Revision of the flexible crinoid genus *Ammonicrinus* and a new hypothesis on its life mode

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The lecanocrinid *Ammonicrinus* (Flexibilia) is newly interpreted based on new material from the Middle Devonian of the Rhenish Massif (Eifel and Bergisches Land, Germany). The species have echinoid-like tubercles on the attachment and on the column, which bear articulated 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 have 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, *Ammonicrinus kongieli* is evaluated as a subjective junior synonym of *Ammonicrinus sulcatus*. The latter species was first recognised from the Eifel (Germany). "*Ammonicrinus wachtbergensis*", from the upper Eifelian of the Eifel, is declared a subjective junior synonym of *Ammonicrinus doliiformis*. The first nearly complete specimen of *Ammonicrinus kerdreoletensis* is described from the lower Eifelian of Vireux-Molhain (southern Ardennes, France). Two new species are described: *Ammonicrinus jankei* sp. nov. and *Ammonicrinus leunisseni* sp. nov. A functional morphologic trend in perfecting the crown encasement 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 in the Eifel area. Several ammonicrinid species are herein defined as spined soft-bottom dwellers, feeding in low-intensity current water, possibly through a self-produced water flow. The first known postmortem encrusting epizoans on ammonicrinid endoskeletons are reported.

Key words: Crinoidea, Flexibilia, *Ammonicrinus*, Devonian, Eifel, Rhenish Massif, Germany.

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Introduction

The idiosyncratic Devonian *Ammonicrinus*, a lecanocrinid flexible crinoid, was described by Springer (1926) and discussed subsequently in comparatively few publications (Krause 1927; Ehrenberg 1930; Wolburg 1938a, b; Wanner 1943, 1954; Ubaghs 1952; Yakovlev and Ivanov 1956; Kongiel 1958; Piotrowski 1977; Moore 1978; Haude 1981; Głuchowski 1993; Hotchkiss et al. 1999; Le Menn and Jaouen 2003; Hauser 2005, 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 (bifacial) articulation on columnals with fulcra aligned and unequal ligmentary areas on either side of each fulcrum, which produced a planispirally coiled proximal column. 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) (Fig. 1). The mesi- and proxistele could coil and show the ability to enclose the crown.

With the exception of two other Palaeozoic genera, *Myelodactylus* Hall, 1852 and *Camptocrinus* Wachsmuth and Springer, 1897, the partly enrolled *Ammonicrinus* (e.g., Fig. 1A) 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). These modifications lead to the most atypical evolutionary model among crinoids by drastically changing a "normal" crinoid crown into a "plate-encased" individual. Accordingly, this 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, corals or bryozoans, or settled completely on hard objects (e.g., brachiopods) by strongly reducing the dististele.
