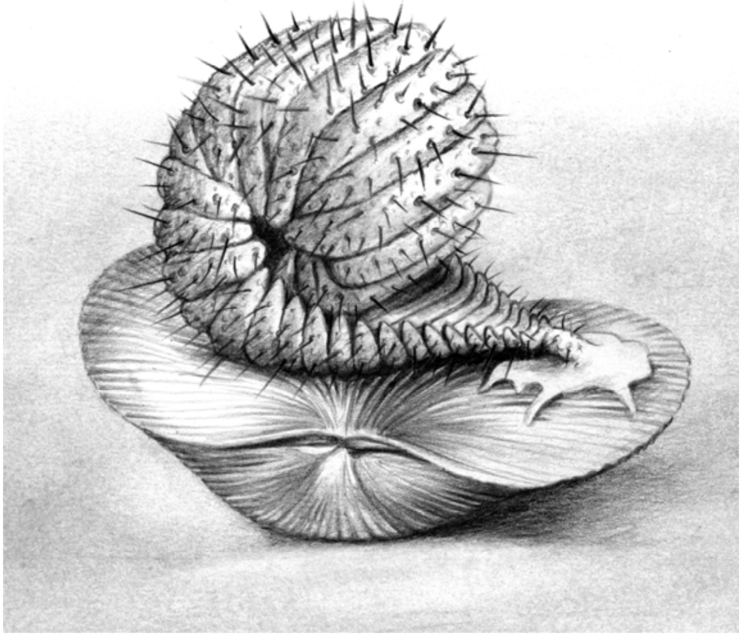


FIGURE 3.4.8—Reconstruction of a spined "settler-type" of *A. leunissi* n. sp. (not to scale), attached on a brachiopod brachial valve (*Schizophoria* sp.); the original (no. GIK-2103) from locality 6 is figured in Pl. 3.4.1, Fig. 14.

3.4.5 INTRA- VS. INTERSPECIFIC VARIABILITY OF THE PROXIMAL-MOST COLUMNALS OF THE DISTISTELE

By studying the connection of the barrel-shaped columnals of the dististele and the mesistele, an interspecific morphological difference between *A. doliiformis* and other species (*A. sulcatus*, *A. wanneri* and *A. leunissi* n. sp.[9]) is recognised. *A. doliiformis*, a form that is only known as a roller-type, developed an uniformly constructed connection in the form of an idealised triangular-shaped, wide columnal-plate between the columnals of the mesistele, with a LCEE, and the barrel-like columnals of the dististele (Figs. 3.4.2.1, 3.4.2.3). In this connection, this species obviously has to be characterised as a relatively constant form, and it developed the most voluminous skeleton of all known ammonicrinids. The wide, triangular-shaped columnal-plate can be used for interspecific differentiation between *A. doliiformis* and the other species.

---

[9] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

In contrast, *A. sulcatus*, *A. wanneri* and *A. leunissi* n. sp.[10] had variously developed connections of the dististele and the mesistele. The distal-most columnal of the mesistele may exhibit an abrupt connection between those ossicles, distinguished by LCEE and the barrel-shaped columnals of the dististele by developing an elongated triangular-shaped ossicle (rare) or a single barrel-like appendage toward the dististele (Figs. 3.4.9.8-10). However, this barrel-like appendage can also be duplicated and directed both, to the dististele and the mesistele (Figs. 3.4.9.11-12). Also a sequence of intermediate shaped ossicles is possible.

The development of all morphologies obviously depends on the hardground on which the crinoids were attached. This intraspecific variability is recognised in *A. sulcatus*, *A. wanneri* and *A. leunissi* n. sp.[11] – all species with the ability to exhibit the encased roller- or the settler-type. That recognition affected PIOTROWSKI's interspecific separation of "*A. kongieli*" and *A. sulcatus*, which is mainly based on the development of either abrupt connection between columnals, distinguished by LCEE and barrel-like columnals or barrel-like plates with extensions (1977, p. 214, tab. 3). Therefore, and because of the recognised intraspecific variability of the ossicular sculpturing, "*A. kongieli*" is declared a subjective junior synonym of *A. sulcatus*.

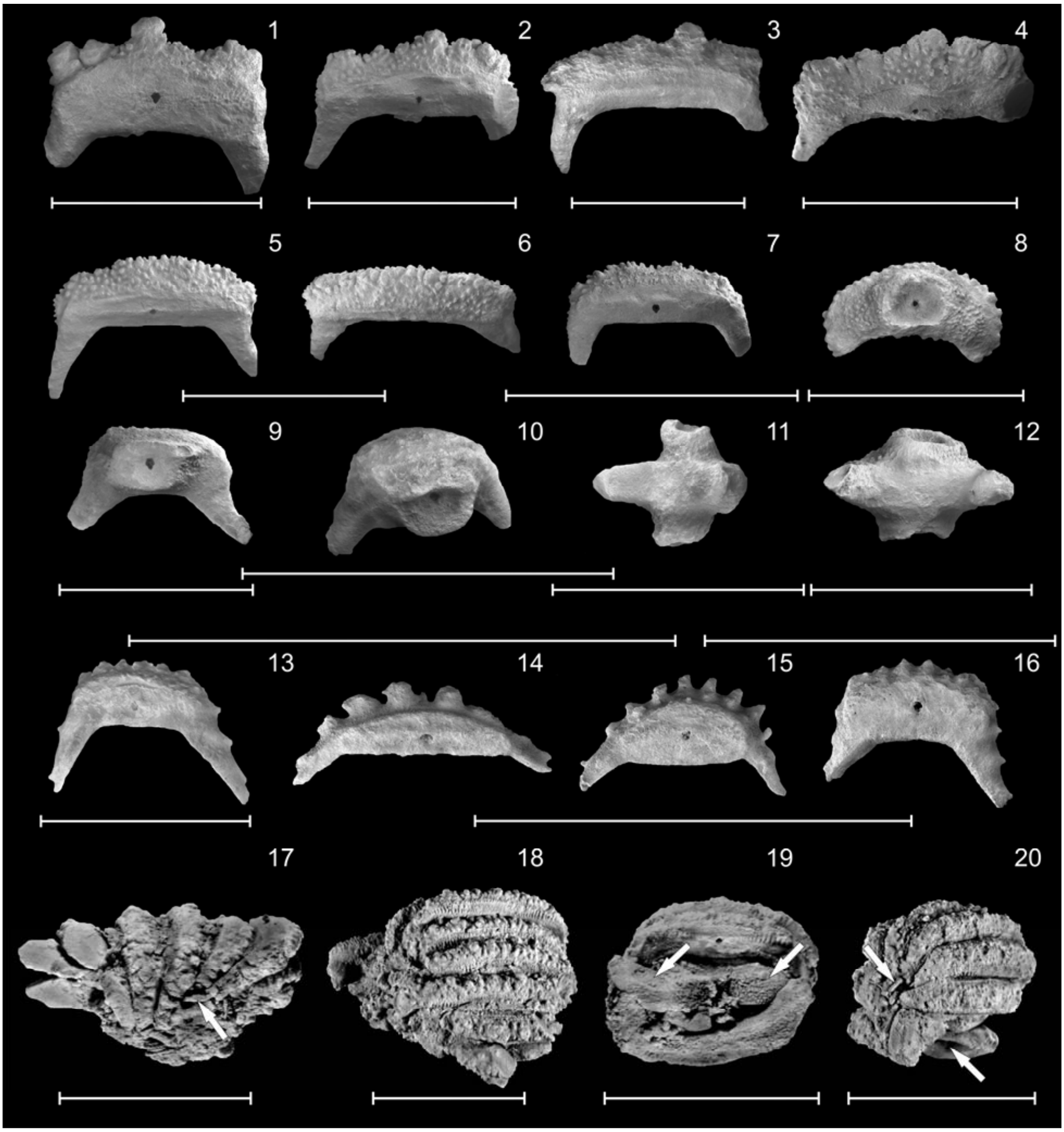
FIGURE 3.4.9 (see p. 157)—Ammonicrinus sulcatus from locality 1 (***1-8***, ***10-20***) and 2 (***9***). ***1-4***, Facet views of nos. GIK-2104-2107, showing nodular tubercles and spine-tubercles on exterior flanks of the columnals of the mesistele; ***5-6***, facet view and view of the exterior flank of a specimen (no. GIK-2108), showing tubercles and spine-tubercles on exterior flank of the columnal of the mesistele; ***7***, facet view of a specimen (no. GIK-2109), showing tubercles and spine-tubercles on exterior flank of the columnal of the mesistele; ***8***, facet view of a strongly sculptured columnal (no. GIK-2110) of the distal-most mesistele, showing connection to the dististele; ***9***, facet view of a columnal of the distal-most mesistele (no. GIK-2111), showing long LCEE and connection to the dististele; ***10***, facet view of a columnal of the distal-most mesistele (no. GIK-2112), showing relatively long LCEE and connection to the dististele; ***11***, interior view of a distal-most, barrel-like columnal of the mesistele (no. GIK-2113) with LCEE; ***12***, interior view of a distal-most, barrel-like columnal of the mesistele (no. GIK-2114), with partly preserved LCEE; ***13***, facet view of a juvenile distal columnal of the mesistele (no. GIK-2115) with nodular tubercles on exterior flank and on LCEE; ***14-15***, juvenile columnals of the proximal mesistele (nos. GIK-2116 and -2117) in facet view, showing well developed nodes on exterior flanks; ***16***, facet view of a juvenile distal columnal of the mesistele (no. GIK-2118) with nodular tubercles on exterior flank and on LCEE; ***17-18***, lateral view (***17***) and view of the exterior flank (***18***) of the partly preserved mesistele (no. GIK-2119); the specimen shows nodular tubercles, spine-tubercles and a few partly preserved spines (arrow); ***19-20***, facet view (***19***) and lateral view (***20***) of a cracked, coiled mesistele (no. GIK-2120), showing several tuberculated and concave ossicles of the cup (arrows). [Scale bars = 1 cm]

---

[10] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

[11] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

FIGURE 3.4.9 (legend p. 156)



3.4.6 POSTMORTEM EPIZONAL ENCRUSTING

Especially the articulated or, typically, isolated ossicles from the localities 1-2 have diverse, postmortem epifaunal encrustation, which infested nearly every hard object lying on – or settling within the soft or moderately stabilised, muddy firmground. The following groups are identified:

1. Brachiopoda. The *A. doliiformis* original of KRAUSE (1927; refigured in Figs. 3.4.1.7-8 and Pl. 3.4.2, Figs. 15-18 of the present work) was infested by a (?)craniid brachiopod. The specimen settled on the exterior side of the former movable mesistele, on top of several spine-tubercles with lost spines. This is clear evidence of an immediate postmortem encrusting.

2. Bryozoa. The following bryozoans were identified on skeletal remains of *A. sulcatus*:

2.1 Trepostomata. One pluricolumnal and one isolated columnal of the mesistele (no. GIK-2147, Fig. 3.4.10.1 and no. GIK-2149, Fig. 3.4.10.3) were postmortem encrusted by the trepostome bryozoan *Leptotrypella* VINASSA & REGNY, 1921. An additional pluricolumnal of the mesistele (no. GIK-2150, Fig. 3.4.10.4) was also postmortem encrusted by the trepostomate bryozoan, *Eostenopora* DUNCAN, 1939. Trepostome bryozoans recently were observed attached to the crown ossicles of the cladid crinoid family Cupressocrinitidae RÖMER, 1854 (compare to BOHATÝ 2009). One brachial of a completely preserved *Abbreviatocrinites nodosus* crown SANDBERGER & SANDBERGER, 1856 (2009, fig. 2.8), one cup of an also entire *A. schreueri* crown BOHATÝ, 2006b (2009, fig. 11.4) and one theca of *Procupressocrinus gracilis* (GOLDFUSS, 1831) [2009, fig. 11.6] were encrusted postmortem by (?)*Eostenopora* sp. The boring trace of an affected arm of *Robustocrinites cataphractus* BOHATÝ, 2009 was also populated by (?)*Eostenopora* sp. (2009, figs. 6.3, 7.2).

2.2 Cystoporata. The erect pluricolumnal of the distal mesistele (no. GIK-2148, Fig. 3.4.10.2) was encrusted by the cystoporate bryozoan *Eridopora* ULRICH, 1882. As strong evidence for a postmortem encrusting, the bryozoan encrusted the external and internal region of the ossicles. Another cystoporate bryozoan, *Cyclotrypa* ULRICH, 1896, is recognised on one columnal (no. GIK-2152, Fig. 3.4.10.6) and one pluricolumnal (no. GIK-2153, Fig. 3.4.10.7) of the mesistele.

2.3 Fenestrata. One isolated mesistele columnal (no. GIK-2155, Fig. 3.4.10.9) was encrusted postmortem by a holdfast of an undetermined fenestrate bryozoan. BOHATÝ (2009, fig. 11.1) reported stems of *Abbreviatocrinites geminatus* BOHATÝ, 2005a and *Procupressocrinus gracilis*, which were encrusted by fenestrate bryozoans. The length of the overgrown pluricolumnals, as well as some observed embedding patterns of bryozoans located underneath the attached stem, allows the presumption of a premortem settlement (compare to BOHATÝ, 2005a, fig. 3B). In contrast, some shorter stem fragments or other disarticulated cupressocrinid ossicles (see 2009, fig. 11.2) were usually encrusted postmortem. This assumption is based on the entire enclosure of some skeletal elements. Similarly, holdfasts of probable rhomboporid bryozoans attached to the columnals of *Schyschcatocrinus creber* DUBATOLOVA, 1975, as reported by GŁUCHOWSKI (2005, figs. 3A-B). GŁUCHOWSKI indicated that the bryozoans lived attached to the fragmented dead stems that lay horizontally on the sea-floor. Strong evidence for the settlement of a living stem of *Cupressocrinites hieroglyphicus* (SCHULTZE, 1866) is given by BOHATÝ (2009, figs. 11.16-18). The example is encrusted by the holdfast of a fenestrate bryozoan (*Cyclopelta* sp.) that grows all around the column without contact to the crenularium. The reticulate bryozoan colony surrounded the stem, whereas the dissepiments built concentric rings characteristic for this genus.

3. Microconchida. One isolated columnal of the mesistele of *A. sulcatus* (no. GIK-2155, Fig. 3.4.10.8) was encrusted by two microconchid-valves, which settled postmortem at the facet region of the ossicle, below and above the crenularium. Microconchids with unstructured or sculptured valves frequently encrusted the ossicles of cupressocrinids from the Middle Devonian of the Eifel, as reported by BOHATÝ (2005a; 2006b; 2009). It is remarkable that larger individuals are rare and isolated (compare to 2006b, pl. 5, fig. 8), whereas numerous smaller microconchids encrusted the crinoids (see 2009, figs. 2.6, 11.7, 11.8). As assumed for *Ammonicrinus*, the microconchid colonisation of the cupressocrinid remains occurred immediately postmortem. The single-species encrusting of microconchids on the columnals of *Tantalocrinus scutellus* LE MENN, 1985 and *Schyschcatocrinus creber*, represent additional settlement examples (GŁUCHOWSKI 2005, p. 323, figs. 5I-L).

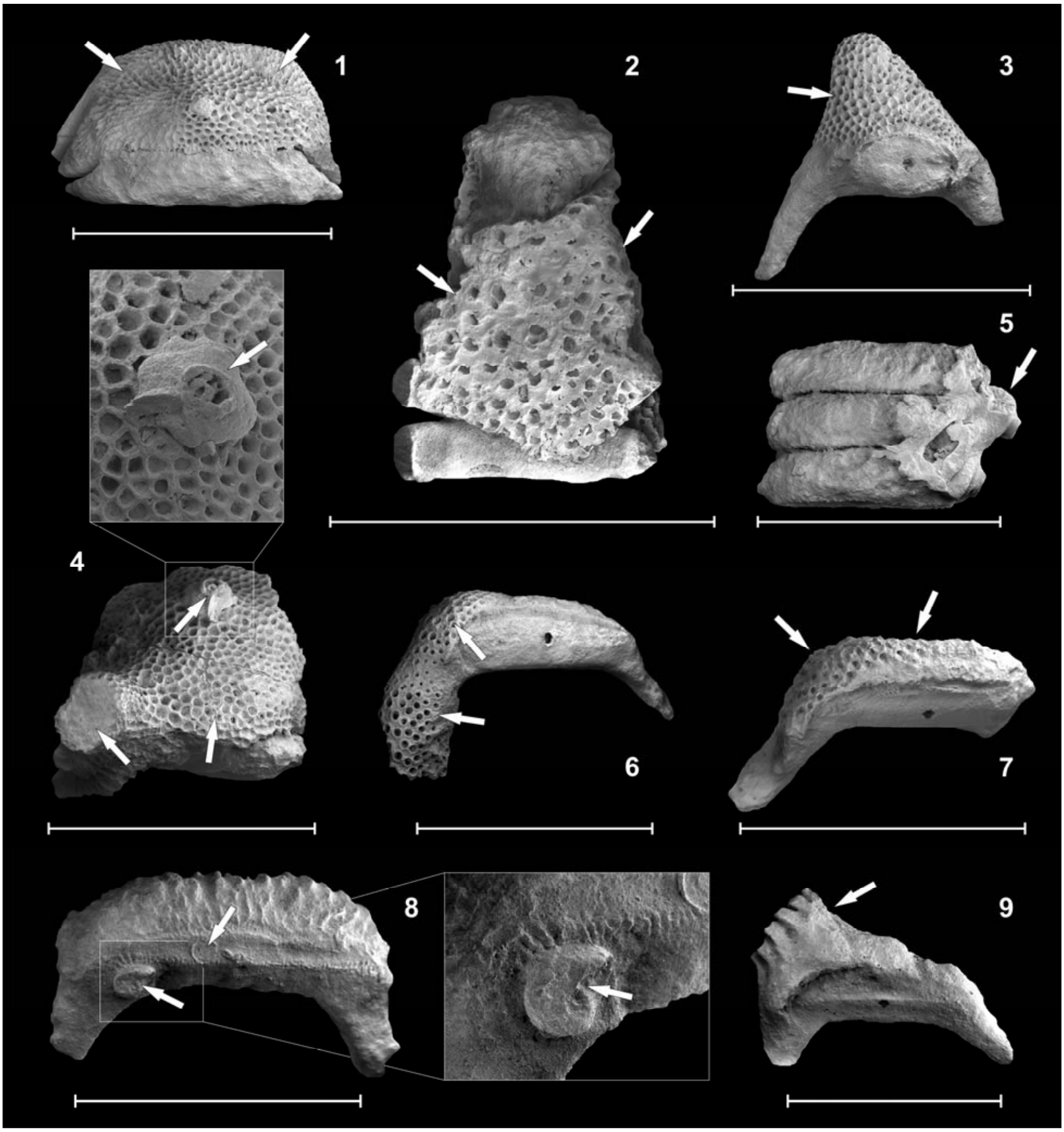
4. Crinoidea. The pluricolumnal of *A. sulcatus* (no. GIK-2151, Fig. 3.4.10.5) was encrusted postmortem by a crinoid holdfast, which settled on several tubercles with lost spines. Another *A. sulcatus* pluricolumnal (no. GIK-2150, Fig. 3.4.10.4) was encrusted postmortem by a trepostomate bryozoan, that was then infested by a small crinoid attachment disc. GŁUCHOWSKI (2005, p. 322) documented the postmortem encrusting of several small crinoid holdfasts attached to Upper Eifelian crinoid columnals. Various

attachments of crinoid juveniles to living or dead adults are known from the Silurian to the Mississippian (see MEYER & AUSICH 1983). Coiling stems, modified discoid holdfasts on the columns of crinoid hosts, as well as dendritic holdfasts distributed on all sides of the column, were reported from Silurian strata by FRANZÉN (1977) and PETERS & BORK (1998). Furthermore, BOHATÝ (2009) reported crinoid holdfasts attached to the crown ossicles of different cupressocrinids. One cup of *Abbreviatocrinites abbreviatus abbreviatus* (GOLDFUSS, 1839) [BOHATÝ, 2009, fig. 11.9] and one isolated radial and arm plate of *A. geminatus* were encrusted by the holdfasts of other cladid crinoids (?*Procupressocrinus gracilis*).

5. Chaetitida. One weathered pluricolumnal of *A. sulcatus* was encrusted by Chaetitida indet. (unfigured material). The encrusting occurred postmortem, because the chaetitid settled on the external and internal regions of the ossicles. BOHATÝ (2009) mentioned *A. a. abbreviatus* cups, which were completely encrusted by indeterminable stromatoporoids. These encrustings were settled again by chaetetids.

FIGURE 3.4.10 (see p. 161)—Postmortem epizoan encrusting on disarticulated columnals of *Ammonicrinus sulcatus* from locality 1 (***1-7***) and 2 (***8-9***). ***1***, View of external flanks of a pluricolumnal of the mesistele (no. GIK-2147), encrusted by a trepostomate bryozoan (?*Leptrotrypella* sp.) [arrows]; ***2***, internal view of a pluricolumnal of the distal-most mesistele (no. GIK-2148), encrusted by a cystoporate bryozoan (?*Eridopora* sp.) [arrows]; ***3***, facet view of an isolated, distal-most columnal of the mesistele (no. GIK-2149), encrusted by a trepostomate bryozoan (?*Leptrotrypella* sp.) [arrows]; ***4***, view of external flanks of a pluricolumnal of the mesistele (no. GIK-2150), encrusted by a trepostomate bryozoan (?*Eostenopora* sp.) [arrows]; the bryozoan is infested by a crinoid attachment disc (see arrows in detail view); ***5***, view of external flanks of a pluricolumnal of the mesistele (no. GIK-2151), encrusted by a crinoid holdfast (arrow); ***6***, facet view of an isolated columnal of the mesistele (no. GIK-2152), encrusted by a cystoporate bryozoan (?*Cyclotrypa* sp.) [arrows]; ***7***, facet view of a pluricolumnal of the mesistele (no. GIK-2153), encrusted by a cystoporate bryozoan (?*Cyclotrypa* sp.) [arrows]; ***8***, facet view of an isolated columnal of the mesistele (no. GIK-2154), encrusted by microconchid valves (see arrows in detail view); ***9***, facet view of an isolated columnal of the mesistele (no. GIK-2155), encrusted by a holdfast of a fenestrate bryozoan (arrow). [Scale bars = 1 cm]

*FIGURE **3.4.10 (legend p. 160)***



3.4.7 CRINOID LOCALITIES AND STRATIGRAPHY

Localities 1-8 (Eifel, Rhenish Massif, Germany)

1. “Auf den Eichen”, NE of Nollenbach within the Hillesheim Syncline; UTM 50°19’45.64”N/6°44’37.94”E. Stratigraphy: Bohnert Member of the Freilingen Formation, Upper Eifelian (Middle Devonian).

2. Abandoned “Weinberg Quarry”, E of Kerpen within the Hillesheim Syncline; UTM 50°18’54.57”N/6°42’53.78”E. Stratigraphy: Bohnert Member of the Freilingen Formation, Upper Eifelian (Middle Devonian).

3. Road cut, S Brühlborn within Prüm Syncline; UTM 50°12’27.14”N/6°27’37.45”E. Stratigraphy: Olifant Member of the Müllert Subformation, Ahbach Formation, Lower Givetian (Middle Devonian).

4. N Niederehe within the Hillesheim Syncline; UTM 50°18’48.87”N/6°45’52.28”E. Stratigraphy: ?Eilenberg Member of the Freilingen Formation, Upper Eifelian (Middle Devonian).

5. “Wachtberg Quarry”, S Sötenich within the Sötenich Syncline; UTM 50°31’18.00”N/6°33’31.34”E. Stratigraphy: ?Eilenberg Member of the Freilingen Formation, Upper Eifelian (Middle Devonian).

6. Abandoned ‘‘Müllertchen Quarry”, S Ahütte within the Hillesheim Syncline; UTM 50°20’05.37”N/6°46’16.77”E. Stratigraphy: Olifant Member of the lower Müllert Subformation, Ahbach Formation, Lower Givetian (Middle Devonian).

7. Brook valley, E of Berlingen within the Gerolstein Syncline; UTM 50°14’20.24”N/6°42’24.26”E. Stratigraphy: Hustley Member of the Loogh Formation, Lower Givetian (Middle Devonian).

8. Hill range near the “Steineberg”, N of Kerpen, S of Flesten within the Hillesheim Syncline (UTM unknown). Stratigraphy: ?Freinilgen Formation, Upper Eifelian (Middle Devonian).

9. Farmland SW of Gondelsheim within Prüm Syncline; UTM 50°13’54.08”N/6°29’42.80”E. Stratigraphy: Eilenberg Member of the Freilingen Formation, Upper Eifelian (Middle Devonian).

Locality 10 (Bergisches Land, Rhenish Massif, Germany)

10 Lindlar-Hartegasse, N Lindlar (UTM unknown). Stratigraphy: Odershäuser Formation, Eifelian/Givetian threshold (Middle Devonian).

Locality 11 (Sauerland, Rhenish Massif, Germany)

11 Plettenberg-Ohle at the Lenne river, SE of Werdohl, Märkischer Kreis, Sauerland (UTM unknown). Stratigraphy: “Selscheider Formation” sensu Wolburg (1938a, p. 230); more probable, the ammonicrinids came from the Odershäuser Formation of the Eifelian/Givetian threshold (Middle Devonian) [pers. information, M. BASSE].

Locality 12 (Vireux-Molhain, France)

12 Vireux-Molhain, southern Ardennes, northern France, close to the Belgian border (UTM unknown). Stratigraphy: Lower Eifelian (Middle Devonian).

3.4.8 MATERIAL AND METHODS

Type species are deposited in the *Forschungsinstitut und Naturmuseum Senckenberg*, Frankfurt am Main, Germany (SMF), the *Institut für Geologie und Mineralogie der Universität zu Köln*, Germany (GIK), the *Museum für Naturkunde der Humboldt-Universität zu Berlin*, Germany (MB.E.), the *Geowissenschaftliches Zentrum der Universität Göttingen*, Germany (without repository-no.), the *Laboratoire de Paléontologie de Brest (Université de Bretagne Occidentale)*, France (LPB), the *National Museum of Natural History (Smithsonian Institution)*, Washington D.C., U.S.A. (USNM) and the *Pracownia Palezoologiczna Muzeum Ziemi*, Warsaw, Poland (MZ).

In addition to a detailed analysis of previously published data, this study focuses on new material, recently discovered within the Rhenish Massif. Specimens were cleaned and dissected using micro-sand streaming methods and studied with a binocular microscope. Photographs of NH_4Cl whitened crinoids were arranged using digital image editing software.

Crinoid descriptive terms follows MOORE & TEICHERT (1978) with the following exception: measurement terms follow WEBSTER & JELL (1999).

3.4.9 SYSTEMATIC PALAEONTOLOGY

3.4.9.1 Introduction

SPRINGER (1926b, p. 23) originally classified *Ammonicrinus* with its type species *A. wanneri* as a possible member of the subclass Camerata WACHSMUTH & SPRINGER, 1885, family Hexacrinitidae WACHSMUTH & SPRINGER, 1885 ("Hexacrinidae" 1926b, p. 23) and mentioned the similarities to *Camptocrinus*. Both assumptions were confirmed by WOLBURG (1938a), who erected the species *A. doliiformis*. This assumption was rejected by BASSLER (1938) and MOORE & LAUDON (1943), who placed *Ammonicrinus* in the "subclass Inadunata", family "Heterocrinidae" (BASSLER) or "Iocrinidae" (MOORE & LAUDON). UBAGHS (1952), who first dissected an *A. wanneri* crown from the surrounding stem and, therefore, was the first author to demonstrate that *Ammonicrinus* is a true member of class Crinoidea MILLER, 1821 (see WANNER 1954, p. 231). UBAGHS assigned the genus to the subclass Flexibilia ZITTEL, 1895, order Sagenocrinida SPRINGER, 1913 and "family Lecanocrinidae SPRINGER, 1913", whereas WANNER (1954, p. 231) identified out the exceptional position of *Ammonicrinus* among the subclass because of its bent crown and the atrophy of the two anterior basals and hypertrophy of the anterior and left anterolateral radial plate. Within the Crinoid Treatise (see MOORE 1978), *Ammonicrinus* was finally assigned to the superfamily "Lecanocrinacea" (= Lecanocrinoidea SPRINGER, 1913 sensu ICZN) and family Calycocrinidae MOORE & STRIMPLE, 1973, characterising lecanocrinids with bilateral symmetry in the plane bisecting the CD interray and the A ray or AE interray, as well as crowns distinctly bent on the stem or the stem coiled around the crown (MOORE 1978, pp. T783-T784).

3.4.9.2 Crinoid systematic

Subclass Flexibilia ZITTEL, 1895
Order Sagenocrinida SPRINGER, 1913
Superfamily Lecanocrinoidea SPRINGER, 1913
Family Calycocrinidae MOORE & STRIMPLE, 1973

3.4.9.2.1 Genus *Ammonicrinus*

Genus *Ammonicrinus* SPRINGER, 1926b

- *Ammonicrinus* SPRINGER, 1926b, p. 22.

Occurrence.—Devonian. Pragian (Lower Devonian) of the Czech Republic (see HOTCHKISS et al. 1999, p. 331, fig. 2.21; PROKOP 2009); Upper Emsian (Lower Devonian) of the Armorican Massif (France); Lower Eifelian (Middle Devonian) of Vireux-Molhain, southern Ardennes (France); Lower Eifelian to Lower (?Middle) Givetian (Middle Devonian) of the Holy Cross Mountains (Poland), the Rhenish Massif (Eifel, Sauerland and Bergisches Land, Germany), Cantabrian Mountains (Spain) and Morocco (material not figured herein).

Because "*Ammonicrinus*? *nordicus*" sensu YAKOVLEV & IVANOV (1956), from the Carboniferous of the Donetz Basin (Russia), is herein excluded from *Ammonicrinus* sensu SPRINGER (1926b), the genus is restricted to the Lower and Middle Devonian (Pragian-Givetian).

Revised description.—The crown is short, rounded asymmetrically and incurved strongly in plane bisecting AE and CD interrays; the cup is either laterally uncovered by the mesistele (*A. kredreoletensis*), partly visible in lateral respectively radial view (*A. doliiformis*), or completely covered by the mesistele (*A. leunissi* n. sp.[12]); infrabasals reduced to 2 subequal, symmetrically disposed plates which are larger than any of the three basals adjoining them on posterior side (AB and EA basals lacking); A and E radials symmetrically disposed and distinctly larger than others, with margins of articular facets rather strongly curved; one single and rhombic radianal plate obliquely at left below C radial. The plates are either unsculptured (?*A. kredreoletensis*), sculptured with fine tubercles (*A. doliiformis*, *A. leunissi* n. sp.[13], *A. sulcatus*, *A. wanneri*) or with radiating ridges on radials (*A. jankei* n. sp.[14]). A large anal X is positioned above CD basal and followed by several smaller anal plates. The arms are formed by wide, short and straight or laterally somewhat curved brachials, branching isotomously on primibrachials 6 to 8 with up to 10 secundibrachials in some branches, followed by at least some tertibrachials. The stem is distinguished by the abrupt xenomorphic change between the dististele, which is composed of more or less elongated and cylindrical to barrel-shaped columnals, the mesistele, composed of columnals with are herein termed "Lateral Columnal Enclosure Extensions" (LCEE) covering the crown, and the proxistele with smaller lateral extensions on columnals in relation to the mesistele; the dististele is either long and composed of numerous columnals ("exposed runner-type",

---

[12] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

[13] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

[14] = *A. jankei* BOHATÝ, submitted *sensu* ICZN

observed in *A. kredreoletensis*; “encased runner-type”, observed in all ammonicrinids, except of *A. kredreoletensis*), short and composed of only few columnals, or reduced (“settler-type”, recognised in *A. leunissi* n. sp.[15], *A. sulcatus* and *A. wanneri*); the dististele can develop radiating cirri (rare, observed in *A. leunissi* n. sp.[16]) and the distal-most dististele is connected with a substrate-controlled holdfast, in form of an attachment disc or a variously formed holdfast composed of radiating cirri; the LCEE of the mesistele are either constantly equally developed (*A. kredreoletensis*, *A. wanneri*), composed of regularly or irregularly arranged columnals with longer and shorter extensions (*A. jankei* n. sp.[17], *A. sulcatus*), or interconnected with several columnals with broadened LCEE that could interlock in coiled position and are combined with smaller, “regular” columnals (*A. doliiformis*, *A. leunissi* n. sp.[18]); the connection between dististele and mesistele is either constant, by the development of a triangular columnal (*A. doliiformis*) or variously formed with floating transitions between those individuals with none or one to several columnals with LCEE on the proximal-most, barrel-like dististele and the following mesistele, which is solely distinguished by LCEE (observed in *A. leunissi* n. sp.[19], *A. sulcatus* and *A. wanneri*); the proxistele causes distinct impressions of columnals on cup. The axial canal is rarely tetralobate but typically pentalobate, with either five similar lumen or one lumen elongated (differences observed in one specimen). *Ammonicrinus* shows synarthrial articulation, with fulcra aligned and unequal ligmentary areas on either side of each fulcrum which produced the planispirally coiled proximal column covering the crown; shape of coiled stem narrow discoidal (*A. wanneri*), oblate spheroidal (*A. leunissi* n. sp.[20], *A. jankei* n. sp.[21]), or wide barrel-shaped (*A. doliiformis*, *A. sulcatus*). The mesi- and dististele are covered by echinoid-like tubercles, which bear movable spines (recognised in *A. doliiformis*, *A. leunissi* n. sp.[22], *A. sulcatus* and assumed in *A. kredreoletensis* and *A. jankei* n. sp.[23]), or mesistele sculptured by irregularly placed tubercles [e.g. in juvenile ossicles of *A. sulcatus* and in “*A. bulbosus*” sensu PROKOP (2009)], tubercles and additional spine-tubercles (*A. sulcatus*) or irregularly arranged ridges without tubercles on the exterior flanks (*A. wanneri*).

---

[15] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN
[16] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN
[17] = *A. jankei* BOHATÝ, submitted *sensu* ICZN
[18] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN
[19] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN
[20] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN
[21] = *A. jankei* BOHATÝ, submitted *sensu* ICZN
[22] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN
[23] = *A. jankei* BOHATÝ, submitted *sensu* ICZN

3.4.9.2.2 Type species *Ammonicrinus wanneri*

Type species: *Ammonicrinus wanneri* SPRINGER, 1926b
Figs. 3.4.1.1-2, 3.4.1.5, 3.4.12.2; Pl. 3.4.2, Figs. 1-10

- *pars Ammonicrinus wanneri* SPRINGER, 1926b, pp. 22-25, pl. 6, figs. 4-4b, only.
- *non Ammonicrinus wanneri* SPRINGER, 1926b, pl. 6, figs. 5-5b = *A. leunissi* n. sp.[24]
- *non Ammonicrinus wanneri* SPRINGER, 1926b, pl. 6, fig. 6 = *A.* cf. *sulcatus*.
- *non Ammonicrinus wanneri* SPRINGER, WOLBURG 1938a, pl. 18, fig. 9.
- *non Ammonicrinus wanneri* SPRINGER, WOLBURG 1938a, pl. 18, fig. 10 = *A. leunissi* n. sp.[25]
- *non Ammonicrinus wanneri* SPRINGER, UBAGHS 1952, p. 210, fig. 2, pl. 1, figs. 1-7, pl. 2, figs. 1-7 = *A. jankei* n. sp.[26]
- *non Ammonicrinus wanneri* SPRINGER, UBAGHS 1978, p. T78, fig. 57, nos. 6-7 = *A. doliiformis*, no. 8 = *A. jankei* n. sp.[27]
- *pars Ammonicrinus wanneri* SPRINGER, MOORE 1978, p. T787, fig. 526, nos. 5a-c, only.
- *non Ammonicrinus wanneri* SPRINGER, MOORE 1978, p. T787, fig. 526, nos. 5d-e = *A. leunissi* n. sp.[28]
- *pars Ammonicrinus wanneri* SPRINGER, WEBSTER 2003, GSA-webpage, *A. wanneri* SPRINGER 1926b, pl. 6, figs. 4-4b, only.

Holotype.—USNM-S2115 (SPRINGER 1926b, pl. 6, figs. 4-4b, only) [Figs. 3.4.1.1-2, 3.4.1.5; also see colour photos of the SPRINGER-original on the webpage-search of the USNM Department of Paleobiology collection].

Locus typicus (assumed).—“Prüm”, within the Prüm Syncline, in the vicinity of Locality 3 (Eifel, Rhenish Massif, Rhineland Palatinate, Germany).

Stratum typicum (assumed).—Uppermost Freilingen Formation (Upper Eifelian) or superposed Ahbach Formation (Eifelian/Givetian threshold, Middle Devonian).

---

[24] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN
[25] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN
[26] = *A. jankei* BOHATÝ, submitted *sensu* ICZN
[27] = *A. jankei* BOHATÝ, submitted *sensu* ICZN
[28] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

Revised description.—Ammonicrinus wanneri shows fine tubercles on the cup ossicles. The stem is mainly distinguished by the characteristic mesistele, composed of columnals with long and relative regularly developed LCEE that nearly orthogonally protrude from both sides of the narrow columnals, forming a narrow discoidal coiled proximal column in closed position; mesistele composed of numerous columnals, which distally passes gradually into the dististele; several specimens show floating transitions between those individuals with none or one to several columnals with LCEE on the proximal-most, barrel-like dististele and the following mesistele; dististele either long and composed of numerous columnals ("encased runner-type"), short and composed of only few columnals, or nearly reduced ("settler-type"); distal-most dististele connected with a substrate-controlled holdfast composed of radiating cirri; axial canal pentalobate; mesistele sculptured by irregularly positioned or oriented ridges, which, idealised, runs parallel to each other on the external flanks of the columnals; no spine-tubercles on the stem.

Differentiation.—The mesistele of *A. wanneri* is composed of regularly developed columnals with narrow and long LCEE that protrude nearly orthogonally from both sides of the columnals, resulting in narrow discoidal coiled proximal column in closed position; the radials are partly visible in lateral view of the coiled stem. In *A. leunissi* n. sp.[29] the LCEE of the mesistele are shorter and interconnected with several columnals showing broadened extensions and combined with smaller, "regular" columnals that cover the cup completely; respectively, the radials are not visible in lateral view of the coiled stem. Additionally, the shape of the coiled stem is oblate spheroidal instead of discoidal. The columnals of the mesistele of *A. wanneri* are sculptured by tubercles, forming irregular ridges on the external flanks of the columnals; no spine-tubercles were observed. In contrast, *A. leunissi* n. sp.[30] is a spined *Ammonicrinus*.

3.4.9.2.3 Species *Ammonicrinus sulcatus*

Ammonicrinus sulcatus KONGIEL, 1958
Figs. 3.4.4.1-2, 3.4.9.1-20, 3.4.10.1-9, 3.4.12.3

- *Ammonicrinus sulcatus* KONGIEL, 1958, pp. 34-36, figs. 6a-b.
- *Ammonicrinus sulcatus* KONGIEL, PIOTROWSKI, 1977, pp. 211-213, p. 208, fig. 2, p. 211, fig. 4, p. 212, fig. 5B, p. 213, fig. 6, pl. 17, figs. 1a-c, 2a-c, 3-4, 5a-b, pl. 18, figs. 4, 5a-b, 6-8, 10.

---

[29] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

[30] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

- *Ammonicrinus kongieli* PIOTROWSKI, 1977, pp. 213-215, pl. 18, figs. 1a-c, 2-3, 9, pl. 19, figs. 1, 2a-b, 3, 4a-b, 5, 6a-b, 7a-b, 8, 9a-b, 10 [not "pl. 18, figs 1-9" as indicated by PIOTROWSKI (1977, p. 213)].
- *Ammonicrinus sulcatus* KONGIEL, UBAGHS 1978, p. T78, fig. 57, no. 9.
- *Ammonicrinus sulcatus* KONGIEL, WEBSTER 2003, GSA-webpage (cum syn.).
- *Ammonicrinus sulcatus* KONGIEL, LE MENN & JAOUEN 2003, p. 208, fig. 1A.
- cf. *Ammonicrinus wanneri* SPRINGER, 1926b, pl. 6, fig. 6 = *A.* cf. *sulcatus*.

Holotype.—MZ-VIII-EP-1/1.

Locus typicus.—Grzegorzowice-Skaly (Holy Cross Mountains, Poland).

Stratum typicum.—Member XIV of the Givetian Skaly beds (Middle Devonian) [see PIOTROWSKI 1977, p. 213].

Revised description.—*Ammonicrinus sulcatus* is distinguished by the fine tubercles on the cup ossicles. The mesistele shows nearly linear and wide external flanks and relatively short LCEE; extensions of the mesistele composed of regularly or irregularly arranged columnals with longer and shorter extensions; adult mesistele "pseudo-tuberculated" by echinoid-like spine-tubercles and movable spines, or distinguished by additional, irregularly arranged, sometimes slightly meandering nodular tubercles bearing the spine-tubercles; columnals of the juvenile mesistele with strongly tuberculated extensions and external flanks; dististele either medium long and composed of numerous columnals ("encased runner-type"), or short and composed of only few columnals, or nearly reduced ("settler-type"); the connection between disti- and mesistele is variously formed with floating transitions between those individuals with none (rare) or one to several columnals (characteristic) with laterally positioned enclosure extensions on the proximal-most, barrel-like dististele and the following mesistele; the planispirally coiled, proximal column is relatively low, wide and barrel-shaped, due to the relatively short LCEE of the mesistele.

Differentiation.—*Ammonicrinus sulcatus* is similar to *A. leunissi* n. sp.[31] and, especially, to *A. jankei* n. sp.[32] *A. sulcatus* developed characteristic and nearly linear external

---

[31] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

[32] = *A. jankei* BOHATÝ, submitted *sensu* ICZN

flanks of the mesistele, showing short LCEE in contrast to the longer extensions of *A. leunissi* n. sp.[33] Several cup ossicles of *A. sulcatus* show rudimentary radiating ridges that are not known in *A. leunissi* n. sp.[34] but developed much stronger in *A. jankei* n. sp.[35] Because of the longer extensions of the mesistele of *A. jankei* n. sp.[36], the shape of the coiled stem is oblate spheroidal, rather than wide and barrel-shaped like in *A. sulcatus*.

3.4.9.2.4 Species *Ammonicrinus doliiformis*

Ammonicrinus doliiformis WOLBURG, 1938a (for 1937)
Figs. 3.4.1.7-8, 3.4.2.1-6, 3.4.3.1-2, 3.4.12.4; Pl. 3.4.2, Figs. 11-18

- *Ammonicrinus doliiformis* WOLBURG, 1938a (for 1937), pp. 230-241, p. 231, fig. 1, p. 232, fig. 2, p. 233, figs. 3-4, p. 240, fig. 5, pl. 17, figs. 1-5, 6a-b, 7, pl. 18, figs. 1(?), 2a-b, 3-4, 5-7(?), 8.
- *Ammonicrinus wanneri* SPRINGER, KRAUSE 1927, pl. VIII, figs. 1-6.
- *Ammonicrinus doliiformis* WOLBURG, UBAGHS 1952, pp. 216-218, pl. 3, figs. 1-5.
- *Ammonicrinus doliiformis* WOLBURG, UBAGHS 1978, p. T64, fig. 44, no. 3.
- *Ammonicrinus wanneri* SPRINGER, UBAGHS 1978, p. T78, fig. 57, nos. 6-7.
- *Ammonicrinus doliiformis* WOLBURG, WEBSTER 2003, GSA-webpage (*cum syn.*).
- *vidi* "*Ammonicrinus wachtbergensis*", HAUSER 2005b, p. 4, fig. 1, pp. 23-25, figs. 15a-b, second unnumbered fig. below on p. 34, pl. 1, figs. 3a-c, + front and backside covers of private publication.

Holotype.—Lost due to world war damages; one cast of the dististele of WOLBURG's type material is deposited in the *Geowissenschaftliches Zentrum der Universität Göttingen*, Germany (without repository-no.).

Locus typicus.—Locality 11.

Stratum typicum.—"Selscheider Formation" sensu WOLBURG (1938a, p. 230); more probable, the type material came from the Odershäuser Formation of the Eifelian/Givetian threshold (Middle Devonian) [pers. information, M. BASSE].

---

[33] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN
[34] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN
[35] = *A. jankei* BOHATÝ, submitted *sensu* ICZN
[36] = *A. jankei* BOHATÝ, submitted *sensu* ICZN

Revised description.—*Ammonicrinus doliiformis* is distinguished by fine tubercles on the surface of the cup ossicles. The arms are relatively long and formed by medium wide, short and straight or laterally somewhat curved brachials. The dististele is long and composed of numerous columnals ("encased runner-type"), the distal-most dististele is connected with a substrate-controlled holdfast, typically in form of a relatively small attachment disc; the LCEE of the wide mesistele are composed of characteristic, regularly or irregularly (rare) arranged columnals with longer and shorter extensions. These are interconnected with several columnals with broadened extensions that could intermesh in a closed coiled position and are combined with smaller, "regular" columnals; connection between disti- and mesistele distinguished by a triangular columnal without extensions; columnals of the mesistele with long, less curved external flanks showing relatively thin cross sections; shape of coiled stem wide barrel-shaped; the cup is partly visible in lateral respectively radial view; mesi- and dististele covered by echinoid-like spine-tubercles, which bear movable spines.

Differentiation.—*Ammonicrinus doliiformis* is similar to *A. leunissi* n. sp.[37] WOLBURG's species has a wider diameter of the coiled stem and a characteristic connection between the disti- and mesistele, which is distinguished by a triangular columnal without extensions in opposition to the variously formed connection between the disti- and mesistele of *A. leunissi* n. sp.[38]

Discussion.—After studying the holotype of "*Ammonicrinus wachtbergensis* HAUSER 2005b" (= original of KRAUSE 1927, figured as *A. wanneri*), it is clearly evident that the specimen is a typical adult and three dimensionally preserved *A. doliiformis*. The specimen came from the Eilenberg Member of the uppermost part of the Freilingen Formation (Upper Eifelian) of locality 5. This stratigraphic level is most famous for *A. doliiformis* and could be correlated with several localities within the Eifel (e.g. with the deposits of the Freilingen Formation of village Gondelsheim within the Prüm Syncline or with locality 4). Also the stratum typicum at the *A. doliiformis* type locality (locality 11, also see locality 10) correlates approximately with the Eifel findings.

Therefore, "*A. wachtbergensis* HAUSER 2005b" is declared a subjective junior synonym of *A. doliiformis*.

---

[37] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

[38] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

FIGURE 3.4.11—*Ammonicrinus kredreoletensis* (no. GIK-2121) from locality 12; lateral view of long mesistele, proxistele and huge cup (arrow) on matrix. [Scale bar = 1 cm]

3.4.9.2.5 Species *Ammonicrinus kredreoletensis*

Ammonicrinus kredreoletensis LE MENN & JAOUEN, 2003

Figs. 3.4.6, 3.4.11, 3.4.12.1

- *Ammonicrinus kredreoletensis* LE MENN & JAOUEN, 2003, p. 207, pp. 210-211, p. 210, figs. 4A-C.

Holotype.—LPB-1073.

Locus typicus.—Coupe de Kerdréolet, niveau K2, L´Hôpital-Camfrout, Département Finistère (Brittany, France).

Stratum typicum.—Kerdréolet Formation, Emsian (Lower Devonian).

Revised descriptions.—Ammonicrinus kredreoletensis shows a subspherical crown with a relatively large cup in comparison to the narrow width of the mesistele; the cup is not covered laterally by the mesistele and is, therefore, clearly visible in lateral view; the ossicles of the cup are unsculptured(?). The mesistele is very long and composed of numerous columnals ("exposed runner-type") that have nearly uncurved to slightly concave external flanks and thin cross sections; LCEE of the mesistele regularly arranged and very short, several columnals of the mesistele have very short and blunt lateral expansions on both lateral edges of the exterior flanks; connection between mesi- and dististele obviously distinguished by a narrow triangular columnal, which follows distally after the rapid narrowing of the columnals of the distal-most mesistele; dististele and attachment unknown; shape of coiled stem narrow discoidal; mesi- and dististele obviously covered by echinoid spine-tubercles, which presumably bear movable spines(?) [not preserved].

Differentiation.—The numerous columnals of the mesistele of *Ammonicrinus kredreoletensis*, the very short lateral expansions of the mesistele and the huge rounded crown clearly separates this species from all other ammonicrinids.

Discussion.—As stated above, the cup of *A. kredreoletensis* is laterally not covered by the LCEE. That possibly implies feeding in the current (Fig. 3.4.6) and negates the internal, respectively pumping proposal assumed for the younger ammonicrinids described herein. Furthermore, the new recovered material indicates that the stem of *A. kredreoletensis* tapers as it approaches the crown, which was obviously elevated up from the substrate into a possible low velocity current for feeding. Therefore, *A. kredreoletensis* can be designated a morphological progenitor of the younger and encased ammonicrinids.

3.4.9.2.6 Species *Ammonicrinus leunissi*

Ammonicrinus leunissi n. sp.[39]

Figs. 3.4.1.3-4, 3.4.1.6, 3.4.5, 3.4.7.1-2, 3.4.8; Pl. 3.4.1, Figs. 1-14

- *Ammonicrinus wanneri* SPRINGER, 1926b, pl. 6, figs. 5-5b.
- *Ammonicrinus wanneri* SPRINGER, WOLBURG 1938a (for 1937), pl. 18, fig. 10.
- *Ammonicrinus wanneri* SPRINGER, MOORE 1978, p. T787, fig. 526, nos. 5d-e.
- *pars Ammonicrinus wanneri* SPRINGER, WEBSTER 2003, GSA-webpage, *A. wanneri* SPRINGER 1926b, pl. 6, figs. 5-5b, only.

---

[39] = *Ammonicrinus leunissi* BOHATÝ, submitted *sensu* ICZN

Holotype.—USNM-S2115 (SPRINGER 1926b, pl. 6, figs. 5-5b, only) [Figs. 3.4.1.3-4, 3.4.1.6; also see colour photos of the SPRINGER-original on the webpage-search of the USNM Department of Paleobiology collection].

Locus typicus (assumed).—"Prüm", within the Prüm Syncline, in the surrounding of Locality 3 (Eifel, Rhenish Massif, Rhineland Palatinate, Germany).

Stratum typicum (assumed).—Uppermost part of the Freilingen Formation (Upper Eifelian) or, more probable, superposed Ahbach Formation (Eifelian/Givetian threshold, Middle Devonian). Within the Eifel, the species shows its maximum distribution within the Olifant and Zerberus members of the Müllert Subformation, Ahbach Formation (lowermost Lower Givetian, Middle Devonian).

Etymology.—The species is named after MR. ROBERT LEUNISSEN (Wollersheim), for his tremendous help in sampling of material for the present work.

Diagnosis.—An *Ammonicrinus*, distinguished by fine tubercles on the surface of the cup ossicles; dististele either long and composed of numerous columnals ("encased runner-type"), short and composed of only few columnals, or nearly reduced ("settler-type"); dististele may develop branching cirri, distal-most dististele connected with a substrate-controlled holdfast (attachment disc or variously formed holdfasts); LCEE of the mesistele interconnected with several columnals with broadened extensions and combined with smaller, "regular" columnals; connection between disti- and mesistele variously formed; axial canal pentalobate; shape of coiled stem oblate spheroidal; cup completely covered by the mesistele; mesistele, dististele and attachment spined.

Description.—The crown is relatively small and distinguished by the short arms with short and wide brachials and the small cup, which is characterised by irregularly arranged, fine tubercles on the surface of all ossicles. The short and narrow proxistele causes distinct impressions of columnals on the cup and spine-tubercles are developed on the external flanks, obviously loosing spines throughout the ontogeny. These tubercles are well developed on the surface of the lateral and external flanks of the mesistele and have very movable spines that allowed coiling over the spined columnals. The LCEE of the mesistele are interconnected with several columnals with broadened extensions that could interlock in a coiled position and are combined with smaller, "regular" columnals. Columnals of the mesistele are less curved external flanks and medium long extensions. The connection between the dististele and the mesistele is variously formed, with floating transitions between those individuals with none or one to several columnals with LCEE on the proximal-most, barrel-like dististele and the following mesistele, which is solely distinguished by these extensions. Dististele is either long and composed of numerous barrel-like columnals, developing the "runner-type", or short and composed of only few or nearly reduced columnals, characterising the "settler-type". Several examples with developed radiating cirri on the columnals of the dististele are known. The distal-most dististele is connected with an attachment disc (rare) or, typically, with a variously formed holdfast composed of radiating cirri. Columnal axial canal pentalobate. The shape of the coiled proximal "stem globe" (proxistele and proximal to middle or nearly complete mesistele), that completely covers the crown, is oblate spheroidal.

For dimensions of the studied material, see indication of size within the figure descriptions.

Differentiation.—*Ammonicrinus leunissi* n. sp.[40] differs from *A. wanneri* by the wider columnals of the mesistele, which have shorter LCEE in comparison with *A. wanneri*. The LCEE of the spined *A. leunissi* n. sp.[41] are interconnected with several columnals with broadened extensions and combined with smaller, "regular" columnals. The unspined *A. wanneri* developed very long and fine extensions that protrude nearly orthogonally from both sides of the narrow columnals, forming a narrow discoidal coiled proximal column in closed position, which is oblate spheroidal in *A. leunissi* n. sp.[42]

3.4.9.2.7 Species *Ammonicrinus jankei*

Ammonicrinus jankei n. sp.[43]

Figs. 3.4.3.3-9

- *Ammonicrinus wanneri* SPRINGER, UBAGHS 1952, p. 210, fig. 2, pl. 1, figs. 1-7, pl. 2, figs. 1-7.
- *Ammonicrinus wanneri* SPRINGER, UBAGHS 1978, p. T78, fig. 57, no. 8.
- *pars Ammonicrinus wanneri* SPRINGER, WEBSTER 2003, GSA-webpage, *A. wanneri* SPRINGER 1926b, UBAGHS 1952, p. 210, fig. 2, pl. 1, figs. 1-7, pl. 2, figs. 1-7 and UBAGHS 1978, p. T78, fig. 57, no. 8., only.

---

[40] = *Ammonicrinus leunissi* BOHATÝ, submitted *sensu* ICZN

[41] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

[42] = *A. leunissi* BOHATÝ, submitted *sensu* ICZN

[43] = *Ammonicrinus jankei* BOHATÝ, submitted *sensu* ICZN

Holotype.—SMF-XXIII.165a.

Locus typicus.—Locality 8.

Stratum typicum.—“Rommersheim Formation” (UBAGHS 1952, p. 206) = Junkerberg Formation sensu HOTZ et al. (1955). My studies at the type locality suggest that the species came from the superjacent ?Freinilgen Formation (Upper Eifelian, Middle Devonian).

Etymology.—The species is named after MR. EBERHARD JANKE (Elsdorf), for his help in sampling of material, especially from time-consuming washings, for this work.

Diagnosis.—An *Ammonicrinus*, distinguished by a crown with a rhombic outline, unpustulated cup ossicles and radiating ridges on radials, radials convex and protrude conically toward the lateral-exterior; arms formed by very wide, V-shaped and medium short brachials; mesistele distinguished by irregularly arranged columnals with longer and shorter LCEE, which are relatively wide, columnals of the mesistele interconnected with several columnals having broadened extensions that could interlock in a coiled position and are combined with smaller, “regular” columnals, mesistele sculptured by irregular tubercles (several tubercles could possibly be spine-tubercles but spines not preserved); shape of coiled stem, covering the crown, oblate spheroidal; cup nearly completely covered by the mesistele. Other skeletal elements unknown.

Description.—The crown is mainly distinguished by its shape that shows a characteristic rhombic outline in lateral-anal view, which is caused by the radials, which are convex and conical extend toward the lateral-exterior. The cup is nearly completely covered by the mesistele. The ossicles of the cup are consistently unpustulated, with up to six radiating ridges on radials. The lateral-most radials have a slightly lobe-like enlarged appendage that could possibly support the lateral water faecal-ejection. The short arms are formed by very wide and V-shaped brachials, which are nearly straight in proximal position; the distal brachials are somewhat curved laterally. The species developed one single rhombic radianal plate obliquely at left below the C radial, followed by a larger anal X and several smaller anal plates forming a short and curved tube that obviously channelled the faecal material toward that point from where the excrements could be ejected toward the lateral-exterior. The short and narrow proxistele causes distinct impressions of columnals on the cup, proximal tube and subsequent arms. The mesistele is sculptured by irregularly arranged tubercles and is distinguished by irregularly arranged columnals with longer and shorter extensions, showing regular columnals that are interconnected with several columnals with broadened LCEE that could interlock in coiled position. Several tubercles could possibly be badly preserved spine-tubercles (spines not preserved). Shape of the coiled stem that cover the crown is oblate spheroidal. The connection between disti- and mesistele, the morphology of the dististele and of the holdfast are unknown.

For dimensions of the studied material, see indication of size within the figure descriptions.

Differentiation.—Ammonicrinus jankei n. sp.[44] is similar to *A. sulcatus*. The species differs in several characteristic morphologies: *A. sulcatus* has fine tubercles on the cup ossicles and the radials are convex and protrude conically toward the lateral-exterior. The cup ossicles of *A. jankei* n. sp.[45] are unpustulated but the radials have as many as six radiating ridges and each one has a slightly lobe-like enlarged appendage. The columnals of the mesistele of *A. jankei* n. sp.[46] are thinner in cross section than those of *A. sulcatus* and show irregularly arranged nodular tubercles instead of finer columnal sculpturing observed in *A. sulcatus*. The planispirally coiled, proximal column of *A. sulcatus* is relatively low, wide and barrel-shaped, due to the relatively short extensions of the columnals of the mesistele. In opposition, the shape of the coiled stem that covers the crown of *A. jankei* n. sp.[47] is oblate spheroidal.

3.4.10 DISCUSSION

Because of the high variability of the substrate-controlled dististele and attachment that strongly affected the overall form of the endoskeleton, *Ammonicrinus* has to be characterised as a lecanocrinid distinguished by high morphologic plasticity. This is mainly expressed by the two recognised main forms, the roller- and the settler-type. As bottom-

---

[44] = *Ammonicrinus jankei* BOHATÝ, submitted *sensu* ICZN

[45] = *A. jankei* BOHATÝ, submitted *sensu* ICZN

[46] = *A. jankei* BOHATÝ, submitted *sensu* ICZN

[47] = *A. jankei* BOHATÝ, submitted *sensu* ICZN

dwellers on muddy firmgrounds or, in particular, on mud substrates, ammonicrinids benefit from this constructional plasticity, which affords anchoring on different hard objects that are lying on the soft-bottom. Radiating cirri, observed in few crinoids, could additionally stabilise the individuals.

Regarding the younger ammonicrinids from the Rhenish Massif, the presumed soft-bottom dwelling, especially in still water habitats, requires two main conditions: (1) It is apparently necessary to protect the crown by encasing it by the proximal mesistele. Furthermore, attacks from vagile benthic predators have to be anticipated with echinoid-like spines. (2) Active “stem pumping”, resulted in a self-generated water flow for feeding and out-pumping of excretory products as well as antagonising sedimentary material. This was possibly enabled by slowly stiffening and relaxation of mutable connective tissues of the mesi- and proxistele. However, it is important to note that this assumed ability doesn’t imply that every ammonicrinid imperatively feeds via “MCT-pumping”. In the same muddy still water habitats that were populated by the roller-type, the settler-type is recognised. This mode of life potentially profited from a low water flow above the nearly unmoved condition at the sediment water interface. Carbonate microfacies analysis within several *Ammonicrinus*-localities of the Eifel indicated former muddy firmgrounds and moving water conditions in which ammonicrinids could passively benefit from water current.

Observations within the Eifel synclines indicate that the *Ammonicrinus* morphology of the coiling of the stem, respectively encasing of the crown, was brought to perfection during the Upper Eifelian. The oldest studied form, *A. kredreoletensis*, has a relative huge crown in relation to the narrow mesistele, which is composed of narrow, similarly shaped columnals with very short extensions. Thus, the crown is nearly unprotected laterally in the resting position of the crinoid and, especially, in the feeding position, which implies feeding in the current and has similarities to the feeding position of camptocrinids and myelodactylocrinids. Younger ammonicrinids encased the crown with modified columnals of the mesistele in a resting- but, herein assumed, also in a feeding position; *A. wanneri* lengthened the LCEE of the similarly shaped columnals of the mesistele, which encased the crown in the coiled position. The developments of smaller columnals of the mesistele, which are interconnected with regular ones, are an advanced or evolved step to afford increase lateral density of the coiled stem. This morphology is recognised in *A. sulcatus*. In *A. doliiformis*, the LCEE of the mesistele is composed of characteristically regularly or irregularly arranged columnals with longer and shorter extensions, which were interconnected with several columnals showing broadened convex and concave extensions that could interlock in coiled position. Especially within the Eifel and the Holy Cross Mountains, the diversity and frequency of vagile benthic predators like platyceratid gastropods increases during the Middle and Upper Eifelian reaching a maximum toward the Eifelian/Givetian boundary (own, unpublished data; see e.g. GAHN & BAUMILLER 2003 for Middle Devonian crinoid/platyceratid interactions). The necessity to increase the ammonicrinid crown protection could speculatively be linked to this ecological circumstance.

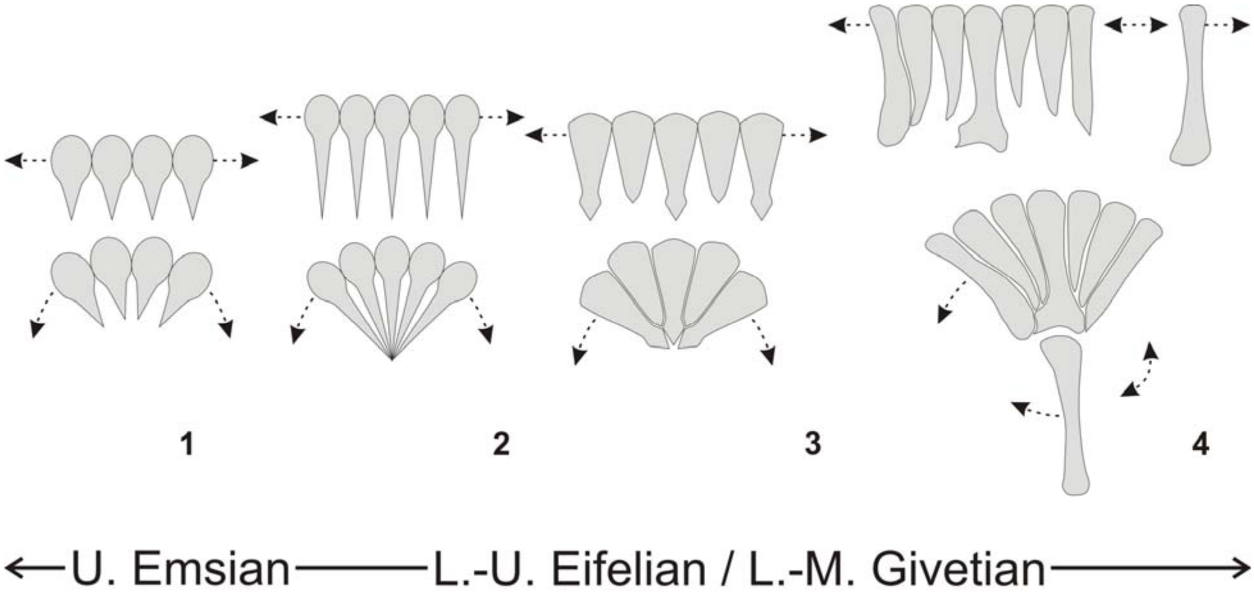


FIGURE 3.4.12—Schematic sketches of different LCEE of the mesistele in uncoiled (above) and coiled positions (below), indicating evolution of perfecting the crown-encasing in coiled position by modifying the extensions form Emsian to Givetian; ***1***, lateral view of *A. kredreoletensis*, showing similar shaped columnals with very short LCEE; thus, the crown is laterally nearly unprotected in coiled position; ***2***, lateral view of *A. wanneri* with lengthened LCEE of the similar shaped columnals, which lattice-like guarded the crown in coiled position; ***3***, lateral view of *A. sulcatus*, showing smaller columnals of the mesistele, which are interconnected with longer ones and afford lateral density of the coiled stem; ***4***, Lateral view of *A. doliiformis*, showing regularly or irregularly arranged columnals with longer and shorter LCEE, which were interconnected with several columnals showing broadened convex and concave extensions that could interlock in coiled position.

PLATE 3.4.1 (see p. 181)

—*Ammonicrinus leunissi* n. sp. from locality 6 (***1-5***, ***9-11***, ***14***), 3 (***6-7***, ***12-13***) and 9 (***8***). ***1***, Lateral view of a specimen (no. GIK-2122) with lost spines, showing complete coiled mesistele and one preserved columnal of the dististele (arrow); ***2***, lateral-facet view of a specimen with lost spines (no. GIK-2123), showing coiled mesistele and proxistele; ***3***, view of the exterior columnal flanks of a slightly compressed specimen (no. GIK-2124) with lost spines, showing proxistele and mesistele with one distal-most, barrel-shaped columnal with LCEE (arrow); ***4***, view of the exterior columnal flanks of a weathered and compressed specimen (no. GIK-2125) with lost spines, showing part of the mesistele and proxistele and rest of disarticulated ossicles of the cup preserved; **5**, lateral view of a partly preserved specimen (no. GIK-2126) with lost spines and well preserved spine-tubercles on the coiled mesistele; ***6***, view of the exterior columnal flanks of a partly preserved, coiled mesistele (no. GIK-2127) with lost spines and one radial plate preserved (arrow); ***7***, view of the exterior columnal flanks of a partly preserved, uncoiled mesistele (no. GIK-2128) with lost spines; ***8***, interior view of a partly preserved, coiled specimen (no. GIK-2129), showing rest of cup and impressions of the lost arms (arrow); ***9***, view of the exterior columnal flanks of an uncoiled specimen (GIK-2130) on matrix (“runner-type”), showing several preserved spines on partly preserved mesistele and dististele and developed radiating cirri on columnals of the dististele (arrow); ***10***, view of the exterior columnal flanks of a specimen on matrix (no. GIK-2131) with coiled proximal-most mesistele and proxistele and uncoiled distal column (“runner-type”) with one barrel-shaped columnal showing short LCEE (arrow on the right); the specimen shows numerous preserved spines on the mesistele; one radial plate is visible (arrow on the left); ***11***, like 10, aboral view of proxistele and base of cup; ***12***, isolated holdfast (no. GIK-2132) of the specimen, figured in Fig. 13; the holdfast is composed of radiating cirri attached to a fenestrate bryozoan (arrow); ***13***, like 12, view of the exterior columnal flanks of uncoiled mesistele on matrix (“runner-type”); ***14***, coiled specimen (no. GIK-2103), attached on a brachiopod brachial valve (*Schizophoria* sp.) [compare to reconstruction, figured in Fig. 3.4.8]; the specimen strongly reduced the dististele and settled with an attachment disc on the brachiopod (“settler-type”). [Scale bars = 1 cm]

PLATE 3.4.1 (legend p. 180)

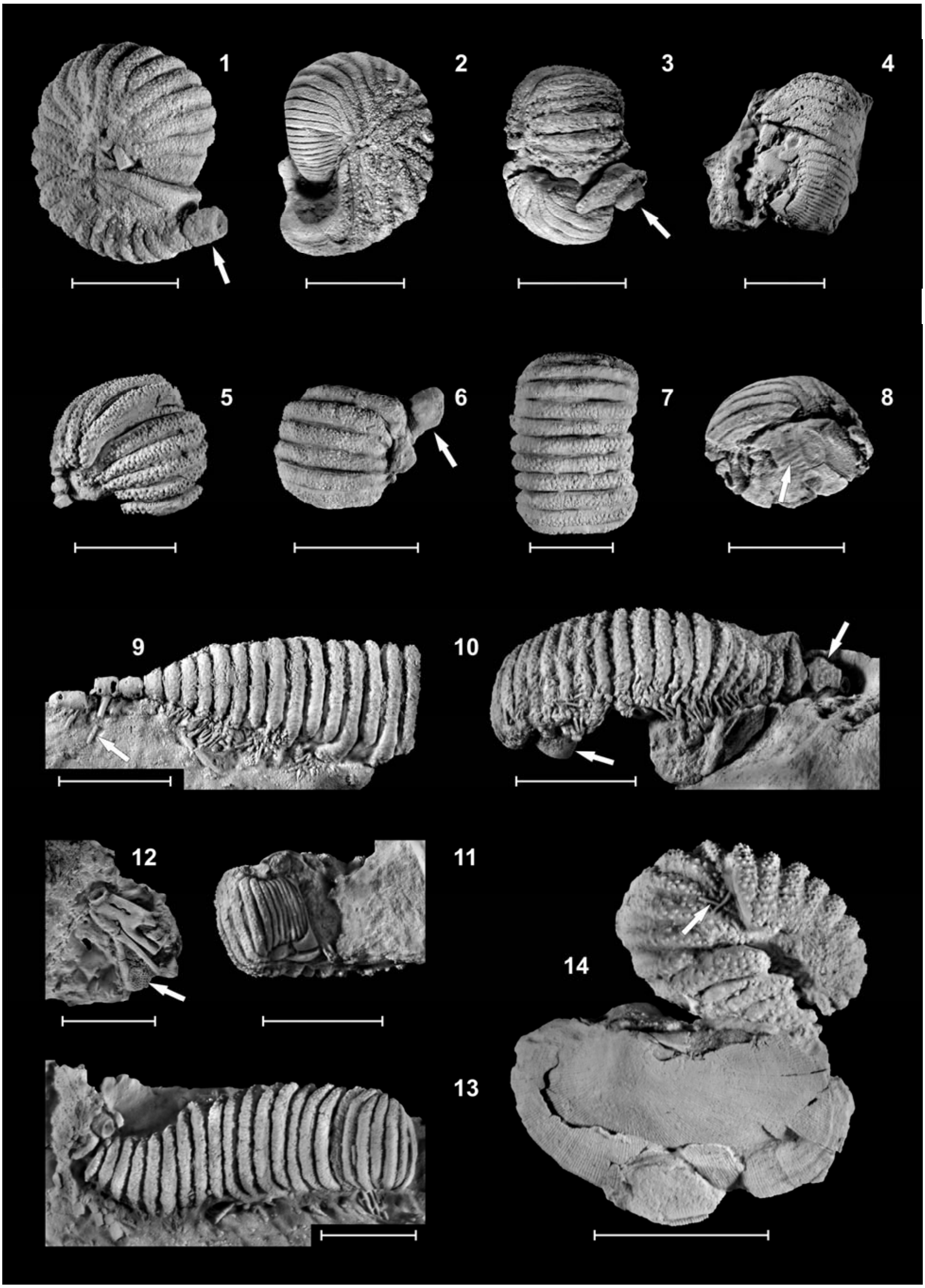
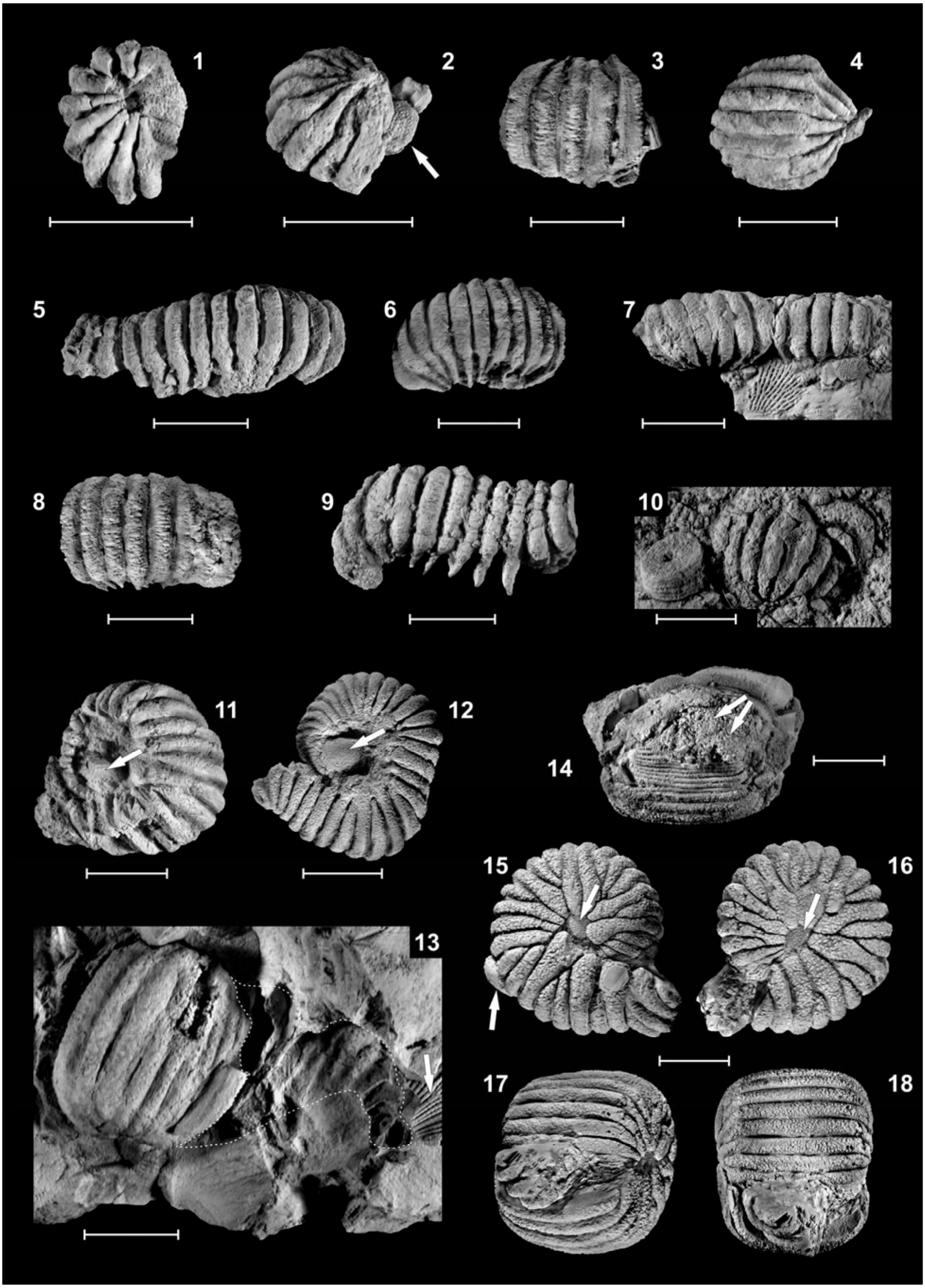


PLATE 3.4.2 (see p. 183)

—*Ammonicrinus wanneri* from locality 3 (***1-9***) and from locality 7 (***10***); *Ammonicrinus doliiformis* from locality 9 (***11-12***), 10 (***13***), 4 (***14***) and 5 (***15-18***). ***1***, Lateral view of a partly preserved specimen (no. GIK-2133) with coiled mesistele; ***2***, lateral view, respectively view of external columnal flanks of the coiled mesistele of a partly preserved specimen (no. GIK-2134) with one preserved, postulated cup ossicle (arrow); ***3***, view of external columnal flanks of the mesistele of a partly preserved specimen (no. GIK-2135); ***4***, lateral view, respectively view of external columnal flanks of the coiled mesistele of a partly preserved specimen (no. GIK-2136), showing typical LCEE; ***5***, view of external columnal flanks of a nearly uncoiled mesistele ("runner-type") [no. GIK-2137]; ***6***, view of external columnal flanks and LCEE of a slightly compressed, coiled mesistele (no. GIK-2138); ***7***, view of external columnal flanks of a nearly uncoiled mesistele ("runner-type") [no. GIK-2139]; ***8***, view of external columnal flanks of the mesistele of a partly preserved specimen (no. GIK-2140); ***9***, view of external columnal flanks of a nearly uncoiled mesistele ("runner-type") [no. GIK-2141]; ***10***, view of external columnal flanks of the coiled mesistele of a weathered specimen (no. GIK-2142) on matrix; ***11***, lateral view of a coiled specimen (no. GIK-2143) with lost dististele and cracked LCEE of the mesistele, exposing the coiled proxistele and several cup ossicles (arrow); ***12***, lateral view of a nearly completely coiled specimen (no. GIK-2144) with lost dististele and cracked LCEE of the mesistele, exposing distal-most part of the coiled proxistele and several cup ossicles (arrow); ***13***, view of external columnal flanks of a preserved, coiled mesistele (no. GIK-2145) on matrix; the imprint of the uncoiled distal mesistele ("runner-type"), of the dististele and of the holdfast, which is attached to a fenestrate bryozoan (imprint, see arrow), is traced by a dashed line; ***14***, facet view of a coiled, adult specimen (no. GIK-2146) with exposed distal part of the proxistele and disarticulated remains of the arms (arrows); ***15***, perfect, three dimensionally preserved, adult specimen (no. MB.E.-287, original of KRAUSE 1927), showing coiled mesistele in lateral view, dististele, attachment and spines missing; centres of tuberculated radials partly visible (arrow); the specimen is infested by a (?)craniid brachiopod (arrow on the left). **16**. Like 15, opposite lateral view; centres of radials partly visible (arrow); ***17***; like *15-16*, oblique lateral view; ***18***, Like *15-17*, view of the external flanks of the mesistele (centre and upper part of the figure) and of the facet area of distal mesistele (below), showing wide barrel-shaped outline. [Scale bars = 1 cm]

PLATE 3.4.2 (legend p. 182)



4. DISCUSSION AND CONCLUSION

4.1 PALAEODIVERSITY

In the following, "Palaeodiversity" is mainly focussed on the number of taxa among the discussed genera.

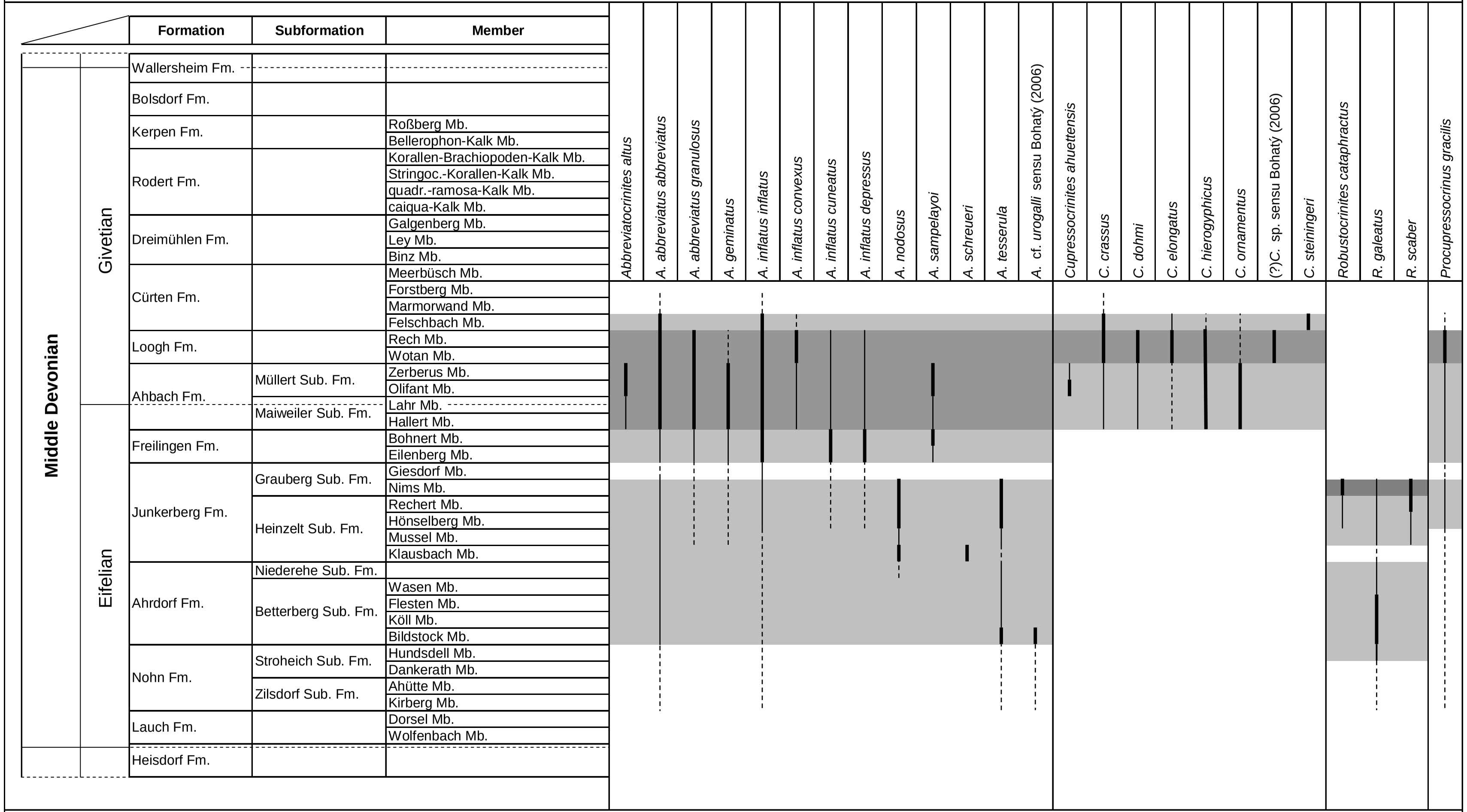
4.1.1 SUBCLASS CLADIDA

Abbreviatocrinites with its species and subspecies, *A. abbreviatus abbreviatus*, *A. inflatus inflatus*, *A. tesserula* and *A.* cf. *urogalli* sensu BOHATÝ (2006b) occurs at the base of the Nohn Formation (Lower Eifelian), as do *Robustocrinites* with its oldest species *R. galeatus* and *Procupressocrinus* with *P. gracilis* (Tab. 4.1.1). This correlates with the establishment of the calcareous sedimentation at the base of the Middle Devonian within the Eifel Synclines. These occurrences coincided with the first proliferation of stromatoporoid/coral-biostromes in the upper part of the Lower Nohn Formation sensu KUCKELKORN (1925).

Three of these oldest, Middle Devonian cupressocrinitids from the Eifel, *A. a. abbreviatus*, *A. i. inflatus* and *P. gracilis*, can be characterised as stratigraphically persisting taxa and can be traced up to the Cürten Formation (Lower Givetian) in the study area.

After the negative influences of increased clastic sedimentation in the northern Eifel realm during the Upper Nohn Formation (HOTZ 1951), stromatoporoid/coral-biostromes re-established at the base of the Ahrdorf Formation. This correlates with the diversification of *Abbreviatocrinites* and *Robustocrinites* between the Bildstock Member of the lower Ahrdorf Formation and the boundary of the Nims and Giesdorf members. Peak diversification was positioned between the Klausbach Member and the border of the Nims and Giesdorf members of the Junkerberg Formation. Furthermore, the number of individuals of the monospecific *Procupressocrinus* increased between the Hönselberg Member and the boundary of the Nims and Giesdorf members (Tab. 4.1.1).

TABLE 4.1.1 **—Stratigraphic distribution of the species of genera *Abbreviatocrinites* , *Cupressocrinites* , *Robustocrinites* and *Procupressocrinus* within the Middle Devonian of the Eifel.**



light grey = minimum distribution, dark grey = maximum distribution of the genera within the Eifel
dashed = minimum distribution, bold = maximum distribution of the species within the Eifel
(based on crowns and cups)

Between the Klausbach Member and the boundary of the Nims and Giesdorf members the palaeodiversity of the cupressocrinitid species doubled in comparison to the Nohn and Ahrdorf formations. Therefore, the first palaeodiversity radiation of cladids is positioned between the Ahrdorf and Freilingen formations (Fig. 4.1.1). This palaeodiversity abruptly declined in the uppermost Junkerberg Formation, with the beginning of the Giesdorf Member, in which nearly every group of the Middle Devonian crinoids of the Eifel is missing due to drastic facies changes associated with the "*otomari* Event" (compare to 4.3.2.3). Similarly, the absence of *Robustocrinites* within the Eifel Synclines coincided with the beginning of the Giesdorf Member (Chapter 3.1.4; Fig. 3.1.8). This resulted in a minimum of genera; nearly one third of the species of *Abbreviatocrinites* disappeared [*A. nodosus* and *A. tesserula* – *A.* cf. *urogalli* and *A. schreueri* already after the Bildstock Member respectively after the Klausbach Member, showing a last increasing of the species number of *A. nodosus* and *A. tesserula* below the Giesdorfian part of the Junkerberg Formation]; the frequency of *P. gracilis* also declined.

The second and larges radiation of the cupressocrinitid palaeodiversity of the Eifel [between the Freilingen Formation (Upper Eifelian) and the lower Cürten Formation (Lower Givetian)], is positioned within the Ahbach Formation. Seven of nine species of *Abbreviatocrinites*, occurs in this time slice within the Freilingen Formation and are associated with *P. gracilis*.

The first occurrence of *Cupressocrinites* is recognised in the Ahbach Formation at the Eifelian/Givetian boundary with five of eight species. This could possibly be correlated to a high sea-level in the course of a transgression during the "*otomari* Event" that presumably allowed faunal migrations (compare to 4.3.2.3).

Except for the absence of the genus *Robustocrinites*, the remaining cupressocrinitids have their maximum diversity and abundance between the Ahbach Formation (Eifelian/Givetian) and Loogh Formation (lowermost Lower Givetium) [Tab. 4.1.1]. The maximum of *Abbreviatocrinites* is within the Ahbach Formation and those of *Cupressocrinites* and *Procupressocrinus* are in the Loogh Formation. This correlates with the maximal facies differentiation of the Eifel (WINTER 1965).

These results complement previously published data of the palaeodiversity development of other cladid crinoids from the Middle Devonian of the Eifel Synclines (BOHATÝ 2006a; HAUDE 2007) [Fig. 4.1.1]. In this context, the distribution of gasterocomoids (*Gasterocoma*, 10 species; *Lecythocrinus*, two species; *Nanocrinus*, two species; *Scoliocrinus*, two species; *Tetrapleurocrinus*, one species and *Trapezocrinus*, one species with two subspecies in the Middle Devonian of the Eifel) correlates with the results presented herein (Fig. 4.1.1). Less distinct, the species-distribution of *Bactrocrinites* traces the pattern in Fig. 4.1.1 (BOHATÝ 2005b). This genus shows two maxima of the palaeodiversity, one within the Junkerberg Formation and one within the Ahbach Formation.

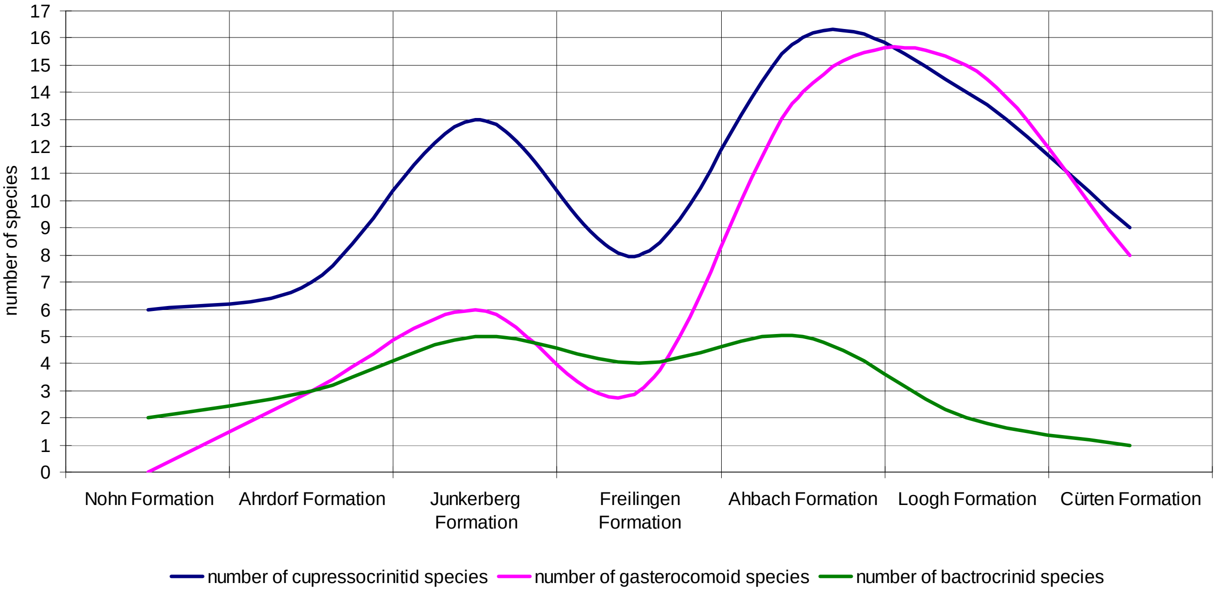


FIGURE 4.1.1—The palaeodiversity history of the studied cupressocrinitid species and comparison with other cladid crinoids of the family Gasterocomidae (after BOHATÝ 2006a, in consideration of the revision of HAUDE 2007) and genus *Bactrocrinites* (after BOHATÝ 2005b), showing maximal diversity in the Junkerberg and Ahbach formations (cupressocrinitids; bactrocrinids) – and in the Junkerberg and boundary of the Ahbach and Loogh formations (gasterocomoids).

4.1.2 SUBCLASS CAMERATA

In contrast to the cladids, the studied camerates have a different pattern of palaeodiversity with only one maximum (Fig. 4.1.2). In the Ahrdorf Formation *Megaradialocrinus* occurs with its oldest Eifel-species *M. thomasbeckeri*; the second oldest species, (?)*M. granuliferus*, occurs primarily in the Junkerberg Formation (Tab. 4.1.2). *Hexacrinites* occurs afterward with four species in the Freilingen Formation. This correlates with the further radiation of the species *Megaradialocrinus*, which occurs in the Freilingen Formation with eight taxa (Tab. 4.1.2). There is an increase from one to two species of *Megaradialocrinus* from the Ahrdorf to the Junkerberg formations. From the Junkerberg to the Freilingen formations, there is an increase from one to two genera, as well as a five-fold increase of species. The radiation continued in the Ahbach Formation with 18 *Megaradialocrinus* and six *Hexacrinites* species. In this time slice, *Hexacrinites* had his maximum palaeodiversity (Tab. 4.1.2). The maximum species richness of *Megaradialocrinus* followed in the superposed Loogh Formation with 22 species. This results in the maximum palaeodiversity of both genera with 25 co-occurring species within the Loogh Formation as figured in the curve-chart (Fig. 4.1.2). Because of the absence of *Hexacrinites* within the Eifel and the decrease of 11 *Megaradialocrinus* species, the diversity decreased in the Cürten Formation.

The curve-chart shows each one single maximum of the palaeodiversity of *Hexacrinitites* and *Megaradialocrinus* between the Junkerberg and Cürten formations. The maximum of the curve of *Hexacrinites* lays within the Ahbach Formation and that of *Megaradialocrinus* in the Loogh Formation. Within the Eifel Synclines this pointed out a sharp increased and relatively continuously curve progression of the palaeodiversity between the Middle Eifelian and lowermost Lower Givetian.

According to own unpublished data, this pattern can also be verified by further camerates of the Eifel Synclines (e.g. genera *Arthroacantha* and *Platyhexacrinus*).

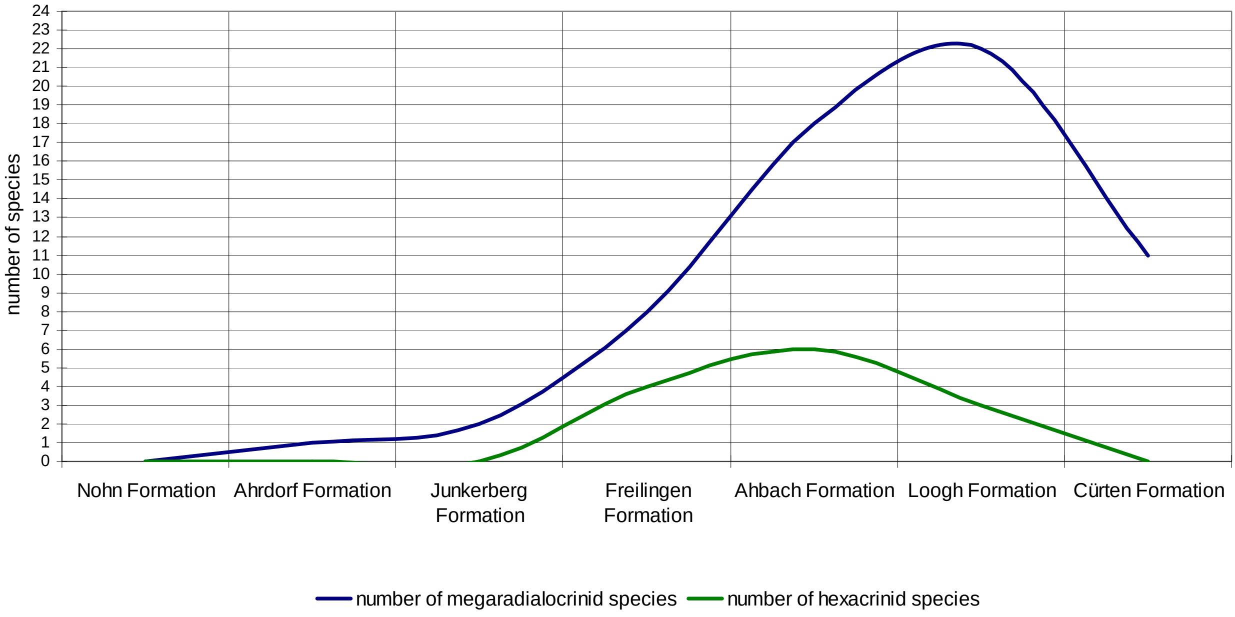
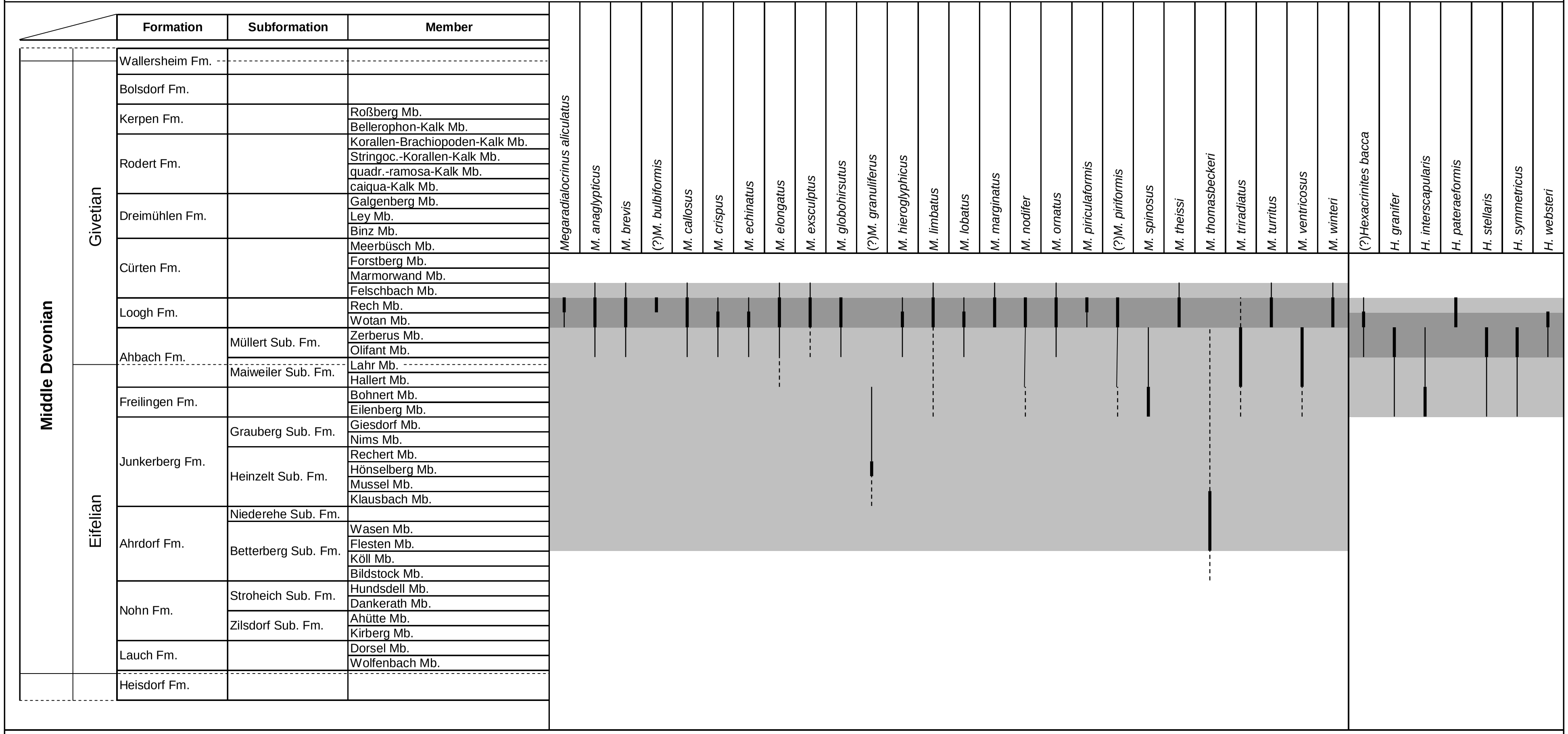


FIGURE 4.1.2—The distribution of the palaeodiversity of studied hexacrinitids and megaradialocrinids with each one single maximum of the palaeodiversity. The maximum of the curve of *Hexacrinites* lays within the Ahbach Formation and that of *Megaradialocrinus* in the Loogh Formation.

***TABLE 4.1.2*—Stratigraphic distribution of the species of genera *Megaradialocrinus* and *Hexacrinites* within the Middle Devonian of the Eifel.**

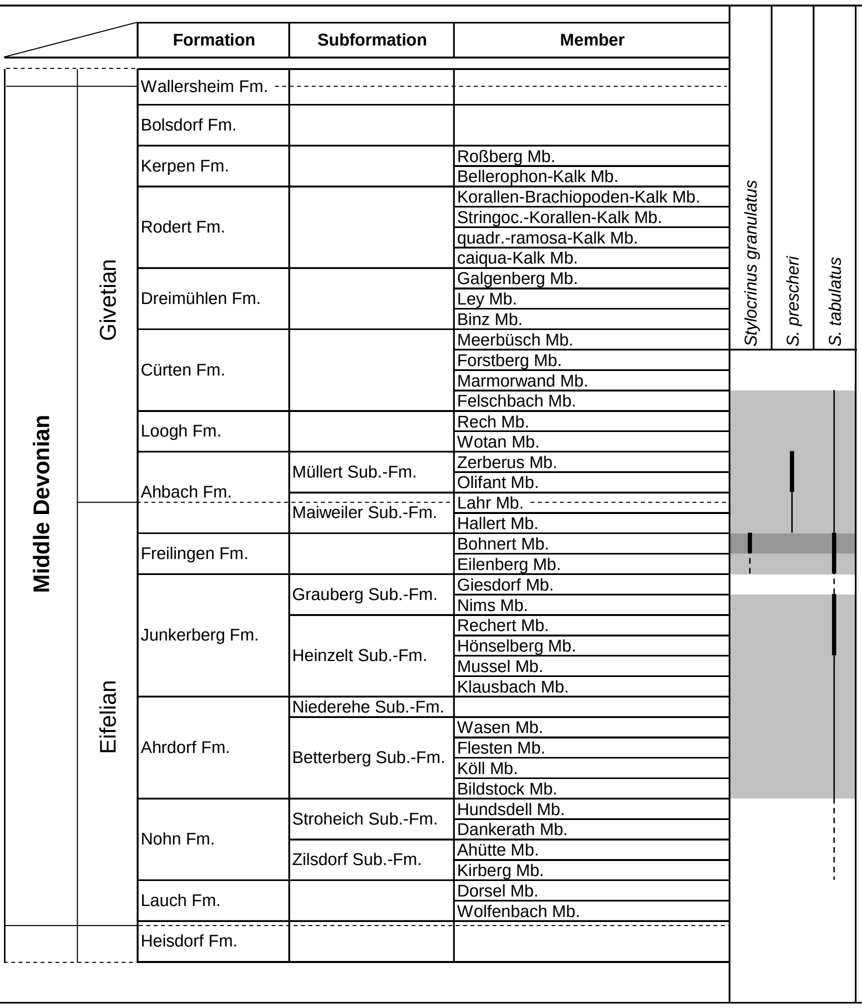


light grey = minimum distribution, dark grey = maximum distribution of the genera within the Eifel
dashed = minimum distribution, bold = maximum distribution of the species within the Eifel
(based on crowns and cups)

4.1.3 SUBCLASS DISPARIDA

Stylocrinus is among the most common and frequent articulated aboral cups collected within the Middle Devonian deposits of the Eifel Synclines.

***TABLE 4.1.3*—Stratigraphic distribution of the species of genus *Stylocrinus* within the Middle Devonian of the Eifel.**



		Formation	Subformation	Member
Middle Devonian	Givetian	Wallersheim Fm.		
		Bolsdorf Fm.		
		Kerpen Fm.		Roßberg Mb.
				Bellerophon-Kalk Mb.
		Rodert Fm.		Korallen-Brachiopoden-Kalk Mb.
				Stringoc.-Korallen-Kalk Mb.
				quadr.-ramosa-Kalk Mb.
				caiqua-Kalk Mb.
		Dreimühlen Fm.		Galgenberg Mb.
				Ley Mb.
				Binz Mb.
		Cürten Fm.		Meerbüsch Mb.
				Forstberg Mb.
				Marmorwand Mb.
				Felschbach Mb.
		Loogh Fm.		Rech Mb.
				Wotan Mb.
		Ahbach Fm.	Müllert Sub.-Fm.	Zerberus Mb.
				Olifant Mb.
				Lahr Mb.
	Eifelian		Maiweiler Sub.-Fm.	Hallert Mb.
		Freilingen Fm.		Bohnert Mb.
				Eilenberg Mb.
		Junkerberg Fm.	Grauberg Sub.-Fm.	Giesdorf Mb.
				Nims Mb.
			Heinzelt Sub.-Fm.	Rechert Mb.
				Hönselberg Mb.
				Mussel Mb.
				Klausbach Mb.
		Ahrdorf Fm.	Niederehe Sub.-Fm.	
			Betterberg Sub.-Fm.	Wasen Mb.
				Flesten Mb.
				Köll Mb.
				Bildstock Mb.
		Nohn Fm.	Stroheich Sub.-Fm.	Hundsdell Mb.
				Dankerath Mb.
			Zilsdorf Sub.-Fm.	Ahütte Mb.
				Kirberg Mb.
		Lauch Fm.		Dorsel Mb.
				Wolfenbach Mb.
		Heisdorf Fm.		

light grey = minimum distribution, dark grey = maximum distribution of the genera within the Eifel
dashed = minimum distribution, bold = maximum distribution of the species within the Eifel
(based on crowns and cups)

The oldest *Stylocrinus* from the Eifel, *S. tabulatus*, came form the Nohn Formation (Lower Eifelian) [Tab. 4.1.3]. From the Ahrdorf up to the upper Junkerberg formations, this species occurred in relatively constant abundance. Maximum abundance is between the Hönselberg and Nims members, after which it abruptly declines in the uppermost Junkerberg Formation (basis Giesdorf Member) [Tab. 4.1.3]. In the lower Freilingen Formation, the abundance of *S. tabulatus* rises abruptly again, and the first occurrence of a second species (*S. granulatus*) is recognised. *S. granulatus* is restricted to the Freilingen Formation and had its maximum abundance in the Bohnert Member, which is the maximum abundance of genus *Stylocrinus* in the Eifel.

With beginning of the Ahbach Formation the new *S. prescheri* first occurs and is restricted to this formation. This species has a maximum distribution in the upper (Lower Givetian) part of the formation (Olifant and Zerberus members of the Müllert Subformation) and is associated with the frequent *S. tabulatus*, which can be traced up to the Cürten Formation with relatively constant abundance.

Stylocrinus mainly occurs between the Junkerberg and Loogh formations and has its maximum abundance between the Freilingen and Ahbach formations, as illustrated in Fig. 4.1.3.

Including other unrevised disparids from the Eifel (e.g. genera *Pisocrinus*, *Trichocrinus*, *Haplocrinites* or *Phimocrinus*), the maximum distribution would be broadened to include the interval from the Ahrdorf and to the Cürten formations.

The single maximum of the *Stylocrinus* palaeodiversity (Fig. 4.1.3) contrasts with the two maxima demonstrated for cladids (Fig. 4.1.1). The cladid maximum is in younger Lower Givetian formations than for the disparid *Stylocrinus*.

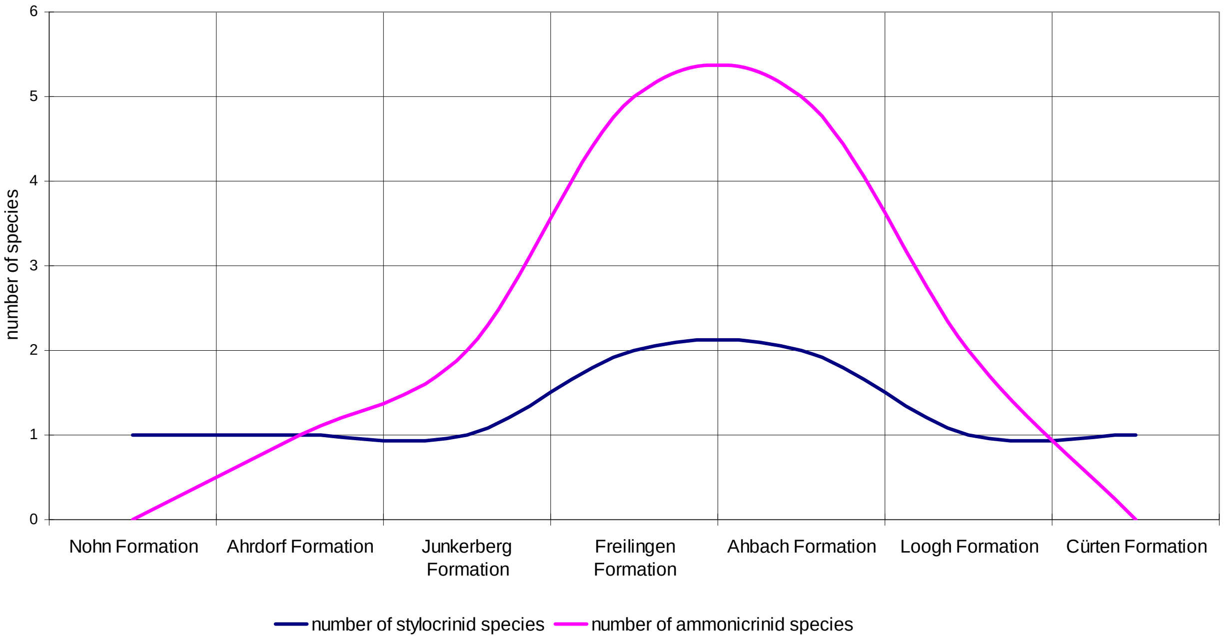


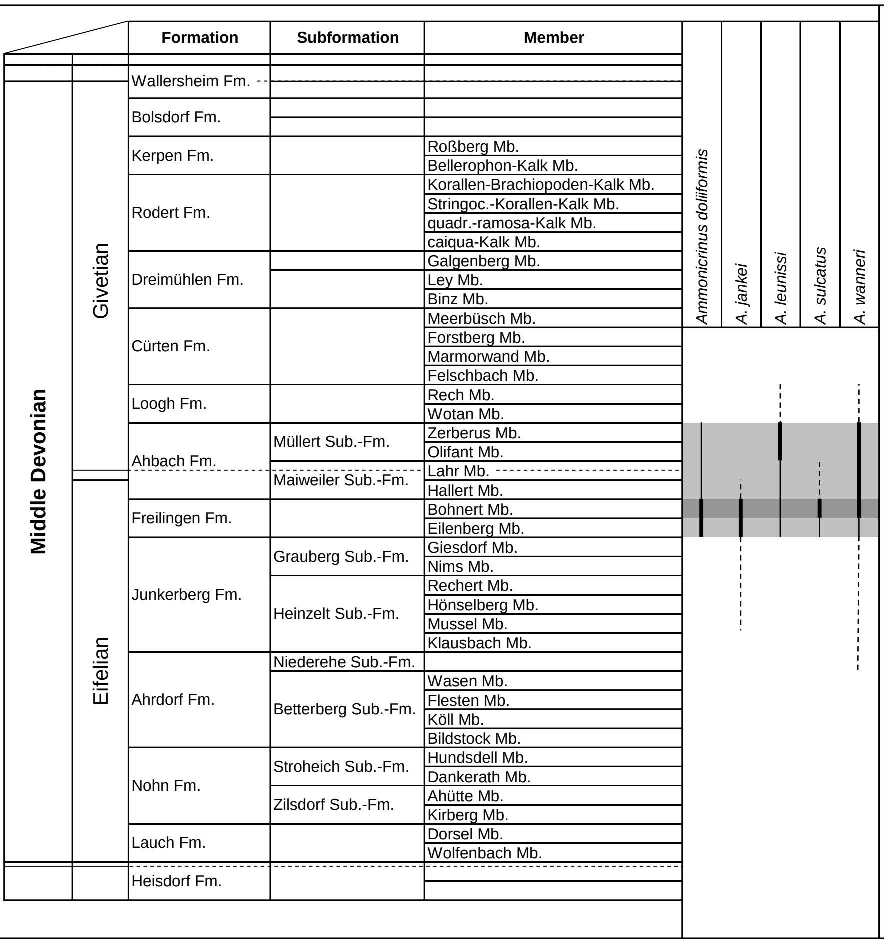
FIGURE 4.1.3—The distribution of the palaeodiversity of the studied disparid stylocrinid and the flexible ammonicrinid species, showing each one single maximum of the palaeodiversity. The maxima of the curves of *Stylocrinus* and *Ammonicrinus* (see Chapter 4.1.4) lay between the Freilingen and Ahbach formations.

4.1.4 SUBCLASS FLEXIBILIA

Columnals are clearly identifiable for *Ammonicrinus* (subclass Flexibilia); they show the following distribution of the palaeodiversity within the Middle Devonian of the Eifel Synclines:

Disarticulated ossicles of the mesi and dististele of *A. wanneri* are rare in the deposits of the upper Ahrdorf Formation (Tab. 4.1.4). As second taxa, *A. jankei,* first occurs in the lower Junkerberg Formation. Beginning in the Freilingen Formation, maximal diversification is recognised with the first appearance of *A. doliiformis*, *A. leunissi* and *A. sulcatus*.

***TABLE 4.1.4*—Stratigraphic distribution of the species of genus *Ammonicrinus* within the Middle Devonian of the Eifel.**



		Formation	Subformation	Member
		Wallersheim Fm.		
Middle Devonian	Givetian	Bolsdorf Fm.		
		Kerpen Fm.		Roßberg Mb.
				Bellerophon-Kalk Mb.
		Rodert Fm.		Korallen-Brachiopoden-Kalk Mb.
				Stringoc.-Korallen-Kalk Mb.
				quadr.-ramosa-Kalk Mb.
				caiqua-Kalk Mb.
		Dreimühlen Fm.		Galgenberg Mb.
				Ley Mb.
				Binz Mb.
		Cürten Fm.		Meerbüsch Mb.
				Forstberg Mb.
				Marmorwand Mb.
				Felschbach Mb.
		Loogh Fm.		Rech Mb.
				Wotan Mb.
		Ahbach Fm.	Müllert Sub.-Fm.	Zerberus Mb.
				Olifant Mb.
	Eifelian		Maiweiler Sub.-Fm.	Lahr Mb.
				Hallert Mb.
		Freilingen Fm.		Bohnert Mb.
				Eilenberg Mb.
		Junkerberg Fm.	Grauberg Sub.-Fm.	Giesdorf Mb.
				Nims Mb.
			Heinzelt Sub.-Fm.	Rechert Mb.
				Hönselberg Mb.
				Mussel Mb.
				Klausbach Mb.
		Ahrdorf Fm.	Niederehe Sub.-Fm.	
			Betterberg Sub.-Fm.	Wasen Mb.
				Flesten Mb.
				Köll Mb.
				Bildstock Mb.
		Nohn Fm.	Stroheich Sub.-Fm.	Hundsdell Mb.
				Dankerath Mb.
			Zilsdorf Sub.-Fm.	Ahütte Mb.
				Kirberg Mb.
		Lauch Fm.		Dorsel Mb.
				Wolfenbach Mb.
		Heisdorf Fm.		

light grey = minimum distribution, dark grey = maximum distribution of the genera within the Eifel
dashed = minimum distribution, bold = maximum distribution of the species within the Eifel
(based on ossicles of the mesi- and dististele and few crown elements)

The maximal diversification in the Freilingen Formation correlates with a successive increase in abundance in the upper part of the formation (Bohnert Member). All five species can be traced to the lower Ahbach Formation (Maiweiler Subformation), respectively up to the top of the Upper Eifelian. Afterward, *A. jankei* and *A. sulcatus* disappeared. The Lower Givetian part of the upper Ahbach Formation (Müllert Subformation) is dominated by *A. leunissi* and *A. wanneri,* and *A. leunissi* had its maximal abundance within the Müllert Subformation. Both species occurred up to the Loogh Formation (lowermost Lower Givetian), with a notable decrease in individual numbers, and *A. doliiformis* disappeared by the base of the Loogh Formation.

No evidence of ammonicrinid remains could be found in the superposed Cürten Formation (Tab. 4.1.4). Therefore, *Ammonicrinus* has a single maximum palaeodiversity between the Junkerberg and the Loogh formations with a peak at the boundary of the Freilingen and Ahbach formations (Fig. 4.1.3). This pattern is similar to the disparid *Stylocrinus* but differs from those of the cladids and camerates (compare to Figs. 4.1.1; 4.1.2).

Further unstudied groups of flexibile crinoids from the Eifel Synclines would result in a similar distribution as Fig. 4.1.3. However, the curve maximum would be younger, because *Eutaxocrinus* and *Dactylocrinus* have a maximal distribution within the Loogh Formation (unpublished data). In contrast, lecanocrinid flexibiles (e.g. genera *Lecanocrinus* and *Geroldicrinus*) flourished between the Junkerberg and Ahbach formations. This would result in a more rapid rise of the diversity curve.

4.1.5 THE GENERAL DEVELOPMENT OF THE CRINOID PALAEODIVERSITY WITHIN THE MIDDLE DEVONIAN OF THE EIFEL SYNCLINES

Between the Nohn Formation (Lower Eifelium) and the Cürten Formation (Lower Givetian) of the Eifel Synclines crinoid palaeodiversity increased (Fig. 4.1.4). This conclusion is based on the analysis of 66 species from eight genera and correlates with the increase in the overall abundance. The diversification can be regarded (Fig. 4.1.4) as tripartite. Although less distinct, the curve for genera follow the same pattern. The first and minimal maximum is in the Nohn and Ahrdorf formations with nine taxa. The second maximum began in the Junkerberg Formation, with an increase of nearly twice as many (i.e., 17 species). The third and highest maximum of diversity is between the boundary of the Freilingen and lower Cürten formations and has a maximum of 45 species. This is a five-fold increase in palaeodiversity in comparison with the first maximum and approximately a 2.6-times higher palaeodiversity than that of the second maximum (Fig. 4.1.4). This third and maximal phase of diversity abruptly declined in the Cürten Formation – a faunal collapse within the Eifel Synclines is, which is herein designated the "Lower Givetian Crinoid Decline" (Fig. 4.1.4) and discussed in 4.3.2.3.

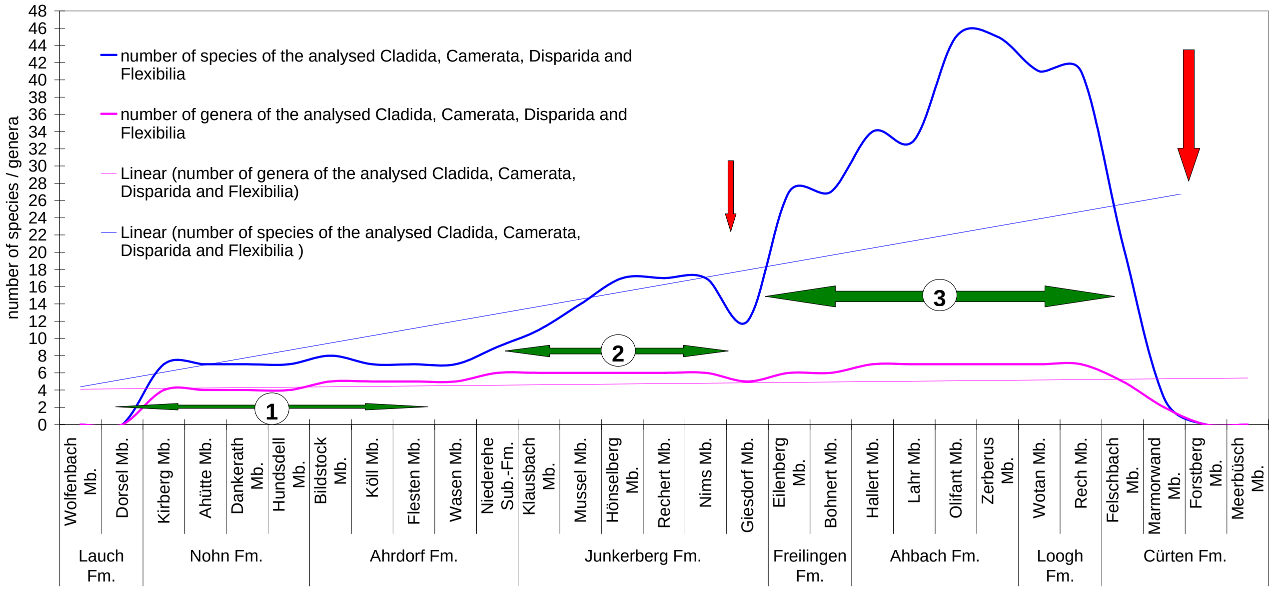


FIGURE 4.1.4—The crinoid palaeodiversity of all studied genera and species within the Middle Devonian of the Eifel Synclines. The species-curve (blue) exemplifies a continuous rising of the palaeodiversity (see average linear), which is tripartite into three separated sections (***1-3***). The rising of the palaeodiversity mainly depend on the differentiation within the studied genera (pink). The small red arrow shows the position of the "*otomari* Event", separating the maxima ***2*** and ***3***; the larger red arrow shows the position of the "Lower Givetian Crinoid Decline", which abruptly declines the highest palaeodiversity (***3***) within the Eifel (compare to 4.3.2.3).

The almost complete disappearance of the crinoids in the Lower Givetian of the Eifel Synclines necessitated study of Givetian crinoids in adjacent sedimentation realms, in order to clarify whether the Lower Givetian Crinoid Decline is a local phenomenon and to understand the development of the crinoid fauna of the Middle Devonian shelf at the SE-margin of the Old Red Continent (compare to Fig. 1.1 within the introduction of this work). Therefore, crinoids of the Bergisch Gladbach-Paffrath Syncline and the Lahn-Dill Syncline, namely the cladid cupressocrinitids and camerate hexacrinitids (Chapter 3.1.3.2.6; BOHATÝ, 2006d; 2008; 2009; BOHATÝ & HERBIG in review) as well as further, the gasterocomoids and sphaerocrinids (BOHATÝ in prep.) are considered. Moreover, stylocrinids (Disparida; Chapter 3.3.3.1; BOHATÝ in review) are known from the Lahn-Dill Syncline, taxocrinids occur in the Bergisch Gladbach-Paffrath Syncline (Flexibilia; BOHATÝ 2006d).

4.1.6 FAUNAL ASSOCIATION AND PALAEODIVERSITY OF THE CRINOIDS FROM THE MIDDLE DEVONIAN OF THE RHENISH MASSIF

Foreword: In the following, famous Devonian crinoid associations of the Rhenish Massif are compared; however, they actually derive from different facies realms (e.g. Rhenish or Hercynic facies).

Lower Devonian

In the Lower Devonian [Upper Siegenian (Upper Pragian) to end of Lower Emsian] approximately 63 crinoid species from 30 genera are known from the "Hunsrückschiefer", exposed between Koblenz, Trier and Mainz (BARTELS et al. 1998; HESS 1999; compare to Fig. 4.1.5). Characteristic pyritised fossils of the four crinoid subclasses are represented by the genera *Codiacrinus*, *Imitatocrinus* and *Parisangulocrinus* (Cladida); *Calycanthocrinus* and *Triacrinus* (Disparida); *Hapalocrinus* and *Thallocrinus* (Camerata) as well as *Eutaxocrinus* (Flexibilia). Furthermore, the "*crinoids of the sandy Lower Devonian up to the Cultrijugatus-Zone*", summarised by SCHMIDT (1941) are also an important fauna. They occur at numerous localities along the western and eastern Rhenish Massif in a time slice between the Upper Siegenian (respectively Upper Pragian) to the Lower Eifelian. 125 species from 34 genera are discussed in this classic monograph, with most specimens preserved as hollow moulds. Especially characteristic are the camerate genera *Ctenocrinus*, *Monstrocrinus* and *Orthocrinus* as well as the cladid *Eifelocrinus*.

Middle Devonian

Within the Eifel Synclines a crinoid association, which is dominated by the diplobathrid camerates *Orthocrinus* and *Monstrocrinus*, is recognised at the Emsian/Eifelian boundary (own, unpublished data). Between the Lower Eifelian and the lowermost Lower Givetian, this highly diverse and abundant crinoid association was established. 66 species from eight genera were studied in the course of this work – more taxa than the famous Hunsrückschiefer(!). Further, the total diversity of the Middle Devonian crinoids from the Eifel Synclines is much more (web-Index of HAUSER 2009: ca. 160 species from ca. 50 genera; however note that this list of species and genera is in need of a taxonomic revision that follows the ICZN) [Fig. 4.1.5]. From an initial critical appraisal, my unpublished data indicates a still higher diversity. Considering the unrevised taxa, approximately 50 genera with more than 200 species are estimated. Therefore, the diversity is approximately 3.4-times higher than that of the Hunsrückschiefer. The HAUSER web-index indicates a crinoid palaeodiversity from the Eifel Synclines as approximately 1.3-times higher, but an initial appraisal of my data indicates a diversity 1.6-times higher than that of the "*crinoids of the sandy Lower Devonian up to the Cultrijugatus-Zone*" of SCHMIDT (1941). This impressively underlines the importance of the crinoids from the Eifel, whose most famous representives are cupressocrinitids and gasterocomoids (Cladida); hexacrinitids, *Eucalyptocrinites* and *Rhipidocrinus* (Camerata); *Stylocrinus*, *Storthingocrinus* and *Haplocrinites* (Disparida) as well as *Eutaxocrinus* and *Ammonicrinus* (Flexibilia).

Hence the Eifel is the most diversified Middle Devonian crinoid region worldwide, whose research essential complement the comparable old, famous crinoid associations of Australia (e.g. JELL et al. 1988); Burma (REED 1908); China (e.g. CHEN & YAO 1993; also see WEBSTER et al. in press), Poland (e.g. GŁUCHOWSKI 1993); the Czech Republik (e.g. PROKOP & PETR 1993; 1995) or the U.S.A. (e.g. GOLDRING 1923).

Between the Lower and the Upper Givetian strata of the Rhenish Massif crinoids are most abundant within the Bergisch Gladbach-Paffrather Syncline and the Lahn-Dill Syncline. This fauna is less diverse and abundant than those of the Hunsrückschiefer and much less so in comparison with the Lower Eifelian to Lower Givetian fauna of the Eifel Synclines. A conservative estimate indicates 20 species (BOHATÝ 2006d; 2008; 2009; BOHATÝ in review; BOHATÝ & HERBIG in review). This could possibly be a result of the Lower Givetian Crinoid Decline (4.3.2.3) – perhaps as much as an eight-fold decrease and, according to own unpublished data, even a ten-fold lower palaeodiversity in comparison to the Lower Eifelian to Lower Givetian crinoid fauna of the Eifel Synclines.

Upper Devonian

Upper Devonian (Frasnian) crinoids also occur within the Eifel, but they are restricted to the vicinity of the Prüm Syncline that yields the only preserved Upper Devonian deposits within the Eifel Synclines (MEYER 1986). In this connection, the famous Frasnian crinoid association of Wallersheim with 24 species from five genera (HAUSER 2002; compare to Fig. 4.1.5) were described. The camerates are represented by the highly diverse and abundant genus *Melocrinitites*, which is associated with the rarer genus *Megaradialocrinus*. The disparids are represented by *Haplocrinites* and *Halysiocrinus*, and the only flexibile is *Dactylocrinus*. Cladids are unknown.

This Frasnian fauna differs from the Middle and Upper Givetian crinoid association of the Rhenish Massif in its taxonomical composition and the dominant taxa as well as in its lower diversity. Considering the so far published number of species of the Eifelian to Lower Givetian of the Eifel Synclines, the species number is about 6.7-times, under consideration of own unpublished data, even ca. 8.4-times lower.

This association of Wallersheim, dominated by *Melocrinites* and *Megaradioalocrinus*, was described as part of an "atypical facies of the Büdesheimer Goniatitenschiefer" by HAUSER (2002). This appraisal cannot be followed herein, because the fossil-rich deposits are part of the *rhenana* Conodont Biozone that characterises the main part of the Oos Formation immediately below the base of the Büdesheim Formation (see GRIMM et al. 2008). Several goniatids, typical for the "Büdesheimer Goniatitenschiefer" (RÖMER 1854; KAYSER 1871), occurred at Wallersheim, as do the rare occurrences of the Oos guide-trilobite *Bradocryphaeus supradevonicus* (pers. information, H. PRESCHER) at Wallersheim, as well as characteristic melocrinids in Oos (own, unpublished data). This fauna indicates an upper Oosian age with a development differing from the type region near village Oos in lithological and facies aspects. However, this corresponds to the upper part of the "Ooser Plattenkalk" of MEYER (1986, p. 173).

The crinoid association of Wallersheim is very similar to the comparably old *Melocrinites*-*Megaradialocrinus*-dominated association of the historical crinoid locality "Breiniger-Berg" near Aachen (NW Rhenish Massif) [own, unpublished data]. In addition, evidence of cladid crinoids is missing within this no longer accessible locality.

Based on the faunal composition, both localities resemble that crinoid association of the Upper Frasnisn Neuville Formation of the Belgian/France Ardennes

(HAUSER 1999; 2003), which are also distinguished by a more diverse *Melocrinites-Megaradialocrinus*-dominated fauna. These localities differ by the presence of the cladid species *Abbreviatocrinites gibber*, *A. inflatus* and *A. sampelayoi* that only was recognised in the Ardennes (HAUSER 1999; 2003).

Within the Rheno-Ardennic Massif these *Melocrinites-Megaradialocrinus*-dominated associations become abruptly distinct directly below the Frasnian/Famennian boundary. This is evidenced by crinoid recoveries from the Büdesheimer Goniatitenschiefer, which can be correlated approximately with the "Matagne Slate" of Belgian (MEYER 1986). At this juncture, pseudo-planktonic amabilicrinitids (WEBSTER et al. 2003), which are attached to drift-wood, were recovered and are associated with platycrinitids (pers. information, G. D. WEBSTER) [own, unpublished data; compare to Chapter 4.3.2.3]. The three(?) species indicate a "Carboniferous character" by morphological and taxonomical similarities to the described Lower Carboniferous fauna of the Rhenish Massif (e.g. of Wülfrath-Aprath, see HAUDE & THOMAS 1992) as well as to those of the Iran [WEBSTER et al. 2003; including revisions of the amabilicrinitids (*sic*!) of HAUDE & THOMAS]. Unpublished data indicates an approximate 70-fold decrease in palaeodiversity of the Büdesheim crinoids in comparison to the crinoids from the Middle Devonian of the Eifel. This extremely low-diverse fauna characterises the herein designated "Frasnian-Famennian Crinoid Decline" (Fig. 4.1.5; see 4.3.2.3).

With consideration of the different facies realms, five faunal groups are recognised in the Rheno-Ardennic Devonian (Fig. 4.1.5): 1, The Lower Devonian crinoids of the Hunsrückschiefer, which lived in Hercynic Facies; 2, the crinoids of the upper Lower Devonian to lowermost Middle Devonian, which lived in the sandy-clayey realm of the Rheinish Facies; 3a, the Middle Devonian crinoids of the Eifel Synclines, which lived in carbonate shelf realms of the Rhenish Facies and were limited within the Eifel by the Lower Givetian Crinoid Decline, but can be traced in low diversity and individual numbers within the eastern Rhenisch Massif (3b); 4, the Frasnian *Melocrinites-Megaradialocrinus*-dominated crinoid association of the deeper water and 5, the Upper Frasnian to Lower Famennian, pseudo-planktonic amabilicrinitid-dominated association of Büdesheim, associated with the "Kellwasser Crisis" [see e.g. SCHINDLER (1990) for this crisis].

Articulated crinoids are not known until the Devonian/Carboniferous boundary of the Rheno-Ardennic Massif. The most famous crinoid locality is Wülfrath-Aprath (see above). These Lower Carboniferous crinoids are not considered further herein.

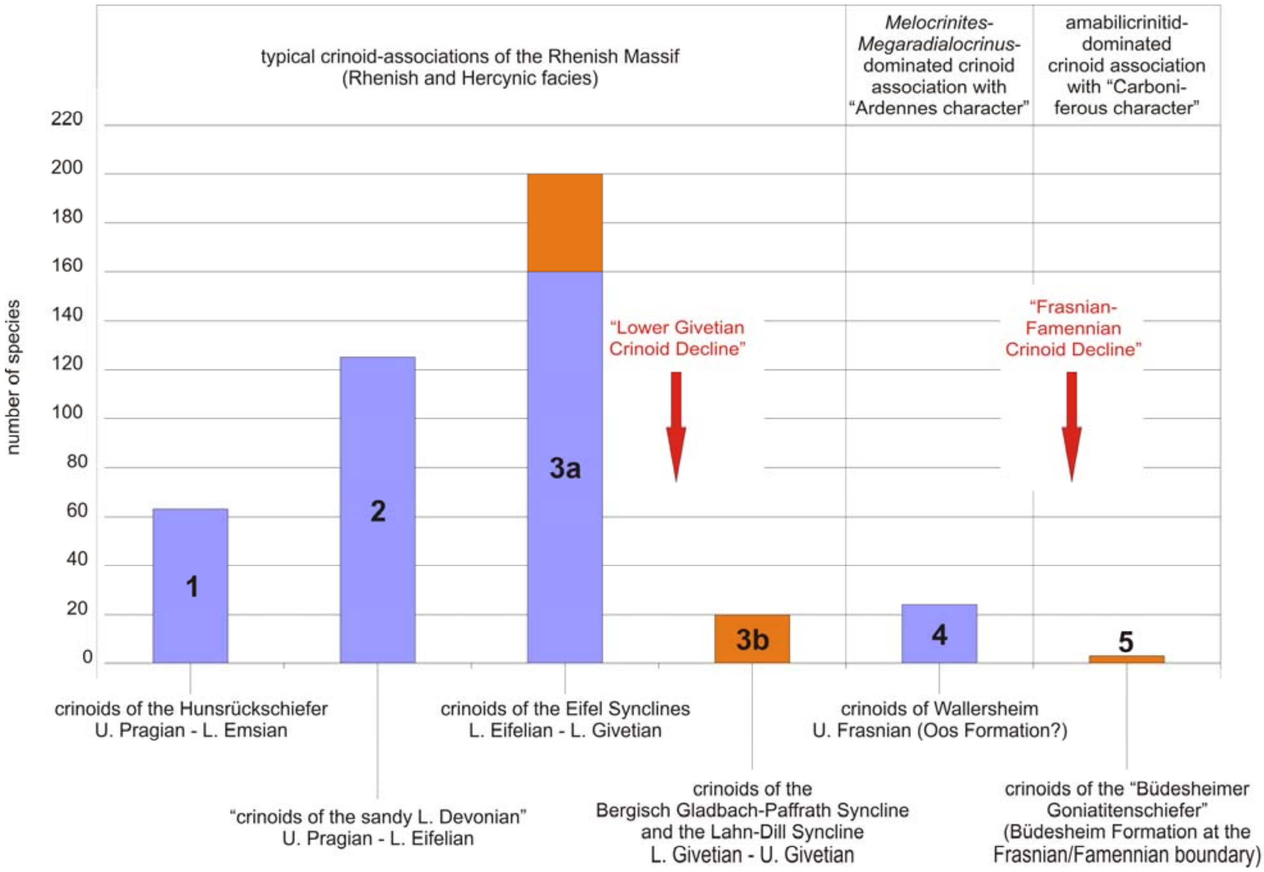


FIGURE 4.1.5—The palaeodiversity of the five crinoid associations within the Rheno-Ardennic Devonian; published number of species = **blue bars**; estimated number of species based on own, unpublished data = **orange bars**. ***1***, Number of Lower Devonian crinoids of the Hunsrückschiefer, which lived in Hercynic Facies (after BARTELS et al. 1998 and HESS 1999: 63 species); ***2***, number of crinoids of the upper Lower Devonian to lowermost Middle Devonian, which lived in Rheinish (sandy-clayey) Facies (after SCHMIDT 1941: 125 species); ***3a***, number of Middle Devonian crinoids of the Eifel Synclines (after HAUSER web-index: 160 species; estimated number of species based on own, unpublished data: 200 species), which lived in carbonate shelf facies and were limited within the Eifel by the Lower Givetian Crinoid Decline; these can be traced in low diversity and abundance up to the Upper Givetian of the eastern Rhenish Massif (***3b***) [estimated number of species based on unpublished data: 20 species]; ***4***, number of the Frasnian *Melocrinites*-*Megaradialocrinus*-dominated crinoids of Wallersheim (after HAUSER 2002: 24 species); ***5***, number of Upper Frasnian to Lower Famennian, pseudo-planktonic amabilicrinitid-dominated crinoids of Büdesheim, associated with the "Kellwasser Crisis" (estimated number of species based on own, unpublished data: three species). Lower Givetian Crinoid Decline and Frasnian-Famennian Crinoid Decline are marked by red arrows.

4.2 PALAEOBIOLOGY

4.2.1 PHYLOGENY AND ECOLOGY ADAPTATIONS RECOGNISED IN MORPHOLOGICAL TRENDS

Several general morphological trends are recognised in the studied Middle Devonian crinoids from the Eifel Synclines. They can be categorised as the following: 1, morphological adaptations based on palaeoenvironmental changes – especially the increasing of biostromal developments within shallow-water realms; 2, morphological trends due to the increased occurrence of "predators" and 3, morphological adaptations based on the competition of habitat colonisation within ecological niches. In this connection it is possible to separate (1) chronological continuously trends, which characterised phylogenetical evolutions from (2) chronologically non-continuously trends that implies morphological adaptations to the ecological parameters.

The increase in biostromal developments within shallow-water realms

A successive establishment of biostromal facies within the shallow-water realm was recognised at the boundary of the Lower and Middle Devonian to the lower Cürten Formation (Lower Givetian) of the Eifel. This does not exclude the development of non-biostromal facies realms, especially at the Eifelian/Givetian boundary (WINTER 1965). In general, the abundance of hydrodynamic turbulent environments increased within this time interval and led to an increased number of crinoid groups with compact, relatively robust skeletons, as exemplified in the cladid cupressocrinitids. This morphological trend is represented by the "faunal group 3a" (see 4.1.6; Fig. 4.1.5) and can be traced up to the Lower Givetian Crinoid Decline of the Eifel Synclines. It is also recognised at additional localities from the Rhenish Massif (Bergisch Gladbach-Paffrather Syncline; Lahn-Dill Syncline; "faunal group 3b") up to the Upper Givetian. In contrast to the Middle Devonian crinoids of the Eifel Synclines, this trend is less apparent in the Frasnian *Melocrinites-Megaradialocrinus*-dominated "faunal group 4" (compare to 4.1.6; Fig. 4.1.5) and was displaced below the Frasnian/Famennian boundary by the more filigree morphologies of the amabilicrinitid-dominated "faunal group 5" (4.1.6; Fig. 4.1.5) of Büdesheim.

The increased occurrence of “predators”

Within the highly diverse palaeocommunities of the Upper Eifelian and the Eifelian/Givetian boundary, a significant predation pressure is assumed by the increased rate of platyceratid gastropods (Chapter 4.3.1.1) and placoderms, in comparison to the Lower to Middle Eifelian (own, unpublished data). This correlates with a morphological adaptation of the studied crinoid skeletons, which e.g. show effective protective mechanisms, like the accelerated development of spines (hexacrinitids, Chapter 3.2; *Ammonicrinus*, Chapter 3.4), a double layered endoskeleton (cupressocrinitids, Chapter 3.1), the “locking” of the arm-crown (*Stylocrinus*, Chapter 3.3) or the “enrolling” of the crown into the stem (*Ammonicrinus*, Chapter 3.4). Therefore, in many instance, predator-driven evolutions have to be assumed.

The competition of habitat colonisation within ecological niches

With the start of the carbonate sedimentation at the boundary of the Lower and Middle Devonian, the abundance and diversity of the epifaunal biota increased in the shallow-water habitats of the Eifel (own, unpublished data). As diversity increased toward the Upper Eifelian, the maximum occurred near the Eifelian/Givetian boundary (WINTER 1965). This palaeodiversity trend also occurs in crinoids (Fig. 4.1.4). Therefore, an increased habitat-population was recognised, and it is herein proposed that the crinoids presumably contra balanced this circumstance by morphological adaptations of the holdfast, the stem and of the crown.

A general morphological plasticity of the holdfasts and stems was recognised in various facies realms of the Eifel. Variability occurs both intraspecifically and among taxa. Adaptation to the specific bottom conditions yielded attachment discs on hardgrounds and dendritic holdfasts on soft-bottoms. Similarly, crinoids with shorter and more compact columns typically occurred in turbulent environments, whereas those with longer and more filigree stems are present mainly in less turbulent habitats. These ecological controlled skeletal variabilities contrast with a recognised evolutional trend, which presumably demonstrate the necessity of settlement in different hydrodynamic levels, or in atypical hydrodynamic habitats. As a result, the regarding taxa occasionally show decided morphological variances of the crown. An example for this are the cladid gasterocomoids (compare to BOHATÝ 2006a; HAUDE 2007), whose upright crown is characterised by five relatively filigree branching arms. They settled predominantly in less turbulent habitats, but presumably were forced to avoid into more turbulent environments due to an increased population-concurrence within their preferred ecological niches (BOHATÝ 2006a). This led to morphologically adaptations of the skeletons, like the sloping of the arm-crown, in combination with the reduction from five to four arms, which obviously allows covering at the bottom and, therefore, living in those turbulent environments. This morphological trend was recognised in several profiles within the Eifel, from the Eifelian up to the Givetian in genera *Gasterocoma*, *Nanocrinus* and *Trapezocrinus* (Chapter 4.3.2.2; Fig. 4.3.4).

Morphological trends in the subclass Cladida

The cupressocrinitids (BOHATÝ 2005a; 2006b; 2009; Chapter 3.1) have three continuous morphological trends: 1, a trend from four to three peripheral columnal axial canals; 2, a trend from longer to shorter arms and 3, only in robustocrinids, on trend from unsculptured plates with thin cross sections to sculptured ossicles with massive cross sections.

Abbreviatocrinites and *Cupressocrinites* include species with both three and four peripheral columnal axial canals. Whereas the majority of older taxa are characterised by four canals (e.g. *A. abbreviatus*, *C. ornamentus*), rare occurrences of species that have three canals occurred between the Eifelian and the Givetian. In this connection, 61.5% of the *Abbreviatocrinites*-species show four, but in contrast only 38.5% three canals. In genus *Cupressocrinites* 75.0% have four but only 25.0% show three canals. Genus *Robustocrinites*, which is restricted to the Eifelian, invariably show four canals – likewise genus *Procupressocrinus*. Chronographically classified, the following distribution was recognised under consideration of all species: 25 species within the Middle Devonian of the Eifel show four canals; seven solely Eifelian, eight in the Eifelian and Givetian and three solely Givetian. In contrast to this the following species have three canals: None in the Eifelian; seven in the Eifelian and Givetian boundary interval; and none in the Givetian. Because no solely Eifelian species with three canals was recognised and this time slice was, therefore, dominated by those showing four canals, the consideration of the exclusive occurrence of species with three canals (*A. gibber*, *A. inflatus* and *A. sampelayoi*) in younger formations outside the working scope, namely within the Frasnian of the Belgian/France Ardennes presumably indicates a morphological trend from older species with four to younger species with three canals (BOHATÝ 2006b; 2009). This obviously is an evolutional respectively phylogenetical trend (Fig. 4.2.1).

The length of the crinoid arms is another morphological trend. Among the 25 crupressocrinitid species in the Middle Devonian of the Eifel, eight species respectively 32.0% have relatively long arms, and 17 species (68.0%) have rather short arms (BOHATÝ 2006b, pls. 1-11). Chronographically through the Eifel strata, the following distribution was recognised: The Eifelian has four species with long but only three with shorter arms. Within the Eifelian and Givetian boundary sequence, only three species with long but 12 with shorter arms are known. In the youngest Givetian only one species with long but two with shorter arms have been found. This trend toward shorter arms corresponds to an increasing of biostromal developments (see above). Presumably, short and compact arms were an advantage in turbulent environments. Also this morphological trend apparently continuous in younger Devonian formations as recognised within the Frasnian of the Belgian/France Ardennes, where only cupressocrinitid species with relatively short arms were found (*A. gibber*, *A. inflatus* and *A. sampelayoi*; compare to BOHATÝ 2006b; 2009).

The arm-shortening trend of *Robustocrinites* is linked to the development of wider brachial cross sections and monolamellar exoplacoid layer plate sculpturing (Chapter 3.1.4; Fig. 3.1.8). The oldest species, *R. galeatus* (Hundsdell Member of the Nohn Formation to upper Nims Member of the Junkerberg Formation, Eifelian), has especially long arms and unsculptured plates with a thin cross section (BOHATÝ 2006b, pl. 7, fig. 2a). The second oldest species, *R. scaber* (Mussel to upper Nims members of the Junkerberg Formation), has shorter arms, wider ossicle cross sections and a fine plate sculpturing (2006b, pl. 7, fig. 3). The youngest species, *R. cataphractus* (Hönselberg to upper Nims members of the Junkerberg Formation), has the shortest arms of the genus, as well as massive plate cross sections and strongly sculptured ossicles (Chapter 3.1.3.2.13; Fig. 3.1.6).

The biostratigraphical distribution of the three robustocrinids is illustrated in Fig. 3.1.8.

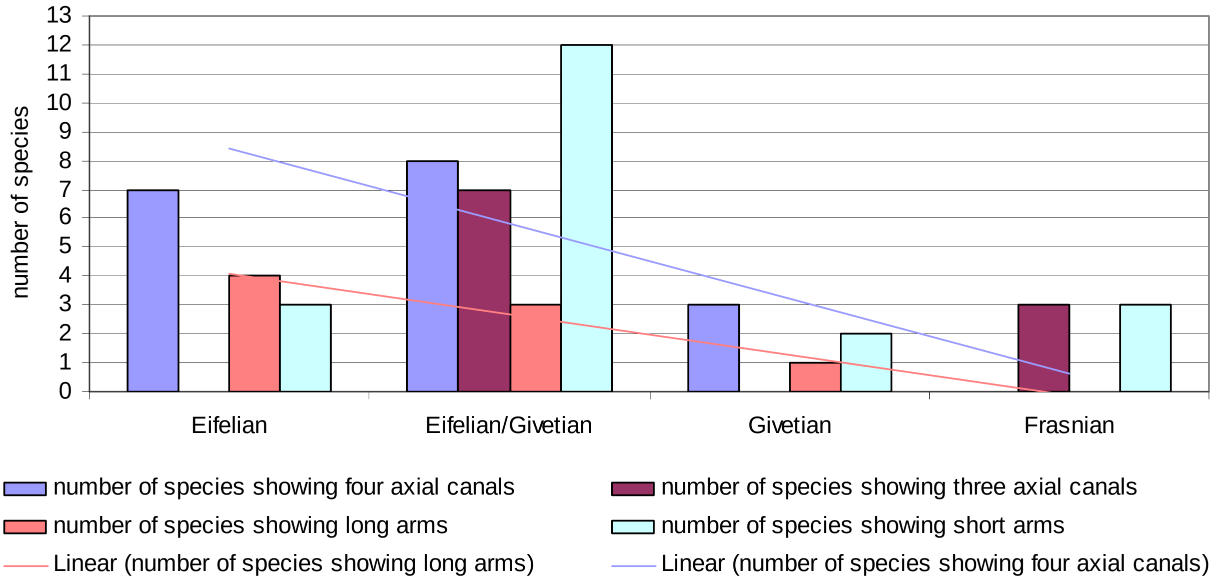


FIGURE 4.2.1—Distribution of cupressocrinitid species with four or three columnal axial canals and long or short arms. Data based on Tab. 4.1.1 under consideration of the three known Frasnian species (*A. gibber*, *A. inflatus* and *A. sampelayoi*) from the Belgian/France Ardennes. The linears indicated the general morphological trends that reduced those taxa with four axial canals and longer arms from the Eifelian to the Frasnian.

Morphological trends in the subclass Camerata

The camerates *Hexacrinites* and *Megaradialocrinus* (Chapter 3.2) have two morphological trends: 1, the first a stratigraphically discontinuous trend from less to more strongly sculptured/spinose crown ossicles, which presumably depended on the ecological framework; and 2, the second a stratigraphically continuous trend of the arm morphology.

Especially in the Upper Eifelian, the Eifelian/Givetian boundary and the lowermost Lower Givetian (Freilingen to Loogh formations), both camerate genera have well-sculptured, spinose plates (e.g., *M. spinosus).* This species occurred in the Freilingen Formation and is associated with strongly sculptured morphotypes of the *Hexacrinites* type species, *H. interscapularis* (**P. interscapularis*).

This general morphological trend of a successive increase in plate sculpturing in the Lower Eifelian through the lowermost Lower Givetian is recognised both inter- and intraspecifically in several species of *Hexacrinites and Megaradialocrinus*. Presumably, this can be interpreted as a reaction of the rising of the palaeodiversity between the boundary of the Lower and Middle Devonian up to the Lower Givetian and was attended by the advanced colonisation of the ecological niches within the manifold facial realms (WINTER 1965).

Fossil localities with strongly sculptured crinoids (e.g. spinose hexacrinitids), are characterised by a high abundance of platyceratid gastropods (Chapter 4.3.1.1). Less sculptured cups from younger formations of the Rhenish Massif (BOHATÝ 2008) indicates that this morphological trend cannot be interpreted as a phylogenetic trend but, rather, as adaptations to specific ecological conditions.

In contrast, *Megaradialocrinus* has a continuous morphological trend in arm branching pattern that indicates a phylogenetical lineage: The oldest form had two straight-lined rami in each ray and the youngest form developed zigzagged rami with few nearly orthogonal branching ramules, as detailed discussed in Chapter 3.2.8 (Fig. 3.2.8).

Morphological trends in the subclass Disparida

Similar to the camerate hexacrinitids, the disparid *Stylocrinus* has a stratigraphically discontinuously morphological trend of less to more strongly sculptured crown ossicles. This is demonstrate by the comparison of the less sculptured *S. tabulatus* (Chapter 3.3.4.1.3; Fig. 3.3.2) from the Lower Eifelian to the intensively sculptured *S. granulatus* (3.3.4.1.4; Fig. 3.3.5), with a first occurrence not until the Upper Eifelian. This species is associated with the strongly sculptured camerates *M. spinosus* and *H. interscapularis* (see above). In contrast, *Stylocrinus* cups from the Middle Givetian of the Lahn-Dill Syncline have less intensively sculptured ossicles. Intraspecific variability toward higher spinosity of the highly plastic *S. tabulatus* occurs in especially diverse palaeocommunities. This is a tendency for sculpturing in the Upper Eifelian and Eifelian/Givetian boundary than in the Lower Eifelian.

In summary, the previous data indicate that, under consideration of the comparison with the camerate hexacrinitids, also the plate sculpturing of *Stylocrinus* have to be characterised as adaptation of special environmental conditions.

Morphological trends in the subclass Flexibilia

The flexibile *Ammonicrinus* has a spectacular and stratigraphically continuous morphological trend from the Emsian to the Givetian, which clearly indicates a phylogenetic lineage (Chapter 3.4). The oldest studied form, *A. kredreoletensis* is characterised by a crown that is nearly unprotected laterally and not encased by the mesistele. Spines are also not present(?). The younger forms have strongly modified mesistele columnals, which allows complete encasement of the crown, and the skeleton developed movable spines. This trend may also indicate a predator-driven evolution.

4.2.2 GROWTH ANOMALIES

In the literature, “growth anomalies” have only been present previously as isolated illustrations (e.g. in HAUSER 1997). Only six publications treated anomalies of Middle Devonian crinoids in detail (MCINTOSH 1979; SIEVERTS-DORECK 1950; 1963; WANNER 1954 and BOHATÝ 2006a; 2009).

Cladida

In the cladid cupressocrinitids growth anomalies could be categorised in two groups; these are: 1, Growth anomalies expressed externally (see Chapter 3.1.5.1) and 2, growth anomalies not expressed externally (Chapter 3.1.5.2). The most common growth anomaly not expressed externally is the cupressocrinitid columnal axial canal (Figs. 3.1.9.5-7). In contrast, individuals with additional (Figs. 3.1.9.4, 3.1.9.7) or reduced number of ossicles (Fig. 3.1.9.5) or with quadrangular or hexagonal symmetry (Figs. 3.1.9.1-3) are visible externally. Because of the frequency of anomalously grown axial canals or symmetry aberrations among several localities, the genetic basis of these interferences is assumed (see detailed discussion in 3.1.5.1).

Individuals with a plate missing or added (Figs. 3.1.9.8, 3.1.9.10-13), with an inexplicable ossicular swelling (Fig. 3.1.9.9) or a modified exobrachial layer (Figs. 3.1.9.14-15) are not recognisable as regeneration, “wound healings” or as documented “generic” abnormalities, and no direct evidence of predatory influence can be recognised. Therefore, these modifications are summarised as growth anomalies without classifiable causes – without indications of external influences (Chapter 3.1.5.2).

Skeletal growth anomalies in cupressocrinitids are relatively common. This conclusion also applies to additional groups in the superfamily Gasterocomoidea [e.g., as proven for *Gasterocoma*, *Lecythocrinus*, *Nanocrinus* and *Tetrapleurocrinus* (BOHATÝ 2006a)]. Abnormalities were more common among gasterocomoids with four arms (*Nanocrinus*, *Tetrapleurocrinus*) or with four arms and sloping of the crowns (e.g. in *Trapezocrinus*), and abnormalities commonly occurred on the radial plate or anal region (BOHATÝ 2006a).

Increased rates of anomalies were also recognised in the cladid bactrocrinids from the Middle Devonian of America (MCINTOSH 1979) that correspond to those recognised herein. Similar modifications were also identified in the Eifel (BOHATÝ 2005b, p. 399, figs. 5a-b; p. 405, fig. 1b).

Camerata

The most common anomalies in the camerate hexacrinitids are similar to those of the gasterocomoids; including anomalies mostly affect the radial and anal regions. In this connection, e.g. the aboral cups, discussed in Chapter 3.2 have shortened radial plates (Fig. 3.2.5.5), additional plates (Fig. 3.2.5.6), horizontally divided radials (Fig. 3.2.5.7) or additional intercalated plates (Fig. 3.2.5.8). However, these growth anomalies are relatively rare. In addition the following anomalies were also recognised: one cup of *M. turritus* with a vertically divided basal plate (BOHATÝ 2006e, fig. 6.4), One cup of *M. crispus* with two combined radials (BOHATÝ 2006c, fig. 3c), one cup of *M. unterthalensis* with one horizontally divided radial plate (BOHATÝ 2006d, fig. 3) and one cup of (?)*M. granuliferus* with the radial facet of two radials combined, resulting in an anomalous four-armed individual (BOHATÝ 2008, fig. 3d).

One type of skeletal modification was formerly considered a growth anomaly of a *M. elongatus*-cup (compare to SIEVERTS-DORECK 1950, p. 81; figs. 1a-c). New findings of those individuals (Chapter 3.2, Figs. 3.2.5.9-10) indicates a sloping in the CD interray or in the A ray direction. This development maybe interpreted as an ecological adaptation of such individuals living in hydrodynamic more turbulent environments (see 4.3.2.2, Fig. 4.3.5).

Relative to the cladids, growth anomalies in camerate crinoids are rare findings. Besides the hexacrinitids, only few abnormal specimens have been reported (see affected *Melocrinites*-cup with tetrahedral symmetry from the Frasnian of Wallersheim; HAUSER 2002, pl. 10, fig. 5).

Disparida

Considering the large number of stylocrinid aboral cups, it is remarkable that only two individuals of this genus with growth anomalies were recovered (Chapter 3.3.5). This contrasts sharply with the cladids and camerates. In the gasterocomoids (*Nanocrinus* and *Trapezocrinus*) nearly one of every 10 cups exhibit a growth anomaly, whereas approximately only one of 750 cups of the disparid *Stylocrinus* is affected. In another disparid, *Storthingocrinus*, isolated aboral cups are also very abundant but abnormalities are extremely rare (own, unpublished data).

Examples of two *Stylocrinus* aboral cups with abnormalities are one aboral cup with an anomalous, additional basal plate (Chapter 3.3.5.1; Figs. 3.3.7.1-2); according to the cupressocrinitid-anomalies, this kind of pathology can be classified as a “growth anomaly without recognisable external influences” and could probably be characterised as ‘‘genetic abnormality”. The second aboral cup (Figs. 3.3.2.18-19) has an uncommon base with a narrow stem-insertion. However, this may be attributed to a skeletal (?)regeneration of the base (compare to 4.2.3). No growth abnormalities from other Middle Devonian disparids have been reported in the literature.

Flexibilia

Preservation of the crown of the flexible *Ammonicrinus* is rare, but no new abnormal specimens have been recovered (Chapter 3.4). However, the second radianal plate in the plate diagram of *Ammonicrinus* (UBAGHS 1952, p. 205, fig. 1) is based on an growth anomaly, as already assumed by WANNER (1954, p. 235).

4.2.3 REGENERATION PROCESSES

In contrast to growth anomalies, regeneration in fossil crinoids have been discussed intensively in the literature (see Chapter 3.1.6.2 for detailed bibliographical references). Especially the work of GAHN & BAUMILLER (2005) can be compared to the Middle Devonian crinoids of the Eifel Synclines.

Evidence for regeneration in Middle Devonian crinoids is from cladids, camerates and, presumably, also from disparids. No evidence of regeneration has been identified among the flexibiles.

Cladida

Skeletal regeneration processes are recognised in the cladid cupressocrinitids (Chapter 3.1.6.2). It was possible to distinguish between “wound healings” (3.1.6.1) and “real regenerations” (3.1.6.2), e.g. indicated by reconstructions of lost arms.

Different sized wound healings in numerous small ossicles were recognised and are obviously a response of nonlethal injured individuals. Possible causes of these wound healings could be injuries caused by predators or possibly impact material in the bedload (see affected cups in Chapter 3.1.5.1; Figs. 3.1.9.16-19).

The recognition of “real regenerations” in the studied skeletons was mainly possible by transferring results of younger literature data (see above) to the crinoids of the Eifel and allowed the identification of regenerated arms. The cupressocrinitid arms herein recognised as regenerated were all smaller than regularly developed arms (Figs. 3.1.6.1; 3.1.7.1; 3.1.9.20). Regeneration in the cupressocrinitid arms was presumably more common than the cup regeneration. Whereas a regenerated arm is smaller, the brachial is nearly as perfectly shaped as the original. The regeneration of the cup principally leads to distorted cup.

Camerata

Similarly, regeneration is recognised in camerates. Smaller and most probably regenerated arms also occurred in the hexacrinitids. This skeletal modification was also recognised in one crown of *M. marginatus,* with one regenerated, smaller and irregularly branched arm (compare to “Remarks” in Chapter 3.2.7.3.1; also see left rami in B ray of the crown figured in BOHATÝ & HERBIG 2007, p. 733, fig. 4). It is most interesting that the disadvantage of the smaller regenerated arms is counterbalanced by additional branching and, therefore, by an increased pinnulated surface.

Disparida

In the disparid *Stylocrinus* one aboral cup (Figs. 3.3.2.18-19) has an uncommon base with a narrow stem insertion, which either can be attributed to a skeletal regeneration of the base or to a growth anomaly (compare to 4.2.2). Thus, regeneration is relatively rare among disparids, if it occurs at all.

4.3 PALAEOECOLOGY

4.3.1 SYNECOLOGY

4.3.1.1 “Predators”

In this study, extensive damage to an individual is inferred to have been the action of predators in the Middle Devonian of the Eifel region. Subsequently, regeneration demonstrated predation, but the lack of regeneration could be either the result of predation that was lethal or no predation at all. The cupressocrinitids exhibited the effects of predation relatively commonly (Chapter 3.1.7). However, only a few examples are known from individuals of the remaining groups, camerates, disparids and flexibles.

Cladida

Chapter 3.1.7 treats pre- and postmortem borings and bite marks on cupressocrinitid crown-ossicles, which partly could be classified. In this regard, it was possible to distinguish between pre- and postmortem borings due to the present or absent of regeneration response in the stereom. A summary of these results is given below:

Postmortem multiple borings are frequent on the skeletons of *C. elongatus* (Chapter 3.1.7.1; Fig. 3.1.10.8) but less frequently in *C. crassus* (Fig. 3.1.10.9). Both species are covered by a thin and monolamellar exoplacoid layer, which apparently offered less resistance against boring organisms, in contrast to the multilamellar layers of *Abbreviatocrinites*. Platyceratid gastropods are discussed as a possible borer (SIEVERTS-DORECK 1963) but this theory cannot be verified.

Pre- and postmortem incurred single borings are present on the ossicles of *A. a. abbreviatus*, *A. geminatus* and *R. cataphractus* but most of the mass occurred postmortem. One of these single boring traces is filled by a trepostome bryozoan (Figs. 3.1.6.3; 3.1.7.2). BAUMILLER & MACURDA (1995) and BAUMILLER (1990; 1993) documented borings on Palaeozoic blastoids and crinoids. Platyceratid gastropods were also discussed as the possible borers.

Fig. 3.1.10.5 presumably has a deep, oval boring on a basal plate of *A. abbreviatus*. The visible stereomatic reaction in the form of an annulus-like swelling indicates that the single boring occurred premortem.

Furthermore, SEM-observations of thin cross-sections of the multilamellar exoplacoid layer of *A. geminatus* exhibits potentially premortem microendolithic borings, which are lined with marcasite-crystal agglomerates (Fig. 3.1.10.10).

Identifiable bite marks at cupressocrinitids (Fig. 3.1.10.7) are rare. They are possibly attributed to cephalopods, placoderms or arthropods. Premortem bite marks are recognised as nonlethal injuries, because they accompanied by "wound healings".

Camerata

Platyceratid gastropods interacted with hexacrinitids. In this context, strongly sculptured calyx plates, such as in spinose hexacrinitids were commonly associated with numerous shells of platyceratid gastropods (own, unpublished data). These taxa have stout spines on the posterior interray plates below the anal openings or a central spine on top of the tegmen (Chapter 3.2.8; Fig. 3.2.9).

Rare cup findings with attached platyceratids proved that these positions correspond to that positions were these gastropods attached the individuals, most likely for coprophages feeding (e.g. HESS et al. 1999, p. 56, fig. 63). This indicates a predator-driven evolution. Several isolated shells of platyceratid gastropods show such specific serrated apertural margins (e.g. KEYES 1888, pl. 1) thus, after the puzzle principle, it was already possible to identify the according hexacrinitid-tegmen on species level(!) [own, unpublished data]. In some instance, a fossil lacks of a former attached platyceratid, but specific marks or stereomatic reactions indicate the former presence of a gastropod. These marks were caused mostly by the lip of the gastropod shell and have been discussed by KEYES (1888, pl. 1, fig. 7). Such marks can also be identified in three Middle Devonian hexacrinitids from the Eifel (Figs. 4.3.1.1-2) and are frequent in the (also monobathrid) camerate *Melocrinites* from the Frasnian of the Belgian/France Ardennes (e.g. HAUSER 1999, pl. 12, fig. 1a).

Certain abnormalities in *Megaradialocrinus* were probably caused by the lip of a gastropod shell. These are in the shape of an annulus as a deep trench with a central node or ridge (Fig. 4.3.1.3). These were incorrectly interpreted as "exceptional development of the anal region" by HAUSER (1997) and named "*Subhexacrinites*", which is, herein, designated a junior synonym of *Megaradialocrinus* (see "Remark" in Chapter 3.2.7.3.1).

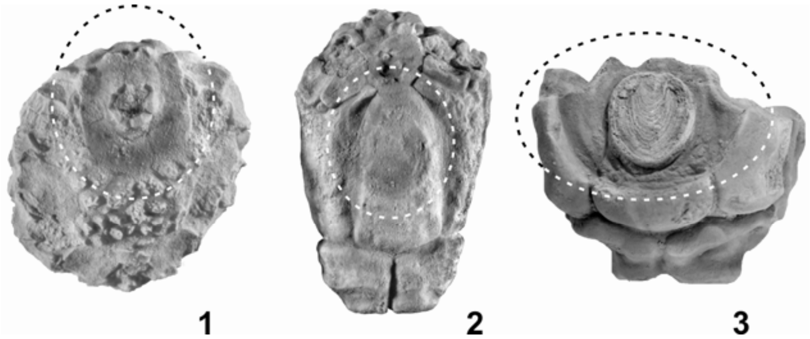


FIGURE 4.3.1—Platyceratid traces on isolated *Megaradialocrinus* aboral cups from the lowermost Lower Givertian of the Gerolstein Syncline. ***1***, Oral view of *M. elongatus* with a platyceratid trace surrounding the anal opening (HEIN collection, no repository), x 2.4; ***2***, lateral view of *M. elongatus* with a platyceratid trace on the anal plate (HEIN collection, no repository), x 1.5; ***3***, lateral view of *M. exsculptus*, showing a annulus like trench with a central ridge coursed by a platyceratid gastropod (LEUNISSEN collection, no repository), x 1.8.

Disparida

Postmortem boring traces in stylocrinid skeletons (Chapter 3.3.5.2) are very similar to the borings on the isolated radials of *Edriocrinus* sp., figured by PROKOP & PETR (1995, pl. 1, figs. 1-16). Two types of borings are recognised: (1) A common rectilinear mostly endolithic boring type of unknown affinity (Figs. 3.3.8.1-3, 3.3.8.6-9) and (2) a rare surficial and meandering boring, which possibly can be attributed to boring bryozoans and/or poriferas (Figs. 3.3.8.4-5). They are discussed in Chapter 3.3.5.2.

One aboral cup of *Stylocrinus tabulatus* represents the first non-platyceratid gastropod trace fossil observed on a crinoid skeleton and was identified as the radular fossil ichnogenus *Radulichnus* (Fig. 3.3.9). The trace can be compared to recently detected gastropod grazing traces on Eifelian brachiopods (GRIGO, in review). These traces were attributed to the activity of polyplacophorid and patellid gastropods (VOIGT 1977), but their affinity remains unclear.

Flexibilia

Clear indications of "predators" could not be verified in the flexible genus *Ammonicrinus*. However, potential adaptation to avoid predation may exist (Chapter 3.4): The older taxa have spineless skeletons, and the younger forms have echinoid-like spines.

4.3.1.2 Epibionts

Epibionts on Palaeozoic crinoids were discussed in numerous publications (see Chapter 3.1.8 for literature data). But the majority of epizoans recognised herein were only described on isolated columnals (compare to GŁUCHOWSKI 2005). Within the Middle Devonian of the Eifel Synclines, epibionts occur on cups and crowns, which allowed differentiating between pre- and postmortem settlement and gave information about the rate of growth of the epizoans or their preferred hardground.

Cladida

Chapter 3.1.8 extensively discussed which epibionts settled pre- and/or postmortem on the studied cupressocrinitids (q.v.), and the majority of the epibiontic encrustations probably occurred postmortem. In summary, the following epibionts could be recognised:

Bryozoans (Chapter 3.1.8.1) are the most abundant epibionts on the skeletons of the Middle Devonian cupressocrinitids of the Rhenish Massif. These are: “Cyclostome bryozoans” (*Hederella* sp.) on *Abbreviatocrinites nodosus* and trepostome bryozoans (?*Eostenopora* sp.) on *A. nodosus*, *A. schreueri* and *P. gracilis*. The length of the columnals of *A. geminatus* and *P. gracilis* that are infested by fenestrate bryozoans (Fig. 3.1.11.1), as well as some embedding patterns of fenestrate bryozoans located underneath the attached stem, allows the presumption of a premortem settlement. Strong evidence for the settlement of a living stem of *C. hieroglyphicus* is given in Figs. 3.1.11.16-18. The example is encrusted by the holdfast of a fenestrate bryozoan (*Cyclopelta* sp.) that grows all around the column without contact to the crenularium.

One observed cup of *A. a. abbreviatus* (Fig. 3.1.11.9) as well as one isolated radial and arm plate of *A. geminatus* have rare postmortem encrustings of the holdfasts of other cladid crinoids (?*P. gracilis*).

Also postmortem encrustings of microconchid valves are common among cupressocrinitids (e.g. Fig. 3.1.11.8).

The predominantly postmortem settlement of tabulate corals was recognised in a few cupressocrinitids. The most common epibiontic tabulates were auloporids, such as *Aulopora* cf. *A. serpens minor* (e.g. Fig. 3.1.11.5), *A.* cf. *A. s. serpens* (Fig. 3.1.11.11) and favositids (*Favosites* cf. *F. goldfussi*) [Fig. 3.1.11.12], settling on *A. geminatus* and *A. nodosus*. Fig. 3.1.11.20 shows a completely overgrown cup of *A. nodosus*.

The rugose corals *Glossophyllum soetenicum* (Fig. 3.1.11.3) and *Thamnophyllum caespitosum* (e.g. Figs. 3.1.11.14-15) settled postmortem on disarticulated cupressocrinitid stems and isolated ossicles.

Furthermore, indeterminable stromatoporoids completely encrusted some articulated cups of *A. a. abbreviatus* (e.g. Fig. 3.1.11.10).

Camerata

Similar to the cladid cupressocrinitids, hexacrinitids have postmortem settlement of diverse epibionts. But based on the lower number of examples, these were relatively rare. Examples include one aboral cup of *Megaradialocrinus globohirsutus* (Figs. 3.2.7.19-21), which was postmortem encrusted by an undeterminable trepostome bryozoan. Another example of a postmortal encrustation is documented in an aboral cup of *Hexacrinites pateraeformis*, which was infested by the favositid coral *Favosites* cf. *F. goldfussi* (Fig. 3.2.3.1).

Disparida

In spite of the huge number of *Stylocrinus* cups discovered, only one example of an attached epibiont was observed. This stylocrinid was infested postmortem by an undeterminable rugose coral (Fig. 3.3.10).

Flexibilia

Postmortem epizoan encrustation of isolated *Ammonicrinus* ossicles is discussed in Chapter 3.4.6. The following epibionts could be recognised:

Most are encrusting of bryozoans on *A. sulcatus* columnals. In this connection, the trepostome genera *Leptotrypella* (e.g. Fig. 3.4.10.1), *Eostenopora* (Fig. 3.4.10.4), the cystoporate genera *Eridopora* (Fig. 3.4.10.2), *Cyclotrypa* (Figs. 3.4.10.6-7) and an indeterminate fenestrate holdfast (Fig. 3.4.10.9) are recognised.

Further postmortal encrustation is relatively rare. These are a (?)craniid brachiopod on an *A. doliiformis* mesistele (e.g. Pl. 3.4.2, Fig. 15), microconchid-valves on one *A. sulcatus*-mesistele (Fig. 3.4.10.9), pluricolumnals of *A. sulcatus* encrusted by small crinoid holdfasts (Figs. 3.4.10.4-5) and, also on *A. sulcatus*, an undetermined chaetitid encrusting on the mesistele (unfigured).

4.3.2 AUTECOLOGY

4.3.2.1 Substrate dependency

The substratum of the sea-floor had a significant influence on the skeletal morphologies of the studied crinoids. Because these elements were in direct contact to the substratum, this is especially true for the holdfasts and stems. Two general types could generally be separated:

The first group settled on soft-bottoms and generally had shorter height. These either lay on the soft-bottom as creeping roots or runners along the substrate or penetrated the substrate with an unbranched or moderately to strongly branched distal stem (see Figs. 4.3.2.B; 4.3.3.A), whose distal stems mostly developed an increased rate of cirri. Furthermore, soft-bottoms could be penetrate by different types of anchors (e.g. AUSICH et al. 1999, p. 14. fig. 20) or roots grown stepwise by successive accretion in the muddy sediment (1999, p. 6, fig. 8).

The second group cemented with attachment discs to numerous types of hardgrounds (Fig. 4.3.3.B). However, on moderately stabilised firmgrounds a commingling of both groups is recognised. For example, mostly creeping roots or runners can lay along the substrate or between hard objects with up to several centimetres of horizontal stem anchored to the substrate by small finger- or lobe-like protrusions of the stereom, typically attached to corals or stromatoporoids with small attachment discs. Several of these protrusions also may penetrate secondary occurring soft-bottom lenses, which could local be developed between hard objects.

The Middle Devonian crinoids of the Eifel Synclines had a highly variable potential of morphological adaptation. Nearly every crinoid studied had the capability to adapt their roots to the respective substrate (e.g. AUSICH et al. 1999, p. 6, fig. 8).

Similarly, higher or shorter stems occurred within turbulent or less turbulent environments. This adaptability surely was one of the most essential reasons for the evolutionally success of the Middle Devonian crinoids that flourished within a manifold diversity of different facies realms and regarding bottom substrates (WINTER 1965).

The development of the two general types, their transitions and the adaptability (see above) were almost comparably recognised in the studied cladids, camerates and disparids. Therefore, the substrate dependency of each group will not be discussed separately. In contrasts, the flexibile *Ammonicrinus* had a more specialised substrate dependency (Chapter 3.4).

On numerous profiles within the Eifel Synclines (e.g. within the Eifelian and Lower Givetian of the Blankenheim, Hillesheim and Gerolstein synclines) these adaptated stems and holdfasts were not only profitable for the crinoids but also for biostromal growth of other faunal elements such as corals, stromatoporoids and bryozoans. The underlying strata of several localities dominated by biostromes were dominated by former soft-bottoms (Fig. 4.3.2.A) that were often penetrated by branching holdfasts, thereby stabilising the sediment. These horizons (Fig. 4.3.2.B) may be designated a pioneer biostromal facies, which made it possible to be settled by additional faunal elements (algae, poriferas, corals and bryozoans).

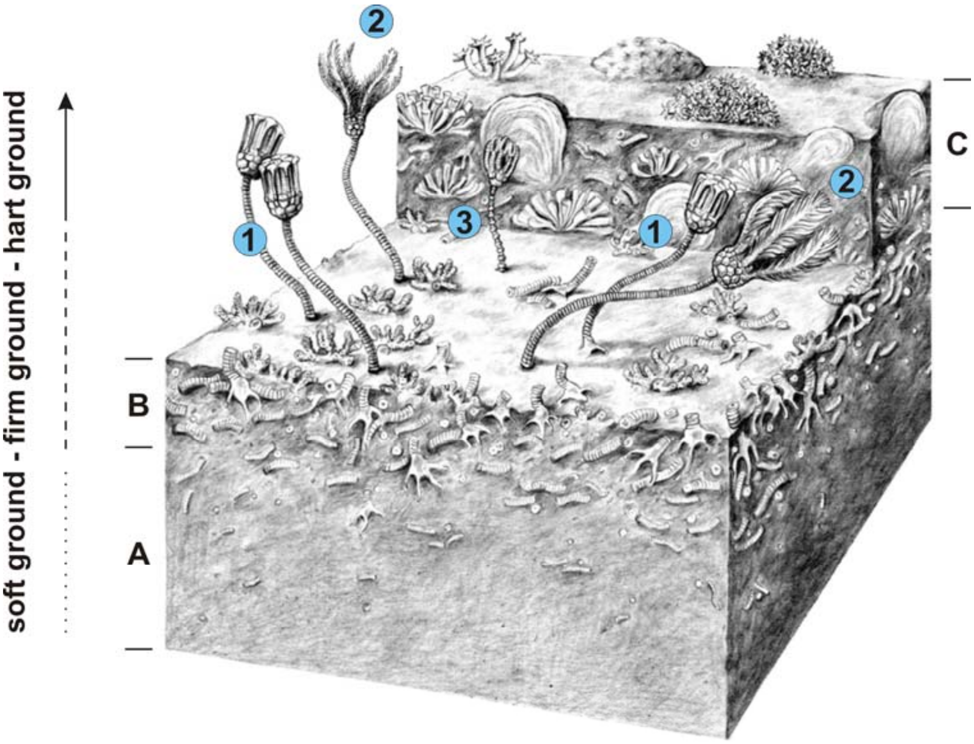


FIGURE 4.3.2—An idealised section of the south-eastern wall of the abandoned "Roderath Quarry" (unpublished data; not to scale) within the Blankenheim Syncline as an example for bottom-stabilisation by crinoid holdfasts in the Eifelian of the Eifel. At the base, a carbonate mudstone indicates a former soft-bottom (**A**). Abundance of crinoid components increases upwards and at the top of the unit first autochthonous crinoid roots crisscrossed the soft-bottom. The roots started to stabilise the substrate by forming local root-meshworks of the biostromal initial facies (**B**). They are associated with thamnoporid meadows, which secondarily stabilised the bottom through sediment baffling. Colonial rugose and tabulate corals as well as stromatoporoids grow on the stabilised crinoid-thamnoporid firmground (**C**). [Crinoids: ***1***, *Eucalyptocrinites rosaceus*; ***2***, *Rhipidocrinus crenatus*; ***3***, *Megaradialocrinus brevis*].

Substrate dependency of the flexibile *Ammonicrinus*

Ammonicrinus skeletons from the Rhenish Massif show substrate-controlled morphological variability of the dististele (distal column and holdfast); the following "morphological groups" are recognised:

The "exposed roller-type" (Chapter 3.4.4, Fig. 3.4.6) settled on firm- or hardground substrates and predominantly show the general skeletal morphology, as illustrated in Fig. 3.4.6. This type is characterised by a laterally unprotected crown that possibly implies feeding in the current. The new material indicates that the stem of *A. kredreoletensis* tapers as it approaches the crown, not in quite as many columnals perhaps, but similar to that of camptocrinids and their crown elevates up from the substrates.

The “encased roller-type” (Chapter 3.4.4, Fig. 3.4.7.1) settled on soft-bottoms. This is the “standard” *Ammonicrinus* and is recognised in all known ammonicrinids, except of *A. kredreoletensis*. These specimens have lateral columnal extensions in the proxistele and mesistele that encloses the crinoids when enrolled. These columnals are followed by several barrel-like columnals of the dististele. The proxi- and mesistele skeleton lay on the soft-bottom, whereas the holdfast was attached to hard objects (brachiopod valves, tabulate corals or bryozoans). The attached hard object affects either the development of an attachment disc or various formed radiating cirri.

In addition to the predominant occurrence of the roller-types, rare discoveries of ammonicrinids (*A. leunissi* n. sp., *A. sulcatus* and *A. wanneri*) with a reduced column length require further study. Mainly attached to dead brachiopod-valves, these ammonicrinids, which are “settler-types”, settling on top of the hard object (Chapter 3.4.4, Fig. 3.4.8).

4.3.2.2 Hydrodynamic dependency

The general trend of a successive establishment of biostromal shallow-water habitats from the boundary of the Lower to Middle Devonian up to the Lower Givetian correlates with the increased rate of hydrodynamically turbulent environments. This leads to the development of more compact, robust crinoids, exemplified in the cladid cupressocrinitids

The Middle Devonian of the Eifel region has a mosaic of numerous small facies realms that were deposited with different levels of turbulence. Thus, it is possible to recognise characteristic crinoid associations that were adapted to either turbulent or less turbulent environments (see Chapter 3.2.4 for one example of the Lower Givetian). In this connection, the facies complexity of the lowermost Lower Givetian deposits (WINTER 1965) is also reflected in the preserved crinoid associations of the Loogh Formation. The higher turbulence within the biostromal habitats led to an association of crinoids with robust skeletons, like cupressocrinitids and some gasterocomoids. Habitats dominated by lower hydrodynamic turbulence were mainly populated by hexacrinitids, rhipidocrinids and eucalyptocrinids. This simplified model must be modified where facies intergrade. Some crinoid localities are dominated by numerous lateral facies interfingering, which leads to a commingling of the crinoid associations at the marginal areas.

Cladida

In cupressocrinitids it was possible to recognise inter- and intraspecific adaptations of the holdfasts, stems and crowns to the hydrodynamic framework of facies. Abbreviatocrinids with relatively short and strong stems and short as well as robust arms, which are covered by a moderately developed multilamellar exoplacoid layer, predominantly populated turbulent habitats (Fig. 4.3.3.B), whereas abbreviatocrinids with long stems, longer arms and a spine-like tapered multilamellar exoplacoid layer preferred less turbulent environments (Fig. 4.3.3.A; also see Bohatý 2005a, p. 205, figs. 3a-b). Both groups were associated with *Procupressocrinus gracilis* that lived in higher or lower turbulence, although this species developed a “gracile” morphology with long stems and arms.

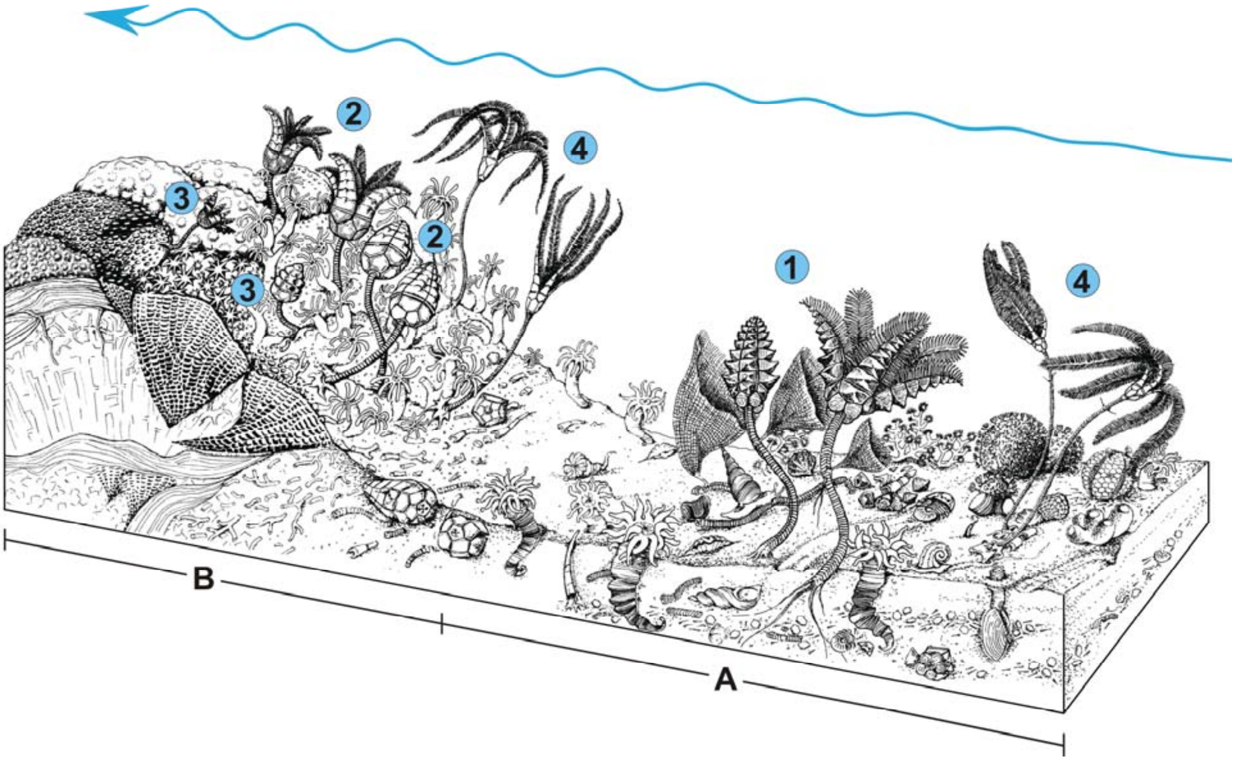


Figure 4.3.3—Idealised section of the lowermost Lower Givetian of the “Wotan Quarry” within the Hillesheim Syncline (modified from Bohatý 2005a; not to scale). The hydrodynamically less turbulent environment (**A**) was populated by abbreviatocrinids with long stems and longer arms as well as spine-like tapered multilamellar exoplacoid layer (***1***, *Abbreviatocrinites geminatus*). The crinoids are anchored with branching roots in the soft-bottom substrate. The turbulent biostrome (**B**) was populated by abbreviatocrinids with relatively short and robust stems as well as short and robust arms covered by a moderately developed multilamellar exoplacoid layer (***2***, *A. a. abbreviatus*; ***3***, *A. a. granulosus*). The individuals developed various attachment discs on hard objects. Both groups were associated with the facies-persisting species *Procupressocrinus gracilis* (***4***). The blue arrow indicates the low to high turbulence.

Further examples indicating the hydrodynamic influence on cladid crinoid skeletons from the Eifel Synclines were the cladid gasterocomoids, whose predominantly upright crown is characterised by five relative filigree branching arms, mainly populated lower turbulent habitats. They were potentially forced to avoid into more turbulent environments because of the increasing rate of competitors within their preferred ecological niches (Chapter 4.2.1; BOHATÝ 2006a). A sloped radial circlet that inclined the crown was a morphological adaptation to facies in higher turbulence (Figs. 4.3.4.1-3). Moreover, the gasterocomoid genera *Nanocrinus* and *Trapezocrinus* (Fig. 4.3.4) and *Tetrapleurocrinus* have a reduction from five to four arms along this turbulence gradient.

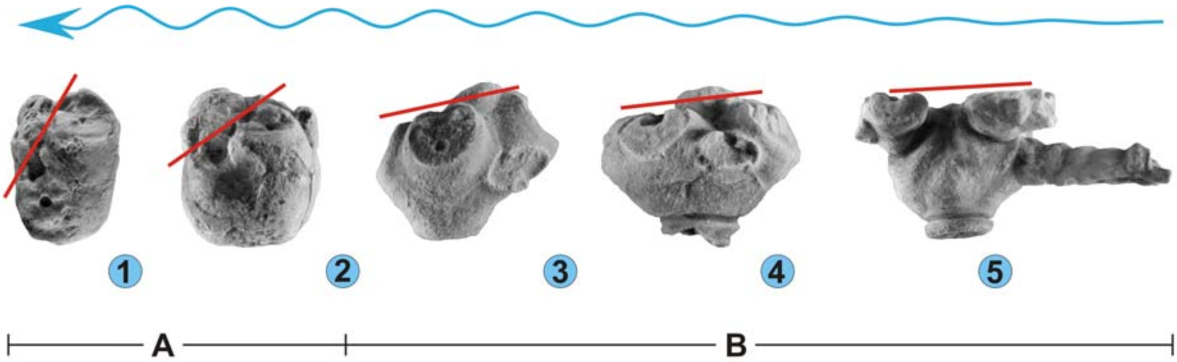


FIGURE 4.3.4—Hydrodynamical adaptations in the cup morphologies of the gasterocomoid genera *Trapezocrinus* (**A**) and *Nanocrinus* (**B**) recovered from the lowermost lower Givetian of one profile (compare to A-B of Fig. 4.3.3) within the "Wotan Quarry" (Hillesheim Syncline). The red line indicates strongly (***1-2***) to minor sloping (***3-5***) of the radial circlet as a morphological adaptation of low hydrodynamic (**B**) to turbulent hydrodynamic conditions (**A**). The blue arrow indicates the low to turbulent hydrodynamic gradient. [Crinoids: ***1***, no CREF34b-172 (PRESCHER collection), x 2.5; ***2***, no CREF34b-173 (PRESCHER collection), x 2.7; ***3***, no CREF34c-28 (BOHATÝ collection), x 3.0; ***4***, no CREF34c-5 (SCHREUER collection), x 3.3; ***5***, no CREF34c-7 (SCHREUER collection), x 2.7].

Camerata

The sloping pattern recognised in cladid crinoids was also documented in the camerate hexacrinitid *Megaradialocrinus elongatus* (Chapter 4.2.2) and interpreted as a "growth anomaly" (Figs. 3.2.5.9-10; 4.3.5.1-2). However, this development is most probably an ecological/facial adaptation. Thus, individuals presumably lived in relatively turbulent conditions between biostromes. These slanted cups only occurred within biostromal deposits, whereas individuals of this species would develop "normal" upright crowns in less turbulent environments.

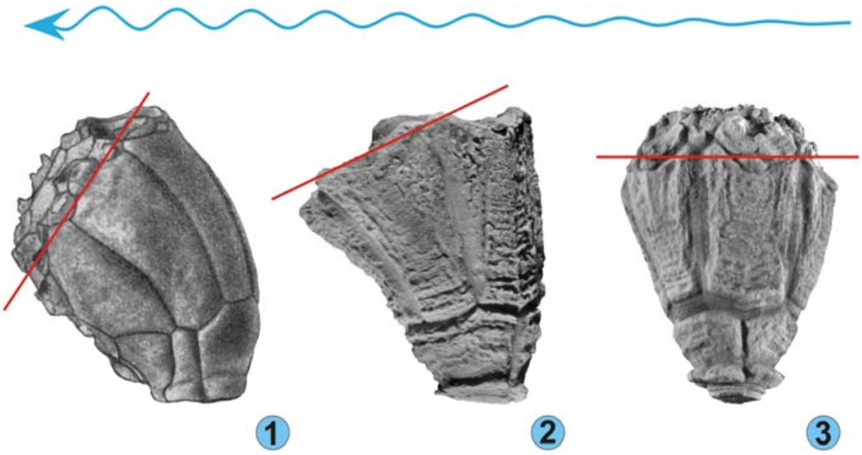


FIGURE 4.3.5—Hydrodynamical adaptations in the cup-morphologies of the hexacrinitid species *Megaradialocrinus elongatus* from the lowermost Lower Givetian of Gerolstein within the Gerolstein Syncline. The red line indicates strongly (***1***) to minor sloping (***2***) and unsloped radial circlet (***3***) as morphological adaptation of low hydrodynamic (***3***) to turbulent hydrodynamic (***1-2***). The blue arrow indicates the low to turbulent hydrodynamic. [Crinoids: ***1***, original of SIEVERTS-DORECK (1950, p. 81, figs. 1a-c), x 1.8; ***2***, no GIK-1960, x 1.6; ***3***, no GIK-1953, x 1.6].

4.3.2.3 The influences of the events and faunal declines and the response of the Middle Devonian Crinoids from the Eifel

Upper Eifelian: Klausbach Event and *otomari* Event

The most significant events for crinoids of the Middle Devonian Eifel Synclines are the "Klausbach Event" (STRUVE 1992) and the "*otomari* Event" (STRUVE et al. 1997).

The Klausbach Event was a regional occurrence at the base of the Junkerberg Formation (Klausbach Member) that is characterised by a rapid increasing of sediment, limiting the Niederehe Subformation, which predominantly was dominated by biostromal developments and lower rates of sedimentation (STRUVE 1992; also see BOHATÝ 2005b, pp. 392-393).

The "*otomari* Event" was a transgression that resulted in sedimentary changes within the Eifel region and occurred in between the base of the Giesdorf and the Eilenberg members (STRUVE et al. 1997).

The response of the analysed crinoids

The palaeodiversity of the studied cupressocrinitids, summarised in Chapter 4.1.1 (Tab. 4.1.1), clearly traces the biogenic impacts of the Klausbach and *otomari* events.

The *otomari* Event reduced the general palaeodiversity of *Abbreviatocrinites*. In contrast, the Klausbach Event had no impact. Moreover the species *A. nodosus* and, especially, *A. schreueri* flourished during this event and *A. a. abbreviatus* could be described a stratigraphically persisting species. Only *A. tesserula* had an apparently negative response of the event.

Cupressocrinites, which populated within the Eifel after both events, thus possibly indicating a faunal migration. This pattern was already recognised after the *otomari* Event for rugose corals within the Rhenish Massif (SCHRÖDER 1997).

Increased sedimentation rate and the development of expanded muddy substrates at the base of the Junkerberg Formation, resulted in a conspicuously decreased occurrence of *Robustocrinites* within the Eifel region (Chapter 3.1.4; Fig. 3.1.8). This loss correlates with the beginning of the Klausbach Event. During times of moderate siliciclastic input, diverse hardground and/or firmgrounds were established between the Mussel and Nims members. Between the basal Hönselberg and the top of the Nims members a species radiation of *Robustocrinites* occurred. All three recognised species became extinct at the top of the Nims Member and, therewith, at the basis of the *otomari* Event.

Also *Procupressocrinus* responded to the *otomari* but not of the Klausbach Event (Tab. 4.1.1.1).

This pattern of the cupressocrinitid palaeodiversity is illustrated in Fig. 4.1.1. The *otomari* Event is represented as a minimum of genera and species curves within the Freilingen Formation. Other cladid crinoids have the same response to the *otomari* Event, (Fig. 4.1.1).

Responses of the Klausbach and *otomari* events are also recognised among camerates, disparids and flexibles:

The hexacrinitids (Chapter 3.2) did not change palaeodiversity in response to the mentioned events (Tab. 4.1.2). However, similar to the cladid genus *Cupressocrinites*, the diversity and individual number rose after the *otomari* Event (compare Tabs. 4.1.1 and 4.1.2).

Similarly, *Stylocrinus* and *Ammonicrinus* (Chapter 3.3 and 3.4) had a decreased abundance during the Giesdorf Member, but a rapid diversification after this member (Tabs. 4.1.3; 4.1.4).

In summary of the influence of these events on Middle Devonian crinoids from the Eifel Synclines, the *otomari* Event acted negatively to the associations (see minimum of the curve within the Giesdorf Member; Fig. 4.1.4). In contrast, the Klausbach Event acted considerably less negatively for some species and some taxa flourished. The crinoids that flourished include the cladids *Abbreviatocrinites nodosus*, *A. schreueri* and *Bactrocrinites tenuis* (especially significant) [BOHATÝ 2005b]. Other echinoderm groups also flourished during the Klausbach Event. These are the echinoid *Lepidocentrus muelleri* and the blastoid *Hyperoblastus eifeliensis*, which are preserved locally in very abundant, monospecific mass occurrences.

Crinoid faunal declines within the Eifel – Lower Givetian Crinoid Decline and Frasnian-Famennian Crinoid Decline

Lower Givetian Crinoid Decline

The maximal palaeodiversity of the Middle Devonian crinoids from the Eifel Synclines is positioned between the Freilingen and lower Cürten formations (Chapter 4.1.5; Fig. 4.1.4). Thereafter, the palaeodiversity abruptly decreased, and this regional faunal break is herein designated the Lower Givetian Crinoid Decline (Chapters 4.1.5-6; Figs. 4.1.4; 4.1.5). The reasons for this decline are unexplained in most instances but it is presumably a reaction to eustatic increase in sea-level during the Givetian (JOHNSON et al. 1985; JOHNSON & SANDBERG 1988). Accordingly, it is possible that the sea-level was too high for the crinoids of the Eifel, which were highly adapted to shallow-water and biostromal facies (based on subjective faunal collecting).

Poor facies condition for crinoids occurred in the Lower to Upper Givetian of the Rhenish Massif. However, this extinction cannot be explained as sampling bias due to unfavourable fossil preservation as a consequence of the incipient Massenkalk Facies with an increasing rate of dolomitisation (MEYER 1986), because even fossil-rich localities of the upper Cürten to Rodert formations document this biodiversity collapse.

Frasnian-Famennian Crinoid Decline – a prospection

Within the deposits of the “Büdesheimer Goniatitenschiefer” (RÖMER 1854; KAYSER 1871), which can approximately be correlated to the “Matagne Slate” of Belgian (MEYER 1986, p. 169), a clear faunal change occurred (compare to 4.1.6). Unpublished pseudo-planktonic amabilicrinitids, which are attached to drift-woods, were recovered from these deposits and are associated with platycrinids. Pseudo-planktonic crinoids were important during the times of the "Kellwasser Crisis" [see SCHINDLER (1990) for this crisis] with their influence of the Devonian reef communities – I also note the (unpublished) correlations to the already described amabilicrinitids from the Upper Frasnian and Famennian of Morocco (WEBSTER et al. 2005; WEBSTER & BECKER 2009).

These finding indicate a significant faunal change between the faunal "groups 3a-b" and "4" to this amabilicrinitid-dominated "faunal group 5" (Chapter 4.1.6) and, therefore, has to be interpreted as reaction of the Frasnium/Famennium Extinction. This faunal change is herein designated the Frasnian-Famennian Crinoid Decline.

Following GRIMM et al. (2008, p. 384) the Büdesheimer Goniatitenschiefer is part of the Büdesheim Formation and includes the two "Kellwasserkalk Horizons" (e.g. GEREKE 2007). These deposits exhibit a significant fauna of pyritised goniatids, orthocerids, brachiopods and gastropods, which are characterised by restricted growth (CLAUSEN 1966). This restricted growth begins abruptly and indicates drastically changes in the environment (MEYER 1986). Presumably, reducing bottom-waters increased and were followed by hydrosulphide-toxication, indicated by the abundance of pyrite (CLAUSEN 1966).

The influence of the Frasnian/Famennian Event for the Devonian crinoids has been discussed in the literature. Following GŁUCHOWSKI (2002, p. 325), the Mid-Late Devonian crisis in crinoid evolution was one of the greatest in Phanaerozoic. It was first manifested globally be a drastic decrease in crinoid preservation during the early Famennian (GŁUCHOWSKI 2002). Despite later expansion of crinoid faunas (MAPLES et al. 1997), their differentiation remained at the lowest level for the entire Devonian. GŁUCHOWSKI (2002) proved that the low diversity of the Holy Cross Mountain Famennian crinoid assemblages (based on stem taxa) may be a consequence of the Frasnian/Famennian mass extinction. However, some studies of the calyx-based crinoid taxa diversity have shown that the major declines appear to coincide with the end of the Givetian (BAUMILLER 1994), and the "Frasnian/Famennian-extinction was a non-event for crinoids" (WEBSTER et al. 1998). This peculiar pattern, however, might be only a consequence of a preservation and/or regional bias (MCINTOSH 2001).

Recent publications argue that this event was, at least for cladid crinoids, a non-event (WEBSTER in press). However, the camerate-dominated crinoid association ("faunal-group 4"; Chapter 4.1.6) of the Rheno-Ardennic Massif had a clear response which indicates the need for further studies.

5. FUTURE RESEARCH

To answer multiple open questions that result from the present thesis, further studies are required that have to be based on the systematical and taxonomical revisions herein. This arises from the high number of species, as given in the chapter “Discussion and conclusion”. It is mainly expressed in the contrast between the number of taxa, which are listed in the literature of the early 19th century as well as in amateur publications (~160 species) that mostly infringe ICZN-guidelines, and a first critical estimation of ~200 species that are based on my own unpublished data and assuredly include numerous undescribed taxa. The upcoming version of the Crinoid Treatise is an inducement for this aim.

Several of the conclusions reached herein concerning the palaeodiversity, palaeobiology and palaeoecology of the studied crinoids have to be more precisely refined. While e.g. the local influences of events (Klausbach Event, *otomari* Event) were adequately described in this thesis, indicated faunal migrations that obviously followed the *otomari* Event, should be analysed in detail to answer the questions from where- and in how many waves of immigration they came. These objectives have to consider data of other faunal groups, like the migration pattern of rugose corals (SCHRÖDER 1997).

Also the controlling factors of regional faunal collapses (Lower Givetian Crinoid Decline, Frasnian-Famennian Crinoid Decline) have to be analysed in detail. It would be most interesting to determine if these faunal breaks also affected other benthic taxa like possibly bryozoans (pers. information, A. ERNST), and to verify to what extent the proposed explanation of a rising sea-level for the Lower Givetian Crinoid Decline, possibly forced the shallow-water adapted crinoids from the Eifel to escape into probably remaining shallow water habitats. These apparently existed within the vicinity of the Lahn-Dill Syncline in the eastern Rhenish Massif and were related to volcanic occurrences in terms of constricted “crinoid island-appearances”. The rising sea-level potentially delimited these low diverse associations and, furthermore, led to migration of the crinoids toward the Ardennes. This could be an explanation for the occurrences of several characteristic cladids and camerates from the Eifel within the Frasnian deposits of the Ardennes that could not be recovered from coeval strata of the Eifel Synclines. Therefore, studies have to be directed toward the comparison between the Givetian crinoid associations of the eastern Rhenish Massif and the Frasnian crinoid faunas of the western Rhenish Massif and the Ardennes.

Considering the postulate that the Frasnian/Famennian Event was a non-event for crinoids (e.g. WEBSTER et al. 1998; WEBSTER in press), an exiting research project would be the detailed analysis of the clearly evidenced response of the Frasnian *Melocrinites*-*Megaradialocrinus*-dominated crinoid association from the Rheno-Ardennic Massif to this crisis, which is characterised by its replacement by an amabilicrinitid-dominated crinoid fauna with a "Carboniferous character". Therefore, the Frasnian/Famennian crinoids of the Eifel and the Ardennes (Büdesheimer Goniatitenschiefer, Matagne Slate) should be analysed and compared to the amabilicrinitids from Morocco (WEBSTER et al. 2003; WEBSTER & BECKER 2009) and Iran (WEBSTER et al. 2003).

The amabilicrinitids from the Frasnian/Famennian boundary interval were often found attached to drift woods (pers. collections, unpublished data; WEBSTER et al. 2003) and, therefore, are considered to be pseudo-planktic. In contrast, the Lower Carboniferous amabilicrinitids of Wülfrath-Aprath (eastern Rhenish Massif; HAUDE & THOMAS 1992, as revised by WEBSTER et al. 2003) indicate a benthic mode of life. It requires further investigation to determine if these contrasting lifestyles might be linked to the Kellwasser Crisis and if this might indicate a high adaptability of these "Carboniferous pioneers" that displaced the Middle Devonian crinoid associations.

The manifold results presented herein and the resulting, even more intriguing open questions show the long-time underestimated potential of crinoids for a better understanding of the complex, interdependent processes controlling evolutionary and palaeoecological changes in the Devonian World.

6. REFERENCES

ALMELA, A. & REVILLA, J. (1950): Especies fósiles nuevas del Devoniano de León. – Notas y Communicaciones del Instituto Geológico y Minero de España, **20**: 45-60.

AMEMIYA, S. & OJI, T. (1992): Regeneration in sea lilies. – Nature, **357**: 546-547.

ANGELIN, N. P. (1878): Iconographia crinoideorum in stratis Sueciae siluricis fossilium. – 62 p., 29 pl. Samson and Wallin (Holmiae).

ARENDT, YU. A. (1983): Novyi rod srednekamennougolnykh podmoskovnykh krinoidei-camerat [A new Middle Carboniferous camerate crinoid genus from the Moscow Basin]. – Paleontologicheskii Zhurnal, **4**: 101-105.

AUSICH, W. I. (1980): A model for niche differentiation in Lower Mississippian crinoid communities. – Journal of Paleontology, **54**: 273-288.

— , BRETT, C. E., HESS, H. & SIMMS, M. (1999): Crinoid Form and Function, pp. 3-30. *In*: HESS, H., AUSICH, W. I., BRETT, C. E. & SIMMS, M. J. (eds.): Fossil crinoids. – 275 p., 238 fig. Cambridge University Press (Cambridge).

AUSTIN, T. & AUSTIN, T. (1843): Description of several new genera and species of Crinoidea. – Annals and Magazine of Natural History, Series 1, **11**(69): 195-207.

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

BARTELS, C., BRIGGS, D. E. G. & BRASSEL, G. (1998): The fossils of the Hunsrück Slate: Marine life in the Devonian. – Cambridge Paleobiology Series, **3**: 1-309.

BASSE, M. (2002): Eifel-Trilobiten. 1. Proetida. – 152 p., 3 fig., 1 tab., 33 pl. Goldschneck-Verlag (Korb).

— (2003): Eifel-Trilobiten. 2. Phacopida (1): Cheiruriden / Acasten / Asteropygen. – 200 p., 3 fig., 4 tab., 29 pl. Goldschneck-Verlag (Korb).

— (2006): Eifel-Trilobiten. 4. Proetida (3), Phacopida (3). – 305 p., 4 tab., 64 pl. Quelle & Meyer (Wiebelsheim).

— & MÜLLER, P. (2004): Eifel-Trilobiten. 3. Corynexochida / Proetida (2) / Harpetida / Phacopida (2) / Lichida. – 261 p., 10 fig., 2 tab., 54 pl. Quelle & Meyer (Wiebelsheim).

BASSLER, R. S. (1938): Pelmatozoa Palaeozoica. *In*: QUENSTEDT, W. (ed.): Fossilium catalogus, I: Animalia; Part 83. – 194 p. W. Junk (s'Gravenhage).

— & MOODEY, M. W. (1943): Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms. – Geological Society of America Special Paper, **45**: 1-734.

BATHER, F. A. (1900): The Echinoderma, Part 3. The Pelmatozoa: *In* LANKESTER, E. R., (ed.) A Treatise on Zoology. – 344 p. Adam and Charles Black (London).

— (1899): A phylogenetic classification of the Pelmatozoa. – British Association for the Advancement of Science, Report, **1898**: 916-923.

— (1919): *Cupressocrinus gibber* n. sp. du Dévonien supérieur de Belgique. – Bulletin de la Société Belge de Géologie de Paléontologie et d'Hydrologie, **28**: 129-136.

— (1926): Notes sur *Cupressocrinus* et *Rhopalocrinus*. – Bulletin de la Société Belge de Géologie de Paléontologie et d'Hydrologie, **36**: 39-51.

BAUMILLER, T. K. (1990): Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. – Palaeontology, **33**(3): 743-748.

— (1993): Boreholes in Devonian blastoids and their implication for boring by platyceratids. – Lethaia, **26**: 41-47.

— (1994): Patterns of dominance and ectinction in the record of Paleozoic crinoids. *In*: DAVID, B., GUILLE, A., FÉRAL, J.-P. & ROUX, M. (eds.): Echinoderms through Time. – pp. 193-198. Balkema (Rotterdam).

— & MACURDA, D. B. JR. (1995): Borings in Devonian and Mississippian Blastoids (Echinodermata). – Journal of Paleontology, **69**(6): 1084-1089.

BECKER, R. T. (2005): Correlation of the proposed Middle Devonian Substage with the global ammonoid record. – Document of the International Subcommission on Devonian Stratigraphy, Annual Meeting, Novosibirsk, 6 p.

— (2007): Correlation of the proposed Middle Givetian Substage with the global ammonoid record. – Subcommission on Devonian Stratigraphy, Newsletter, **22**: 17-23.

BERGOUNIOUX, F. M. (1939): Crinoïdes du Fransnien de Château-Gaillard près Trélon (Nord). – Bulletin de la Société Géologique de France, ser. 5, **9**: 81-92.

BEYER, E. (1896): Beitrag zur Kenntnis der Fauna des Kalkes von Haina bei Waldgirmes (Wetzlar). – Verhandlungen des Naturhistorischen Vereins der Preußischen Rheinlande und Westfalens, **53**: 56-102.

BIRENHEIDE, R. (1995): Motility and stiffness of cirri of the stalked crinoid *Metacrinus rotundus*. Conference Information: 4th European Echinoderms Colloquium, Date: APR 10-13, 1995, London, England. – Echinoderm Research, **1995**: 91-94.

— (1996): Contractile connective tissue in crinoids. – Biological Bulletin, **191**(1): 1-4.

— & MOTOKAWA, T. (1994): Morphological basis and mechanics of arm movement in the stalked crinoid *Metacrinus rotundus* (Echinodermata, Crinoidea). – Marine Biology, **121**(2): 273-283.

— , YOKOYAMA, K. & MOTOKAWA, T. (2000): Cirri of the stalked crinoid *Metacrinus rotundus*: neural elements and the effect of cholinergic agonists on mechanical properties. – Proceedings of the Royal Society of London, series B, Biological Sciences, **267**(1438): 7-16.

BOHATÝ, J. (2001): Wachstumsanomalien mitteldevonischer Crinoidenkelche aus den Kalkmulden der Eifel (Rheinisches Schiefergebirge). *In*: REICH, M. & HINZ SCHALLREUTER, I. (eds.): 1. Arbeitstreffen deutschsprachiger Echinodermenforscher, Greifswald, 11.-13. Mai 2001 - Arbeiten und Kurzfassungen der Vorträge und Poster. – Greifswalder Geowissenschaftliche Beiträge, **9**: 7-9.

— (2005a): Doppellagige Kronenplatten: Ein neues anatomisches Merkmal paläozoischer Crinoiden und Revision der Familie Cupressocrinitidae (Devon). – Paläontologische Zeitschrift, **79**(2): 201-225.

— (2005b): *Bactrocrinites* (Crinoidea) aus dem Mittel-Devon der Eifel (linksrheinisches Schiefergebirge, Deutschland) - Taxonomie, Biostratigraphie und Fazieskontrolle. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **235**(3): 381-410.

— (2006a): Seltene Gasterocomidae (Crinoidea) aus dem Mittel-Devon der Eifel (linksrheinisches Schiefergebirge, Deutschland). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **239**(3): 399-443.

— (2006b): Neue Cupressocrinitidae (Crinoidea) aus den mitteldevonischen Kalkmulden der Eifel (linksrheinisches Schiefergebirge, Deutschland). – Senckenbergiana lethaea, **86**(2): 151-189.

— (2006c): Über den taxonomischen Status des mitteldevonischen *Hexacrinites crispus* (QUENSTEDT, 1861) [Crinoidea, Camerata] aus dem linksrheinischen Schiefergebirge Deutschlands. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **2006**(8): 471-482.

— (2006d): Camerate Crinoiden aus dem Givetium (Mittel-Devon) der Bergisch Gladbach-Paffrather Mulde (Bergisches Land, rechtsrheinisches Schiefergebirge). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **242**(2/3): 243-260.

— (2006e): A new Middle Devonian *Hexacrinites* (Crinoidea, Camerata) from the Gerolstein syncline (Eifel-Hills, Germany). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **242**(2/3): 261-274.

— (2008): Paläozoische Crinoiden (Echinodermata) aus der historischen Petrefaktensammlung SANDBERGER (Wiesbaden), Teil 1: Camerata (Hexacrinitidae). – Jahrbuch des Nassauischen Vereins für Naturkunde, **129**: 5-27.

— (2009): Pre- and postmortem skeletal modifications of the Cupressocrinitidae (Crinoidea, Cladida). – Journal of Paleontology, **83**(1): 45-62.

— (in press): Revision of the Hexacrinitidae (Crinoidea) based on a classical Lower Givetian crinoid deposit (Gerolstein, Eifel/Germany). – Neues Jahrbuch für Geologie und Paläontologie.

— (in review): Revision of the disparid *Stylocrinus* (Crinoidea) from the Devonian of Europe, Asia and Australia. – Palaeontology.

— (submitted): New mode of life interpretation and revision of the idiosyncratic lecanocrinid genus *Ammonicrinus* (Crinoidea, Flexibilia). – Palaeontology.

— (in prep.): Paläozoische Crinoiden (Echinodermata) aus der historischen Petrefaktensammlung SANDBERGER (Wiesbaden), Teil 2: Cladida (Gasterocomoidea). – Jahrbuch des Nassauischen Vereins für Naturkunde.

— & HERBIG, H.-G. (2007): The validity of the Middle Devonian camerate crinoid species *Hexacrinites hieroglyphicus* (Goldfuss, 1839) and *H. marginatus* (Schultze, 1866). – Geobios, **40**(6): 731-736.

— & HERBIG, H.-G. (in review): Middle Givetian echinoderms from the Schlade Valley (Rhenish Massif, Germany) - habitats, taxonomy and ecostratigraphy. – Paläontologische Zeitschrift.

BREIMER, A. (1962): A monograph on Spanish Palaeozoic Crinoidea. – Leidse geologische Mededelingen, **27**: 1-189.

BRETT, C. E. & ECKERT, J. D. (1982): Paleoecology of a well-preserved crinoid colony from the Silurian Rochester Shale in Ontario. – Life Science Contribution, Royal Ontario Museum, **131**: 1-20.

BRONN, H. G. (1848-1849): Index palaeontologicus - oder Übersicht der bis jetzt bekannten fossilen Organismen, bearbeitet unter Mitwirkung der Herren PROF. H. R. GÖPPERT und HERM. VON MEYER, bearbeitet von DR. H. G. BRONN: Handbuch einer Geschichte der Natur. – v. 5, Abt. 1, (1, 2), pt. 3, A. Nomenclator Palaeontologicus; A-M, pp. 1-775; N-Z, pp. 776-1381. Schweizerbart'sche (Stuttgart).

BRÜHL, D. (1999): Stratigraphie, Fazies und Tabulaten-Fauna des oberen Eifelium (Mittel-Devon) der Dollendorfer Mulde/Eifel (Rheinisches Schiefergebirge. – Kölner Forum für Geologie und Paläontologie, **4**: 1-155.

BYRA, H. (1983): Revision der von C. L. SCHLÜTER (1880-1889) beschriebenen Chaetetida und Tabulata aus dem Rheinischen Devon. – Courier Forschungs-Institut Senckenberg, **59**: 1-127.

CHARLESWORTH, J. K. *In* FRECH, F. (1914) [ed.]: Die Fauna des devonischen Riffkalkes; III Die Crinoiden. – Zeitschrift der Deutschen Geologischen Gesellschaft, **66**: 330-347.

CHEN, Z-T. & YAO, J-H. (1993): Palaeozoic echinoderm fossils of western Yunnan, China. – 102 p., 16 pl. Geological Publishing House (Beijing).

CLAUSEN, C.-D. (1966): Oberdevonische Cephalopoden aus dem Rheinischen Schiefergebirge. 264 p., 59 fig., 15 pl. Unpublished dissertation (University of Bonn).

COEN-AUBERT, M. & LÜTTE, B.-P. (1990): Massive rugose corals from the Middle Devonian of the North Eifel Hills (Rheinisches Schiefergebirge, West Germany). – Geologica et Palaeontologica, **24**: 17-39.

DEWALQUE, G. *In* FRAIPONT, J. (1884): Recherches sur les crinoïdes du famenien (devonien superieur) de Belgique I-III. – Annales de la Société Géologique de Belgique, **1883**(11): 105-118.

DOHM, B. (1930): Die Kalkmulde von Gerolstein in der Eifel. Eine Einführung in die Geologie. – 64 p. Georg Fischer (Wittlich).

— (1976): Die geologischen Verhältnisse im Landkreis Daun in der Vulkaneifel - 2. erweiterte Auflage. – 79 p. Görres (Koblenz).

DONOVAN, S. K. & LEWIS, D. N. (1999): An epibiont and the functional morphology of the column of a platycrinitid crinoid. – Proceedings of the Yorkshire Geological Society, **52**: 321-323.

D'ORBIGNY, A. D. (1850-52): Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés faisant suite au cours élémentaire de paléontologie et de géologie stratigraphique. – v. 1 [1849 (1850)], pp. 1-392; v. 2 [1850 (1852)], pp. 1-427; v. 3 (1852), p. 196 + table alphabétique et synonymique des genres et des espèces, pp. 1-189. Victor Masson (Paris).

DUBATOLOVA, YU. A. (1964): Morskie lilii devona Kuzbassa [Devonian crinoids of the Kuznetz Basin]. – Akademiya Nauk SSSR, Sibirskoe Otdeleniye Trudy Instituta Geologii i Geofiziki: 1-153.

— (1971): Morskie lilii rannego i srednego Devona Altaya i Kuzbassa. – Akademiya Nauk SSSR, Sibirskoe Otdelenie Trudy Instituta Geologii i Geofizki, **124**: 1-159.

— (1975): Devonian crinoids of the Minusin Basin [in Russian]. – Trudy Instituta Geologii i Geofiziki AN SSSR, Sibirskoe Otdelenie, **272**: 1–58.

— & YELTYSHEVA, R. S. (1967): Stratigraphic importance of the Devonian Crinoids of Siberia. *In*: OSWALD, D. H. (ed.): International Symposium on the Devonian System, **2**: 537-542. Alberta Society of Petroleum Geologists (Calgary).

DUJARDIN, F. & HUPÉ, L.-H. (1862): Histoire naturelle des Zoophytes, échinodermes; Librairie Encyclopédique. – 628 p. Roret (Paris).

DUNCAN, H. (1939): Trepostomatous Bryozoa from the Traverse Group of Michigan. – University of Michigan Paleontology Contributions, **5**(10): 171-270.

EHRENBERG, K. (1930): Die “Nebenformen” der Crinoiden, ihre stammesgeschichtliche Entwicklung und Bedeutung. – Palaeobiologica, **3**: 257-324.

ERNST, A. (2008): Non-fenestrate bryozoans from the Middle Devonian of the Eifel (western Rhenish Massif, Germany). – Neues Jahrbuch für Geologie und Mineralogie, **250**(3): 313-379.

— & BOHATÝ, J. (in press): *Schischcatella* (Fenestrata, Bryozoa) from the Devonian of the Rhenish Massif, Germany. – Palaeontology.

— & SCHRÖDER, S. (2007): Devonian bryozoans of Rhenish Slate Massif. – Neues Jahrbuch für Geologie und Paläontologie, **246**(2): 205-233.

FABER, P. (1980): Fazies-Gliederung und -Entwicklung im Mittel-Devon der Eifel (Rheinisches Schiefergebirge). – Mainzer gewissenschaftliche Mitteilungen, **8**: 83-149.

FRANZÉN, C. (1977): Crinoid holdfasts from the Silurian of Gotland. – Lethaia, **10**: 219-234.

GAHN F. J. & BAUMILLER T. K. (2003): Infestation of Middle Devonian (Givetian) camerate crinoids by platyceratid gastropods and its implications for the nature of their biotic interaction. – Lethaia, **36**(2): 71-82.

— & — (2005): Arm regeneration in Mississippian crinoids: evidence of intense predation pressure in the Paleozoic? – Paleobiology, **31**(1): 151-164.

GALLE, A. (1978): Favositidae (Tabulata) from the Devonian of Bohemia. – Sbornik Geologických Věd, Paleontologie, **20**: 33-62.

— & PROKOP, R. J. (2000): Complex parasitism and symbiosis of crinoid, subepidermal parasite, and tabulate coral. Lower Devonian (Pragian), Barrandian, Czech Republic. – Věstnik Českého Geologického Ústavu, **75**: 441-444.

GEREKE, M. (2007): Die oberdevonische Kellwasser-Krise in der Beckenfazies von Rhenoherzynikum und Saxothuringikum (spätes Frasnium/frühestes Famennium, Deutschland). – Kölner Forum für Geologie und Paläontologie, **17**: 1-228.

GŁUCHOWSKI, E. (1993): Crinoid assemblages in the Polish Givetian and Frasnian. – Acta Palaeontologica Polonica, **38**(1/2): 35-92.

— (2002): Crinoids from the Famennian of the Holy Cross Mountains, Poland. – Acta Palaeontologica Polonica, **47**(2): 319-328.

— (2005): Epibionts on upper Eifelian crinoid columnals from the Holy Cross Mountains, Poland. – Acta Palaeontologica Polonica, **50**(2): 315-328.

GOLDFUSS, G. A. (1826-44): Petrefacta Germaniae tam ea, quae in museo universitatis regiae Borussicae Fridericiae Wilhelmiae Rhenanae servantur, quam alia quaecunque in Museis Hoeninghusiano, Muensteriano aliisque extant iconibus et descriptionibus illustrate (Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angrenzenden Länder, unter Mitwirkung des Herrn GRAFEN GEORG ZU MÜNSTER, herausgegeben von Dr. AUG. GOLDFUSS). – **1** (1826-33): Divisio secunda: Radiariorum Reliquiae – Strahlenthiere der Vorwelt, p. 115-221. Arnz and Co (Düsseldorf).

— (1839): Beiträge zur Petrefactenkunde. – Nova Acta Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum [= Kaiserlich Leopoldinisch-Carolinische Akademie der Naturforscher, Verhandlungen], **19**(1): 329-352.

GOLDRING, W. (1923): The Devonian crinoids of the state of New York. – New York State Museum, Memoir, **16**: 1-670.

GRIGO, M. (in review). Bioerosional traces in brachiopod shells from the Middle Devonian of the Rhenish Massif (Eifel, Germany). – Neues Jahrbuch für Geologie und Paläontologie.

GRIMM, M. C., PIECHA, M., PRICK, R. & JOACHIMSKI, M. M. (2008): Höheres Mitteldevon und Oberdevon der Prümer Mulde (Givetium bis tiefes Famennium/Eifel). *In*: Deutsche Stratigraphische Kommission (ed.): Stratigraphie von Deutschland VIII, Devon. – Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften, **52**: 375-391.

GÜRICH, G. (1909): Leitfossilien, 2. Lieferung: Leitfossilien des Devon. – pp. 97-199, pls. 29-52. Gebrüder Borntraeger (Berlin).

HALL, J. (1852): Palaeontology of New York, v. 2, Containing descriptions of the organic remains of the lower middle division of the New-York system. – Natural History of New York; vol. **6**. – pp. 1-362. D. Appleton & Co. (New York) and Wiley & Putnam (Boston, Gould, Kendall and Lincoln).

HALLECK, M. S. (1973): Crinoids, hardgrounds, and community succession: The Silurian Waldron–Laurel contact in southern Indiana. – Lethaia, **6**: 239-252.

HAUDE, R. (1981): Mechanik, Morphogenese und Palökologische Bedeutung der "Pelmatozoen"-Stiele. *In*: RIEF, W.-E. (ed.): Paläontologische Kursbücher, 1: Funktionsmorphologie. – pp. 187-203. Published by the Paläontologische Gesellschaft (München).

— (2007): Mode of life of fan-hand-like *Scoliocrinus* according to functional form and syntopy with two other irregular crinoids from the Middle Devonian of the Rhenish Massif (Germany). – Annales de Paléontologie, **93**: 291-316.

— & THOMAS, E. (1992): Die unter-karbonischen Crinoiden von "Kohleiche" bei Wuppertal. *In*: THOMAS, E., (ed.): Oberdevon und Unterkarbon von Aprath im Bergischen Land (Nördliches Rheinisches Schiefergebirge). – pp. 307-361. Sven von Loga (Köln).

HAUSER, J. (1997): Die Crinoiden des Mittel-Devon der Eifler Kalkmulden. – 274 p., 48 text-fig., 20 tab, 76 pl. Private published (Bonn).

— (1999): Die Crinoiden der Frasnes-Stufe (Oberdevon) vom Südrand der Dinant-Mulde (Belgische und französische Ardennen). – 156 p., 45 text-fig., 46 tab., 38 pl. Privately published (Bonn).

— 2001. Neubeschreibung mitteldevonischer Eifel-Crinoiden aus der Sammlung Schultze (Museum of Comparative Zoology, The Agassiz Museum, Harvard University, Mass., USA), nebst einer Zusammenstellung der Eifelcrinoiden (Holotypen) der Goldfuss Sammlung. – 199 p., 126 text-fig., 37 tab., 28 pl. Private published (Bonn).

— (2002): Die Crinoiden der Frasne-Stufe (Oberdevon) von Wallersheim/Loch (Prümer Mulde; Eifel) nebst einer Zusammenstellung sämtlicher Melocriniten weltweit, 70 p, 15 pl. *In*: HAUSER, J. & HAUSER, A.: Oberdevonische Echinodermen aus den Dolomit-Steinbrüchen von Wallersheim-Loch (Rheinisches Scheifergebirge, Prümer Mulde; Eifel). – pp. 1-70a, pls. 1-15a (Crinoidea) and pp. 1-13b, pls. 1-4b (Echinoidea). Privately published (Bonn).

— (2003): Über *Jaekelicrinus* und andere Crinoiden aus dem Frasnium (Oberdevon) vom Südrand der Dinant Mulde (Ardennen, Belgien). – 49 p., 59 text-fig., 4 tab., 10 pl. Privately published (Bonn).

— (2004): Neue Crinoiden (Echinodermata) aus dem Mitteldevon der Eifelkalkmulden (Rheinisches Schiefergebirge). – 53 p., 45 text-fig., 2 tab., 2 pl. Privately published (Bonn).

— (2005a): *Hexacrinites elongatus* (G.A. GOLDFUSS, 1839) - Ein Faziesfossil des Eifeler Givetiums. – Privately published on private web-page: <http://www.devon-crinoiden.de/Hexacriniteselongatus.pdf> (Bonn) [does not meet ICZN regulations, J.B.].

— (2005b): *Ammonicrinus* (Crinoidea, Flexibilia) aus dem Paläozoikum von Deutschland (Eifel, Sauerland) und dem Heilig-Kreuz-Gebirge (Polen). – 52 p., 16 tab., 68 text-fig., 6 pl. Privately published (Bonn).

— (2006a): *Cupressocrinites goldfussi* n. sp. - Ein neuer Vertreter der Gattung *Cupressocrinites* GOLDFUSS, 1831 aus dem Mitteldevon der Eifel (Deutschland, Rheinisches Schiefergebirge). – Privately published on private web-page: <http://www.devon-crinoiden.de/cupressogoldfussi.pdf> (Bonn) [does not meet ICZN regulations, J.B.].

— (2006b): *Dachsbergcrinites* nov. gen. (Crinoidea, Inadunata) - Eine neue Crinoiden-Gattung aus dem Mitteldevon der Eifel (Rheinisches Schiefergebirge). – Privately published on private web-page: <www.devon-crinoiden.de/Dachsbergcrinites.pdf> (Bonn) [does not meet ICZN regulations, J.B.].

— (2006c): Über einen neuen *Hexacrinites* (*Hexacrinites magnificus* n.sp.) (Crinoidea, Camerata) aus dem Mitteldevon (Rheinisches Schiefergebirge) der Eifel (Deutschland). – Privately published on private web-page: <http://www.devon-crinoiden.de/hexacrinitesmagnificus.pdf> (Bonn) [does not meet ICZN regulations, J.B.].

— (2006d): *Hexacrinites breimeri* n. sp. und *Hexacrinites taluxaiensis* n. sp. (Crinoidea, Camerata) aus dem Givetium der asturischen Küste (N Spanien). – Privately published on private web-page: <http://www.devon-crinoiden.de/Hexacrinites%20breimeri.pdf> (Bonn) [does not meet ICZN regulations, J.B.].

— (2007a): Die Crinoidenwelt der Eifel vor 350.000.000 Jahren - Neue Crinoiden aus dem Mitteldevon der Eifel, Teil 2. – 83 p., 88 text-fig., 3 tab., 4 pl. Private published (Bonn).

— (2007b): Systematik, pp. 22-73, pls. 1-2. *In*: HAUSER J. & LANDETA F. G. (eds.): Neue Crinoiden aus dem Paläozoikum von Nordspanien. – 78 p., 113 text-fig., 4 tab., 2 pl. Private published (Bonn, Oviedo).

— (2008): Crinoiden und Begleitfauna des Ahbachiums der Rommersheimer Trasse (Prümer Mulde, Eifel, Rheinisches Schiefergebirge). – 80 p., 92 text-fig, 18 pl. Privately published (Bonn).

— (2009): Private web-page: <http://www.devon-crinoiden.de>.

— , LANDETA, F. G. & SAVILL J. J. (2009): *Ammonicrinus wanneri* SPRINGER, 1926 (Crinoidea, Flexibilia) from the Portilla Formation, Givetian (Cantabrian Mountains, Province Leon, Northern Spain), pp. 54-58. *In*: HAUSER J. & LANDETA F. G. (eds.): Crinoiden aus dem Unter- und Mitteldevon von Asturien und Leon (Nordspanien). – 58 p., 6 tab., 48 text-fig., 4 pl. Private published (Bonn).

HEESEMANN, J. & DAHM, H.-D. (1965) [eds.]: Das Mitteldevon des Rheinischen Schiefergebirges. – Fortschritte in der Geologie von Rheinland und Westfalen, **9**: 1-938.

HESS, H. (1999): Lower Devonian Hunsrück Slate of Germany, pp. 111-121. *In*: HESS, H., AUSICH, W. I., BRETT, C. E. & SIMMS, M. J. (eds.): Fossil crinoids. – 275 p., 238 fig. Cambridge University Press (Cambridge).

— , AUSICH, W. I., BRETT, C. E. & SIMMS, M. J. (1999): Fossil crinoids. – 275 p., 238 fig. Cambridge University Press (Cambridge).

HOLLIS, K. A. & AUSICH, W. I. (2008): The Holdfast of *Gilbertsocrinus tuberosus* (Mississippian, Crinoidea). – Canadian Journal of Earth Sciences, **45**: 135-140.

HOLZAPFEL, E. (1895): Das Obere Mitteldevon (Schichten mit *Stringocephalus burtini* und *Maeneceras terbratum*) in Rheinischen Gebirge. – Abhandlungen der Preußischen Geologischen Landesanstalt, **16**: 1-460.

HOTCHKISS, F. H. C., PROKOP, R. J. & PETR, V. (1999): Isolated vertebrae of brittlestars of the Family Klasmuridae SPENCER, 1925 (Echinodermata: Ophiuroidea) in the Devonian of Bohemia (Czech Republic). – Journal of the Czech Geological Society, **44**(3-4): 329-333.

HOTZ, E. E. (1951): *Coelotrochium canis* n. sp. und seine Bedeutung für die Stratigraphie des Mittel-Devons der Eifel. – Senckenbergiana, **32**: 31-36.

— , KRÄUSEL, W. & STRUVE, W. (1955): Die Kalkmulden von Hillesheim und Ahrdorf. *In*: KRÖMMELBEIN, K., HOTZ, E. E., KRÄUSEL, W. & STRUVE, W. (eds.): Zur Geologie der Eifelkalkmulden. – Beiheft Geologisches Jahrbuch, **17**: 45-192.

JAEKEL, O. (1895): Beiträge zur Kenntniss der palaeozoischen Crinoiden Deutschlands. – Paläontologische Abhandlungen, Neue Folge, **3**: 1-116.

— (1918): Phylogenie und System der Pelmatozoen. – Palaeontologische Zeitschrift, **3**(1): 1-128.

JELL, P. A. (1999): Silurian and Devonian crinoids from central Victoria. – Memoirs of the Queensland Museum, **43**(1): 1-114.

— & JELL, J. S. (1999): Crinoids, a blastoid and a cyclocystoid from the Upper Devonian reef complex of the Canning Basin, Western Australia. – Memoirs of the Queensland Museum, **43**(1): 201-236.

— , — , JOHNSON, B. D., MAWSON, R. & TALENT, J. A. (1988): Crinoids from Devonian limestones of eastern Australia. – Memoirs of the Queensland Museum, **25**: 355-402.

JOHNSON, J. G. & SANDBERG, C. A. (1988): Devonian Eustatic Events in the Western United States and their Biostratigraphic Responses. *In*: MCMILLAN, N. J., EMBRY, A. F. & GLASS D. J. (eds.): Devonian of the World, Vol. I. Regional Synthesis. – Canadian Society of Petroleum Geologists, Memoir, **14**: 171-178.

— , KLAPPER, G. & SANDBERG, C. A. (1985): Devonian eustatic fluctuations in Euamerica. – Geological Society of America Bulletin, **96**: 567-587.

KASIG, W. & NEUMANN-MAHLKAU, P. (1969): Die Entwicklung des Eifeliums in Old-Red-Fazies - zur Riff-Fazies im Givetium und Unteren Frasnium am Nordrand des Hohen Venns (Belgien/Deutschland). – Geologische Mitteilungen, **8**: 327-388.

KAUFMANN, B. (2006): Calibrating the Devonian Time Scale: a synthesis of U-Pb ID-TIMS ages and conodont stratigraphy. – Earth Science Reviews, **76**: 175-190.

KAYSER, E. (1871): Studien aus dem Gebiete des rheinischen Devon. II. Die devonischen Bildungen der Eifel. – Zeitschrift der Deutschen Geologischen Gesellschaft, **23**: 289-376.

KEYES, C. R. (1888): On the attachment of *Platyceras* to palaeocrinoids and its effects in modifying the form of the shell. – American Philosophical Society, Proceedings and Transactions, **25**(128): 231-243.

KOENEN, A. VON (1886): Die Crinoiden des norddeutschen Ober-Devons. – Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, **1**: 99-116.

KONGIEL, R. (1958): Nowy gatunek *Ammonicrinus* i jego wystepowanie w Polsce - Une espece now velle de l'*Ammonicrinus* de givetian inferieur de Skaly (Mts. de Snte Croix). – Poland Institute of Geology, Museum Ziemi, Proceedings, **2**: 31-40.

KORN, D. (2008): Rheinische Masse. Geologische Übersicht. *In*: Deutsche Stratigraphische Kommission (ed.): Stratigraphie von Deutschland VIII, Devon. – Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften, **52**: 116.

KÖNIG, C. D. E. (1825): Icones Fossilium Sectiles. – 4 p., 8 pls. [pls. 9-19 unpubl.] (London).

KRAUSE, P. G. (1927): Über *Ammonicrinus* aus dem Mitteldevon der Eifel. – Zeitschrift der Deutschen Geologischen Gesellschaft, **79**: 448-456.

KREBS, W. (1970): Nachweis von Oberdevon in der Schwerspatgrube Eisen (Saargebiet) und die Folgerung für die Paläogeographie und Lagerstätten des linksrheinischen Schiefergebirges. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1970**: 465-480.

— (1974): Devonian carbonate complexes of Central Europe. *In*: LAPORTE, L. F. (ed.): Reefs in time and space. – Special Publication of the Society Economic Paleontology and Mineralogy, **18**: 155-208.

KUCKELKORN, L. (1925): Die Süd-West-Enden der Blankenheimer und Dollendorfer Mulde in der Hohen Eifel. – Sitzungsbericht des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalen, Abteilung C, **1924**: 78-105.

LAMARCK, J. B. P. A. DE (1801): Systême des animaux sans vertèbres, ou tableau général des classes, des ordres et des genres de ces animaux; présentant leurs caractères essentiels et leur distribution, d'après la considération de leurs rapports naturels et de leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Hist. Naturelle, parmi leurs dépouilles conservées; précédé du discours d'ouverture du Cours de Zoologie, donné dans le Muséum National d'Histoire Naturelle l'an 8 de la République. – viii + 432 p. Lamarck & Deterville (Paris).

— (1816): Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie, Vol. 2. – 568 p. Verdière (Paris).

LANE, N. G. & SEVASTOPULO, G. D. (1986): Micromorph crinoid fauna of the McCraney Limestone (Mississippian, Kinderhookian) of western Illinois. – Journal of Paleontology, **60**: 736-743.

LE MENN, J. (1975): Un nouveau genre d'Hexacrinitidae (Crinoidea, Camerata). – Annales de la Société Géologique du Nord, **95**: 243-250.

— (1985): Les Crinoides du Dévonien inferieur et moyen du Massif armoricain. Mémoires de la Societé géologique et minéralogique de Bretagne, **30**: 1-268.

— & JAOUEN P. A. (2003): Nouvelles espèces d'*Ancyrocrinus* et d'*Ammonicrinus*, crinoïdes à pédoncule spécialisé du Dévonien armoricain (Brest, France). – Comptes Rendus Palevol, **2**(3): 205-212.

LÜTTE, B.-P. (1984): Rugose Korallen aus dem Mitteldevon (Givetium) der Sötenicher Mulde (Rheinisches Schiefergebirge, Nord-Eifel). – Münstersche Forschungen zur Geologie und Paläontologie, **61**: 175-243.

— (1987): *Glossophyllum*-Arten aus dem Mittel-Devon der Eifel (Rugosa; Rheinisches Schiefergebirge). – Senckenbergiana lethaea, **67**(5/6): 433-457.

— (1990): Horn- und kegelförmige rugose Korallen aus dem Mittel-Devon der Eifel. – Senckenbergiana lethaea, **70**(4/6): 297-395.

LYON, S. S. (1869): Remarks on thirteen new species of Crinoidea from the Palaeozoic rocks of Indiana, Kentucky, and Ohio, and a description of certain peculiarities in the structure of the columns of *Dolatocrinus,* and their attachment to the body of the animal. – American Philosophical Society, Transactions, **13**: 443-466.

MAILLIEUX, E. (1940): Les Echinodermes du Frasnien de la Belgique. – Mémoires du Musé d'Histoire Naturelle de Belgique, **92**: 3-48.

MANNIFIELD, K. & SEVASTOPULO, G. D. (1998): Long stemmed crinoids from the Carboniferous of Ireland. *In*: MOOI, R. & TELFORD, M. (eds.): Echinoderms: San Fransisco; Proceedings of the Ninth International Echinoderm Conference, San Fransisco, August 1996. – pp. 183-186, 3 fig. Balkema (Rotterdam, Brookfield).

MAPLES, C. G., WATERS, J. A., LANE, N. G., MARCUS, S. A., LIAO, Z., HOU, H., WANG, J. & LIU, L. (1997): "Carboniferous" echinoderms in the Late Devonian? Refugia, rebound, and repopulation. *In*: CEJCHAN, P. & HLADIL, H. (eds.): Recoveries from Mass Extinctions, Final Conference Recoveries 97', Abstract Book. – 11 p. Geological Institute AS CR (Praha).

MAURER, F. (1875): Paläontologische Studien im Gebiet des rheinischen Devon. 2. Die Fauna des Rotheisenstein der Grube Haina. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, **1875**: 596-618.

MCINTOSH, G. C. (1979): Abnormal specimens of the Middle Devonian crinoid *Bactrocrinites* and their effect on the taxonomy of the genus. – Journal of Paleontology, **53**: 18-28.

— (1987): Review of the Devonian camerate crinoid *Bogotacrinus scheibei* Schmidt from Colombia. – Journal of Paleontology, **61**: 750-757.

— (2001): Devonian cladid crinoids: Families Glossocrinidae Goldring, 1923, and Rutkowskicrinidae new family. – Journal of Paleontology, **75**: 783-807.

MEEK, F. B. & WORTHEN, A. H. (1869): Descriptions of new Crinoidea and Echinoidea from the Carboniferous rocks of the western states, with a note on the genus *Onychaster*. – Proceedings of the Academy of Natural Sciences of Philadelphia, **21**: 67-83.

MEYER, D. L. & AUSICH, W. I. (1983): Biotic interactions among recent and among fossil crinoids, pp. 377-427. *In*: TEVESZ, M. J. S. & MCCALL P. L. (eds.): Biotic Interactions in Recent and Fossil Benthic Communities. – xviii + 837 p. Plenum Press (New York).

— & OJI, T. (1993): Eocene crinoids from Seymour Island, Antarctic Peninsula: paleobiogeographic and paleoecologic implications. – Journal of Paleontology, **67**(2): 250-257.

— , Miller, A. I., Holland, S. M. & Dattilo, B. F. (2002): Crinoid distribution and feeding morphology through a depositional sequence: Kope and Fairview Formations, Upper Ordovician, Cincinnati Arch region. – Journal of Paleontology, **76**(4): 725-732.

MEYER, W. (1986): Geologie der Eifel. – 614 p., 153 fig., 13 tab., 1 geol. map. Schweizerbart'sche (Stuttgart).

— , STOLTIDIS, J. & WINTER, J. (1977): Geologische Exkursion in den Raum Weyer-Schuld-Heyroth-Niederehe-Üxheim-Ahütte. – Decheniana, **130**: 322-334.

MIESEN, J. (1971): Crinoiden der Eifel. – 70 p., 431 fig., 16 textfig., 20 pl. Privately published (Leverkusen).

— (1974): Die Versteinerungen im Devon der Eifel. – 199 p., 1427 text-fig. Privately published (Leverkusen).

MILICINA, V. S. (1977): Crinoidei iz eifelskikh otlozhenii vostochnogo sklona Severnogo i Srednego Urala; Novie materiali po paleontologii Urala. – Akademiya Nauk SSSR, Uralskii Nauchnii Tsentr, Institut Geologii i Geokimii, **12**: 123-143.

— (1989): Devonskie morskie lilii semeistva Hexacrinitidae Urala [On Hexacrinitidae from the Devonian deposits of the Urals]. *In*: KALJO, D. L., (edit.): Problemy izucheniya iskopaemykh i sovremennykh iglokozhikh [Fossil and recent echinoderm researches]. – Akademiya Nauk Estonskoi SSR, Tallin: 98-110.

MILLER, J. S. (1821): A natural history of the Crinoidea, or lily-shaped animals; with observations on the genera, Asteria, Euryale, Comatula and Marsupites. – 150 p. + unnumbered pls. Bryan & Co. (Bristol, England).

— (1883): The American Palaeozoic fossils: A catalogue of the genera and species, with names of authors, dates, places of publication, groups of books in which found, and the etymology and signifcation of the words, and an introduction devoted to the stratigraphical geology of the Palaeozoic rocks. – Echinodermata pp. 247-334. Private published (Cincinnati, Ohio).

— (1889): North American geology and paleontology. – 664 p. (Echinodermata pp. 665-718). Western Methodist Book Concern (Cincinnati, Ohio).

— & GURLEY, W. F. E. (1890): Description of some new genera and species of Echinodermata from the Coal Measures and Subcarboniferous rocks of Indiana, Missouri, and Iowa. – Journal Cincinnati Society of Natural History, **13**(1): 3-25.

MOORE, R. C. (1978): Flexibilia, pp. T759-T812. *In*: MOORE, R. C. & TEICHERT, C. (eds.): Treatise on Invertebrate Paleontology; Part T, Echinodermata 2, vols. 1-3. – I-XXXVIII + pp. T1-T1027. The Geological Society of America and The University of Kansas (Boulder, Colorado & Lawrence, Kansas).

— & JEFFORDS, R. M. (1968): Classification and nomenclature of fossil crinoids based on studies of dissociated parts of their columns. – The University of Kansas Paleontological Contributions, **46**: 1-86.

— & LAUDON, L. R. (1943): Evolution and classification of Paleozoic crinoids. – Geological Society of America, Special Paper, **46**: 1-153.

— & STRIMPLE, H. L. (1973): Lower Pennsylvanian (Morrowan) crinoids from Arkansas, Oklahoma, and Texas. – University of Kansas Paleontological Contributions, **60**(Echinodermata 12): 84.

— & TEICHERT, C. (1978) [eds.]: Treatise on Invertebrate Paleontology; Part T, Echinodermata 2, vols. 1-3. – I-XXXVIII + pp. T1-T1027. The Geological Society of America and The University of Kansas (Boulder, Colorado & Lawrence, Kansas).

— , LANE, N. G. & STRIMPLE, H. L. (1978): Cladida, pp. T578-T759. *In*: MOORE R. C. & TEICHERT C. (eds.): Treatise on Invertebrate Paleontology; Part T, Echinodermata 2, vols. 1-3. – I-XXXVIII + pp. T1-T1027. The Geological Society of America and The University of Kansas (Boulder, Colorado & Lawrence, Kansas).

— , LANE, N. G., STRIMPLE, H. L. & SPRINKLE, J. (1978): Disparida, pp. T520-T564. *In*: MOORE, R. C. & TEICHERT, C. (eds.): Treatise on Invertebrate Paleontology; Part T, Echinodermata 2, vols. 1-3. – I-XXXVIII + pp. T1-T1027. The Geological Society of America and The University of Kansas (Boulder, Colorado & Lawrence, Kansas).

MOTOKAWA, T., SHINTANI, O. & BIRENHEIDE, R. (2004): Contraction and stiffness changes in collagenous arm ligaments of the stalked crinoid *Metacrinus rotundus* (Echinodermata). – Biological Bulletin, **206**(1): 4-12.

MOZZI, D., DOLMATOV, I. Y., BONASORO, F. & CARNEVALI, M. D. C. (2006): Visceral regeneration in the crinoid *Antedon mediterranea*: basic mechanisms, tissues and cells involved in gut regrowth. – Central European Journal of Biology, **1**(4): 609-635.

MURRAY, J. W. (1990): Wirbellose Makrofossilien - Ein Bestimmungsatlas (German translation by SCHNEIDER, J. & WALTER, H.). – 266 p., 1596 text-fig. Ferdinand Enke Verlag (Stuttgart).

MÜLLER, J. (1855): Über die Echinodermen in der Umgegend von Coblenz und in dem Eifeler Kalke. *In*: ZEILER, F. & WIRTGEN, P.W. (eds.): Bemerkungen über die Petrefacten der älteren devonischen Gebirge am Rheine, insbesondere über die in der Umgegend von Coblenz vorkommenden Arten. – Verhandlungen des Naturhistorischen Vereins der Preußischen Rheinlande und Westfalen, **12**: 1-28.

— (1856): Über neue Crinoiden aus dem Eifeler Kalk. – Verhandlungen der Königlichen Akademie der Wissenschaften, Monatsberichte, **1856**: 353-356.

— (1857) [1856]. Über neue Echinodermen des Eifeler Kalkes. – Köngliche Akademie der Wissenschaften, Abhandlungen, **1857**: 243-268.

PAECKELMANN, W. (1913): Das Oberdevon des Bergischen Landes. – Abhandlungen der Königlich Preußischen Geologischen Landesanstalt, Neue Folge, **70**: 1-358.

PAPROTH, E. & STRUVE, W. (1982): Bemerkungen zur Entwicklung des Givetium am Niederrhein. Paläogeographischer Rahmen der Bohrung Schwarzbachtal 1. – Senckenbergiana lethaea, **63**(1/4): 359-376.

PETERS, S. E. & BORK, K. B. (1998): Secondary tiering on crinoids from the Waldron Shale (Silurian: Wenlockian) of Indiana. – Journal of Paleontology, **72**: 887-893.

PHILLIPS, J. (1836): Illustrations of the geology of Yorkshire, or a description of the strata and organic remains. Part. 2. The Mountain Limestone districts, 2nd edition. – pp. 203-208, pls. 3-4. John Murray (London).

PHILLIPS, J. (1841): Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon and West Somerset. – xii + 232 p., 60 pl. Longman, Brown, Green & Longmans (London).

PIOTROWSKI, A. (1977): Genus *Ammonicrinus* Crinoidea, from the Middle Devonian of the Holy Cross Mountains, Poland. – Acta Palaeontologica Polonia, **22**(2): 205-219.

POLYARNAYA, ZH. A. (1973): Members of the genus *Cupressocrinites* (Crinoidea) from the Givetian of the Southern Urals. – Paleontological Journal. **7**(4): 562-565. [Original: Predstaviteli Tyada *Cupressocrinites* (Crinoidea) iz Zhivetskikh Otlozhenii Yuzhnogo Urala. Paleontologicheskiy Zhurnal, **4**(1973): 132-135].

— (1986): Zhivetskie morskie lilii vostochnogo sklona yuzhnogo urala [Givetian crinoids in the eastern slope of the Southern Urals]. – Zapiski Leningradskogo Ordena Lenina, Ordena Oktyabrskoy Revolyutsshch i Ordena Trudovogo Krashogo Znameni Gornnogo Instituta, **107**: 76-81.

POWERS, B. G. & AUSICH, W. I. (1990): Epizoan associations in a Lower Mississippian Paleocommunity (Borden Group, Indiana, U.S.A.). – Historical Biology, **4**: 245-265.

PRICK, R. (1983): Inadunate Crinoiden aus dem Mittel-Devon der Eifel. – Senckenbergiana: lethaea, **64**(2/4): 227-235.

PROKOP, R. J. (1982): Some new hexacrinitids (Crinoidea, Camerata) from the Lower Devonian of Bohemia. – Věstník Ústředního ústavu geologického, **57**(5): 277-283.

— (1987): The stratigraphical distribution of Devonian crinoids in the Barrandian area (Czechoslovakia). – Newsletter on Stratigraphy, **17**(2): 101-107.

— (2009): *Ammonicrinus bulbosus* sp. n. (col.) (Crinoidea, Flexibilia) from the Lower Devonian Koněprusy Limestone, Barrandian area (Czech Republic). Journal of the National Museum (Prague), Natural History Series, **177**(12): 161-164.

— & Petr, V. (1993): *Taxocrinus* sp. (Crinoidea, Flexibilia) in the Middle Devonian of Moravia (Czech Republic). *In*: Prokop, R. J. & Petr, V. (eds.): New flexible crinoids from the Silurian and Devonian of the Czech Republic: Folia Musei Rerum Naturalium Bohemiae Occidentalis. Geologica, **38**: 16-19.

— & — (1995): New finds of isolated cup plates of the crinoid genus *Edriocrinus* in the Bohemian Lower and Middle Devonian. – Časopis Národniho muzea, Řada přirodovědná, **164**(1-4): 49-50.

Quenstedt, F. A. (1852): Handbuch der Petrefactenkunde. – I-IV, 1-792, 62 pl. Laupp (Tübingen) [delivery 1: 1-256, pl. 1-19 – 1851; delivery 2: 257-528, pl. 20-42 – 1851; delivery 3: I-IV, 529-792, pl. 43-62 - 1852].

— (1861): Epochen der Natur. – 853 p. + unnumbered woodcuts. Laupp (Tübingen).

— (1865-1866): Handbuch der Petrefaktenkunde, 2. Edition. – 320 p., 24 pl.; [delivery 1: 1865], pp. 321-640, pls. 25-51, 54-56 [delivery 2: 1866], pp. 641-982, pls. 52-53, 57-86 [3. Lieferung 1866]. Laupp (Tübingen).

— (1874-1876): Petrefactenkunde Deutschlands, 1. Abteilung, 4. Band: Echinodermen (Asteriden & Encriniden). – pp. 1-742 [1876]; Atlas zu den Echiniden. – pp. 62-89 [1874]; Atlas zu den Asteriden & Encriniden. – pp. 90-114 [1876]. Fuess (Leipzig).

— (1885): Handbuch der Petrefaktenkunde. 3. Edition. – I-VIII, 1-1239, 443 fig., 100 pl. Tübingen (H. Laupp).

Reed, F. R. C. (1908): The Devonian faunas of the Northern Shan states. – Memoirs of the Indian Geological Survey, **2**(5): 1-157.

Römer, C. F. (1844): Das Rheinische Übergangsgebirge. Eine palaeontologisch-geognostische Darstellung. – 96 p., 6 pl. Hahn (Hannover).

— (1851): Beiträge zur Kenntnis der fossilen Fauna des devonischen Gebirges am Rhein. – Verhandlungen des Naturhistorischen Vereins der preußischen Rheinlande und Westfalens, **8**: 357-376 [**9** addendum 1852: 281-288].

— (1852): Beiträge zur Kenntnis der fossilen Fauna des devonischen Gebirges am Rhein, I. Crinoidea – addendum of no. VIII, p. 358 seq. – Verhandlungen des Naturhistorischen Vereins der preußischen Rheinlande und Westfalens, **9**: 281-288.

— (1852-1854): Erste Periode, Kohlen-Gebirge, pp. 210-291. *In*: Bronn, H. G. (1851-1856): Lethaea Geognostica, **3**(2): 1-788.

Römer, F. A. (1843): Die Versteinerungen des Harzgebirges. – 40 p., 12 pl. Hahn (Hannover).

SANDBERGER, G. & SANDBERGER, F. (1856): Ordnung III. Crinoïdea, Meerlilien MILLER, pp. 383-403. *In*: SANDBERGER, G. & SANDBERGER, F. (eds.) [1849-1856]: Die Versteinerungen des Rheinischen Schichtensystems in Nassau. Mit einer kurzgefassten Geognosie dieses Gebietes und mit steter Berücksichtigung analoger Schichten anderer Länder. – I-XV, 564 p., 41 pls. (atlas) [1849: pp. 1-40, pls.1-5; 1850: pp. 41-72, pls. 6-8, 11-12; 1851: pp. 73-104, pls. 9-10, 10a-b, 13; 1852: pp. 105-168, pls. 14-23; 1854: pp. 169-232, pls. 24-33; 1856: I-XV, pp. 233-564, pls. 34-39]. Kreidel & Niedner (Wiesbaden).

SCHINDLER, E. (1990): The late Frasnian (Upper Devonian) Kellwasser Crisis. *In*: KAUFFMAN, E. G. & WALLISER, O. H. (eds.): Extinction Events in Earth History, Proceedings of the Project 216: Global Biological Events in Earth History. – Lecture Notes in Earth Sciences, **30**: 151-159.

SCHLOTHEIM, E. F. VON (1820): Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert. – p. 1-437, pl. 15-29. Beckersche Buchhandlung (Gotha).

SCHLÜTER, C. A. (1885): Über einige neue Anthozoen aus dem Devon. – Sitzungsberichte der Niederrheinischen Gesellschaft für Natürliche Heilkunde, **42**: 144-151.

— (1934): Die Crinoideen des Rheinischen Devons, I. Teil; Die Crinoideen des Hunsrückschiefers. – Abhandlung der Preußischen Geologischen Landesanstalt, **163**: 1-149.

— (1937): Fósiles paleozoicos de la Cordillera Oriental de Colombia (Cordillera de Bogotá). – Republic de Colombia, Ministerio de Industrias y Trabajo, Estudios Geologicos y Paleontologicos Sobre la Cordillera Oriental de Colombia, **2**: 1-6.

— (1941): Die Crinoiden des Rheinischen Devons II. Teil. A. Nachtrag zu: Die Crinoiden des Hunsrückschiefers; B. Die Crinoideen des Unterdevons bis zur *cultrijugatus*-Zone (mit Ausschluß des Hunsrückschiefers). – Abhandlungen der Preußischen Geologischen Landesanstalt, **182**: 1-253.

SCHNUR, J. (1849): Crinoiden, pp. 21-22. *In*: STEININGER J. (ed.): Die Versteinerungen des Übergangsgebirges der Eifel. – Jahrbuch des Schulcursus an dem Gymnasium zu Trier, **1848/1849**: 1-34.

SCHÖNE, B. R., BASSE, M. & MAY, A. (1998): Korrelationen des Eifelium/Givetium-Grenzbereichs im Rheinischen Schiefergebirge. – Senckenbergiana lethaea, **77**(1/2): 233-242.

SCHRÖDER, S. (1995): Rugose Korallen aus der Freilingen-Formation der Dollendorfer Mulde (Ober-Eifelium/Mitteldevon; Eifel/Rheinisches Schiefergebirge). – Senckenbergiana lethaea, **75**(1/2): 33-75.

— (1997): Upper Eifelian (Middle Devonian) rugose corals from the Eifel Hills (Germany) and their relation to North American and Eastern European taxa. – Boletin Real de la Sociedad Española de Historia Natural, Seccion de Geología, **92**(4): 271-279.

— (2001): On some western European Siphonophrentidae. – Bulletin Tohoku University Museum, **1**: 245-259.

— & SALERNO, C. (2001): Korallenfauna und Fazies givetischer Kalksteinabfolgen (Cürten-/Dreimühlen-Formation) der Dollendorfer Mulde (Devon, Rheinisches Schiefergebirge/Eifel). – Senckenbergiana lethaea, **81**(1): 111-133.

SCHULTZE, L. (1866): Monographie der Echinodermen des Eifler Kalkes. – 118 p., 13 pls; Carl Gerold's Sohn (Wien) [presented at the meeting of the "mathematisch-naturwissenschaftlichen Classe" at the 07.12.1865 *via* E. SUESS; also published as: SCHULTZE, L. (1867): Monographie der Echinodermen des Eifler Kalkes. – Denkschrift der Mathematisch Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, **26**(2): 113-230].

SEILACHER, A. & MACCLINTOCK, C. (2005): Crinoid anchoring strategies for soft-bottom dwelling. – Palaios, **20**(3): 224-240.

SIEVERTS, H. (1934): Neues über *Cupressocrinus* Goldfuss. – Sitzungsbericht, herausgegeben vom Naturhistorischen Verein der Preussischen Rheinlande und Westfalen, Verhandlung für 1932/1933, **26/27**: 89-102.

SIEVERTS-DORECK, H. (1950): Über *Hexacrinus* und *Bactrocrinus*. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **3**: 80-87.

— (1953): Über einige inadunate Crinoiden aus dem rheinischen Devon. – Notizblatt des Hessischen Landesamt für Bodenforschung, **81**: 75-87.

— (1957): Neufunde von *Diamenocrinus* und *Ctenocrinus* aus dem Mittel Devon der Eifel. – Notizblatt des Hessischen Landesamt für Bodenforschung, **85**: 62-66.

— (1963): Über Missbildungen bei *Cupressocrinus elongatus* aus dem Mitteldevon der Eifel. – Decheniana, **115**(2): 239-244.

SIMMS, M. J. & SEVASTOPULO, G. D. (1993): The origin of articulate crinoids. – Palaeontology, **36**(1): 91-109.

SMITH, A. B. (1985): Crinoidea (Echinodermata, Chapter 7), pp. 153-181, pls. 7.1.1.-7.8.1. *In*: MURRAY, J. W., (ed.): Atlas of invertebrate macrofossils. – xiii + 241 p. Logman, The Palaeontological Association (Harlow, Essex).

SPRENG, W. P. & PARKS, J. M. (1953): Evolution in basal plates of monocyclic camerate crinoids. – Journal of Paleontology, **27**: 585-595.

SPRINGER, F. (1913): Crinoidea. *In*: ZITTEL, K. A. VON: Textbook of paleontology, 2nd edit., vol. 1. – pp. 173-243. Macmillan & Co. (London).

— (1926a): Upper Devonian crinoids from the Mackenzie River valley. – Canada Geological Survey, Museum Bulletin, **42**: 127-132.

— (1926b): Unusual forms of fossil crinoids. – Proceedings of the U.S. National Museum, **67**(9): 1-137.

STEININGER, J. (1848): Die Versteinerungen des Übergangsgebirges der Eifel. – Jahrbuch des Schulcursus an dem Gymnasium zu Trier, **1848/1849**: 1-34.

— (1853): Geognostische Beschreibung der Eifel. – 144 p., 10 pl., 1 map. Lintz (Trier).

STEININGER, F. F. & PILLER, W. E. (1999): Empfehlungen (Richtlinien) zur Handhabung der stratigraphischen Nomenklatur. – Courier Forschungsinstitut Senckenberg, **209**: 1-19.

STEINMANN, G. (1903): Einführung in die Paläontologie. – 466 p., 818 fig. W. Engelmann (Leipzig).

— (1907): Einführung in die Paläontologie, 2. Auflage. – 542 p. W. Engelmann (Leipzig).

— & DÖDERLEIN L. (1890): Elemente der Palaeontologie. – 848 p., XIX, 1030 textfig. Wilhelm Engelmann (Leipzig).

STRIMPLE, H. L. (1952): Some new species of crinoids from the Henryhouse Formation of Oklahoma. – Journal of the Washington Academy of Science, **42**: 75-79.

— (1963): Crinoids of the Hunton Group. – Oklahoma Geological Survey Bulletin, **100**: 1-169.

STRUVE, W. (1961): Das Eifeler Korallen-Meer - Mineralogische und geologische Streifzüge durch die nördliche Eifel. – Aufschluß, Sonderheft, **10**: 81-107.

— (1963): Das Korallen-Meer der Eifel vor 300 Millionen Jahren - Funde, Deutungen, Probleme. – Natur und Museum, **93**(6): 237-276.

— (1982a): The Eifelian within the Devonian frame, history, boundaries, definitions, pp. 401-432. *In*: ZIEGLER, W. & WERNER, R. (eds.): On Devonian Stratigraphy and Palaeontology of the Ardenno-Rhenish Mountains and related Devonian Matters. – Courier Forschungsinstitut Senckenberg, **55**: 1-498.

— (1982b): The Great Gap in the record of marine Middle Devonian, pp. 433-447. *In*: ZIEGLER, W. & WERNER, R. (eds.): On Devonian Stratigraphy and Palaeontology of the Ardenno-Rhenish Mountains and related Devonian Matters. – Courier Forschungsinstitut Senckenberg, **55**: 1-498.

— (1992): Neues zur Stratigraphie und Fauna des rhenotypen Mittel-Devon. – Senckenbergiana lethaea, **71**(5/6): 503-624.

— (1996a): On *Athyris* (Brachiopoda) and its type species '*Terebratula*' *concentrica* von Buch. *In*: ALVAREZ, F., BRUNTON, C. H. C. & STRUVE, W. (1996): Beiträge zur Kenntnis devonischer Brachiopoden, 26. – Senckenbergiana lethaea, **76**(1/2): 65-105.

— (1996b): Eifel (Venn, Bergisches Land); Unterstufen, Formationen, Subformationen; Mitteldevon. *In*: WEDDIGE, K. (ed.): Devon-Korrelationstabelle. – Senckenbergiana lethaea, **76**(1/2): 280, tab. R160dm96.

— (1996c): Trilobiten, Rheinisches Schiefergebirge; Mitteldevon. *In*: WEDDIGE, K. (ed.): Devon-Korrelationstabelle. – Senckenbergiana lethaea, **76**(1/2): 280, tab. B100dm96.

— (1996d): Brachiopoden, Rheinisches Schiefergebirge; Mitteldevon. *In*: WEDDIGE, K. (ed.): Devon-Korrelationstabelle. – Senckenbergiana lethaea, **76**(1/2): 208, tab. R160dm96.

— & WERNER, R. (1982): The Lower/Middle Devonian boundary and the Eifelian Stage in the "Type Eifelian" region. *In*: PLODOWSKI, G., WERNER R. & ZIEGLER, W. (eds.): Field meeting on Lower and Lower Middle Devonian stages in the Ardenno-Rhenish type area, guidebook. – pp. 81-151, figs. 1-6, 2 maps (1:10.000). International Union of Geological Sciences, Subcommission on Devonian Stratigraphy (Frankfurt am Main).

— (†), PLODOWSKI, G. & WEDDIGE, K. (1997): Tagesexkursion I (27.09.1997) Biostratigraphische Stufengrenzen und Events in der Prümer und Hillesheim Mulde, p. 123-167. *In*: ESCHGHI, I. & RUDOLF, H. (eds.): 67. Jahrestagung der Paläontologischen Gesellschaft, 21.-28.09.1997 in Daun/Vulkaneifel, Exkursionsführer. – Terra Nostra, Schriften der Alfred-Wegener-Stiftung, **97**(7): 1-202.

TAYLOR, P. D. T. & WILSON, M. A. (2007): Morphology and affinities of hederelloid "bryozoans", p. 88. *In:* HAGEMAN, S. J. & MCKINNEY, F. K. (eds.): 14th Meeting of the International Bryozoology Association, 02.-07.07.2007, Abstracts with Program. – IBA Website, p. 88, <http://www.iba.appstate.edu/IBAfiles/AbstrastWprogram.pdf>. Boone, (North Carolina).

THOMAS, A. O. (1924): Echinoderms of the Iowa Devonian. – Iowa Geological Survey, Annual Reports 1919 and 1920, **29**: 385-552.

UBAGHS, G. (1952): *Ammonicrinus* SPRINGER, Crinoidea Flexibilia du Dévonien moyen d'Allemagne. – Senckenbergiana, **33**: 203-226.

— (1978): Skeletal morphology of fossil crinoids, pp. T58-T216. *In*: MOORE, R. C. & TEICHERT, C. (eds.): Treatise on Invertebrate Paleontology; Part T, Echinodermata 2, vols. 1-3. – I-XXXVIII + pp. T1-T1027. The Geological Society of America and The University of Kansas (Boulder, Colorado & Lawrence, Kansas).

— (1978): Camerata, pp. T408-T519. *In*: MOORE, R. C. & TEICHERT, C. (eds.): Treatise on Invertebrate Paleontology; Part T, Echinodermata 2, vols. 1-3. – I-XXXVIII + pp. T1-T1027. The Geological Society of America and The University of Kansas (Boulder, Colorado & Lawrence, Kansas).

ULRICH, E. O. (1882): American Palaeozoic Bryozoa. – The Journal of the Cincinnati Society of Natural History, **5**: 121-175, 233-257.

— (1896): Bryozoa. *In*: EASTMAN, C. (ed.): Zittel's Textbook of Palaeontology, vol. 1. – pp. 257-291. Macmillan (London).

VINASSA DE REGNY, P. (1921): Sulla classificazione die trepostomidi. – Societa Italiana di Scienze Naturali Atti, **59**: 212-231.

VOIGT, E. (1977): On grazing traces produced by the radula of fossil and Recent gastropods and chitons. *In*: CRIMES, T. P. & HARPER, J. C. (eds.): Trace Fossils **2**: 335-346.

WACHSMUTH, C. & SPRINGER, F. (1880): Revision of the Palaeocrinoidea I, the families Ichthyocrinidae and Cyathocrinidae. – Proceedings of the Academy of Natural Sciences of Philadelphia, **1879**: 226-378.

— & — (1885): Revision of the Palaeocrinoidea. Discussion of the classification and relation of the brachiate crinoids, and conclusion of the generic descriptions. – Proceedings of the Academy of Natural Sciences of Philadelphia, **3**(1): 223-364.

— & — (1880-1886): Revision of the Palaeocrinoidea. – Proceedings of the Academy of Natural Sciences of Philadelphia, Part **I**: The families Ichthyocrinidae and Cyathocrinidae (1880), pp. 226-378, pls. 15-17 (separate repaged pp. 1-153, pls. 1-3). Part **II**: Family Sphaeroidocrinidae, with the subfamilies Platycrinidae, Rhodocrinidae, and Actinocrinidae (1881), pp. 177-411, pls. 17-19 (separate repaged, pp. 1-237, pls. 17-19). Part **III**(1): Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions (1885), pp. 225-364, pls. 4-9 (separate repaged, pp. 1-138, pls. 4-9). Part **III**(2): Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions (1886), pp. 64-226 (separate repaged to continue with section 1, 139-302).

— & — (1889): Crinoids. *In*: MILLER, S. A. (ed.): North American geology and paleontology. – 664 p. Western Methodist Book Concern (Cincinnati).

— & — (1897): The North American Crinoidea Camerata. – Harvard College Museum of Comparative Zoology, Memoir, **20**: 1-359; **21**: 360-897 (+ sep. atlas).

WALTER, R. (1995): Geologie von Mitteleuropa. – 566 p. Schweizerbart (Stuttgart).

WANNER, J. (1942): Einige neue Krinoiden aus dem Mittel-Devon der Eifel. – Decheniana, **101**(A/B): 25-38.

— (1943): Die Krinoiden des Rheinischen Devons. – Rheinische Heimatpflege, **13**(1941, no. 1/2): 27-38.

— (1954): Die Analstruktur von *Ammonicrinus* Springer nebst Bemerkungen über Aberranzen und Anomalien bei Krinoiden. – Neues Jahrbuch für Geologie und Paläontologie, Monatschafte, **5**(1954): 231-236.

WEBSTER, G. D. (1973): Bibliography and index of Paleozoic crinoids, 1942-1968. – Geological Society of America, Memoir, **137**: 1-341.

— (1977): Bibliography and index of Paleozoic crinoids, 1969-1973. – Geological Society of America, Microform Publication, **8**: 1-235.

— (1986): Bibliography and index of Paleozoic crinoids, 1974-1980. – Geological Society of America, Microform Publication, **16**: 1-405.

— (1988): Bibliography and index of Paleozoic crinoids and coronate echinoderms 1981-1985. – Geological Society of America, Microform Publication, **18**: 1-235.

— (1993): Bibliography and index of Paleozoic crinoids, 1986-1990. – Geological Society of America, Microform Publication, **25**: 1-204.

— (2003): Bibliography and Index of Paleozoic crinoids, coronates and hemistreptocrinoids 1758-1999, Index of the crinoid crowns and parts of crowns. – GSA Website: <http://crinoid.gsajournals.org/crinoidmod>. Geological Society of America (Boulder).

— (2007): Inplenary and explenary radial facets in cladid crinoids. – Palaeoworld, **16**(2007): 325-328.

— (in press): Summary observations on Devonian cladid crinoid evolution and extinctions. UNESCO/International Year of Planet Earth, 'life theme' volume. – Springer (Berling, Heidelberg).

— & BECKER, R. T. (2009): Devonian (Emsian to Frasnian) crinoids of the Dra Valley, western Anti-Atlas Mountains, Morocco. – Geological Society, London, Special Publications, **2009**(314): 131-148.

— & JELL, P. A. (1999): New Carboniferous crinoids from eastern Australia. – Memoirs of the Queensland Museum, **43**(1): 237-278.

— , LANE, N. G., MAPLES, C. G., WATERS, J. A. & HOROWITZ, A. B. S. (1998): Frasnian-Famennian extinction was a non-event for crinoids, blastoids and bryozoans. – Geological Society of America, Abstracts with Programs, **30**: 30-31.

— , HAFLEY, D. J., BLAKE, D. B. & GLASS, A. (1999): Crinoids and stelleroids (Echinodermata) from the Broken Rib Member, Dyer Formation (Late Devonian, Famennian) of the White River Plateau, Colorado. – Journal of Paleontology, **73**(3): 461-486.

— , MAPLES C. G., MAWSON, R. & DASTANPOUR, M. (2003): A cladid-dominated Early Mississippian crinoid and conodont fauna from Kerman Province, Iran and revision of the glossocrinids and rhenocrinids. – Journal of Paleontology, Memoir, **60**(77) [supplement to no. 3]: 35 p.

— , BECKER, R. T. & MAPLES, C. G. (2005): Biostratigraphy and paleoecology of Devonian (Emsian and Famennian) crinoids from southeastern Morocco. – Journal of Paleontology, **79**(6): 1052-1071.

— , MAPLES, C. G. & YAZDI, M. (2007): Late Devonian and early Mississippian echinoderms from central and northern Iran. – Journal of Paleontology, **81**(5): 1101-1113.

—, WATERS, J. & CHEN X. (in press): Revision of the Chen and Yao Devonian to Permian crinoids from Western Yunnan. – Palaeobiodiversity and Palaeoenvironments.

WEDDIGE, K. & ZIEGLER, W. (2000): Das bibliographische Lebenswerk von DR. WOLFGANG STRUVE. – Senckenbergiana lethaea, **79**(2): 603-636.

WEISSMÜLLER, A. (1998): Ein umfangreicher Fund von *Encrinus liliiformis* Lamarck im Oberen Muschelkalk (mo2) des Diemeltales (Nordhessen). – Philippia, **8**(4): 245-270.

WHIDBORNE, G. F. (1889): On some fossils of the limestones of south Devon. – Geological Magazine, series 3, **6**: 78-80.

— (1895): A monograph of the Devonian fauna of the south of England. The fauna of the limestone of Lummaton, Wolborough, Chircombe Bridge, and Chudleigh. – Palaeontographical Society, Monograph 48, **2**(4): 161-212.

WILKIE, I. C. (1984): Variable tensility in echinoderm collagenous tissues - a review. – Marine Behavior & Physiology, **11**(1): 1-34.

— , EMSON, R. H. & YOUNG, C. M. (1993): Smart collagen in sea lilies. – Nature, **366**: 519-520.

— , CANDIA CARNEVALI, M. D. & TROTTER, J. A. (2004): Mutable collagenous tissue: recent progress and an evolutionary perspective. *In*: HEINZELLER, T. & NEBELSICK, J. H. (eds.): Echinoderms München: pp. 371-378. – A. A. Balkema (Rotterdam).

WILLIAMS, H. S. (1883): On a crinoid with movable spines (*Arthroacantha ithacensis*). – American Philosophical Society, Proceedings, **21**: 81-88.

WILSON, H. E. (1916): Evolution of the basal plates in monocyclic Crinoidea Camerata. – Journal of Geology, **24**: 488-510, 533-553, 665-684.

WILSON, M. A. & TAYLOR, P. D. T. (2001): “Pseudobryozoans” and the problem of encruster diversity in the Paleozoic. – PaleoBios, **21** (addendum of no. 2): 134-135.

WINTER, J. (1965): Das Givetium der Gerolsteiner Mulde (Eifel). – Fortschritte in der Geologie von Rheinland und Westfalen, **9**: 277-322.

WOLBURG, J. (1938a) [for 1937]: Bau und Biologie von *Ammonicrinus doliiformis* n. sp. – Jahrbuch der preußischen geologischen Landesanstalt, **58**: 230-241.

— (1938b): Zur Frage der Lebensweise der eingerollten Crinoiden. – Zentralblatt für Mineralogie, Geologie und Paläontologie, Abt. B, **7**: 254-261.

XU, I-W. (1963): Some hexagonal crinoids (*Hexacrinites*) from the Middle Devonian section in the Syansyan District of Kwangsi Province. – Acta Palaeontologica Sinica, **11**: 108-118.

YAKOVLEV, N. N. (1930): Notes sur les Crinoides paleozoiques. Part 1. Contribution a la connaissance de *Hexacrinus pateraeformis* SCHULTZE et du genre *Hexacrinus*. – pp. 907-908, 1 pl. Part 2. Crinoides du Permien de la Sicile, pp. 908-910, 1 pl. Part 3. Un nouveau crinoide du bassin du Donetz, pp. 910-911, 1 pl. Izvestiya Akademii Nauk SSSR (Bulletin de l'Academie Sciences de l'URSS): 907-911, 3 pl.

— (1964): Klass Crinoidea. Mosskie lilii. Obstchaya chast, Osnovy paleontologii. Spravotchnik dlia paleontologov i geologov SSR. Echinodermata, Hemichordata, Pogonophora, and Chaetognatha [Class Crinoidea, crinoids, general part, characteristics, and morphology. *In*: ORLOV, YU. A., (ed.): Fundamentals of palaeontology, Echinodermata, Hemichordata, Pogonophora, and Chaetognatha]. – pp. 54-74, figs. 51-113. Izdatel'stvo Nedra (Moscow).

— & IVANOV, A. P. (1956): Morskie lilii i blastoidei kamennougolnykh i permskikh otlozhenii SSSR [Marine crinoids and blastoids of the Carboniferous and Permian deposits of Russia]. – Vsesoyuznogo Nauchno-Issledovatelskii Geologicheskogo Institut, Trudy, **11**: 1-142.

ZITTEL, K. A. VON (1876-1880): Handbuch der Palaeontologie, v. 1, Palaeozoologie. – 765 p. R. Oldenbourg (München).

— (1895): Grundzüge der Palaeontologie (Palaeozoologie). – 971 p. R. Oldenbourg (München, Leipzig).

— (1903): Grundzüge der Paläontologie (Paläozoologie) – 1. Abteilung: Invertebrata, zweite verbesserte und vermehrte Auflage. – 558 p., 1405 textfig. R. Oldenbourg (München & Berlin).

Erklärung

Ich versichere, dass ich die von mir vorgelegte Dissertation selbstständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit – einschließlich Tabellen, Karten und Abbildungen-, die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie – abgesehen von unten angegebenen Teilpublikationen – noch nicht veröffentlicht worden ist sowie, dass ich eine solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde.

Die Bestimmungen dieser Promotionsordnung sind mir bekannt.

Die von mir vorgelegte Dissertation ist von Herrn Prof. Dr. Hans-Georg Herbig betreut worden.

Zur Wahrung der Priorität wurden Teile dieser Arbeit bereits publiziert (1) – bzw. liegen als Manuskript im Druck (2) oder in Begutachtung (3-4) vor:

(4) BOHATÝ, J. (submitted): New mode of life interpretation and revision of the idiosyncratic lecanocrinid genus *Ammonicrinus* (Crinoidea, Flexibilia). – Palaeontology.

(3) BOHATÝ, J. (in review): Revision of the disparid *Stylocrinus* (Crinoidea) from the Devonian of Europe, Asia and Australia. – Palaeontology.

(2) BOHATÝ, J. (in press): Revision of the Hexacrinitidae (Crinoidea) based on a classical Lower Givetian crinoid deposit (Gerolstein, Eifel/Germany). – Neues Jahrbuch für Geologie und Paläontologie.

(1) BOHATÝ, J. (2009): Pre- and postmortem skeletal modifications of the Cupressocrinitidae (Crinoidea, Cladida). – Journal of Paleontology, **83**(1): 45-62.

Dipl.-Geol. Jan Bohatý
Köln, den 10. September 2009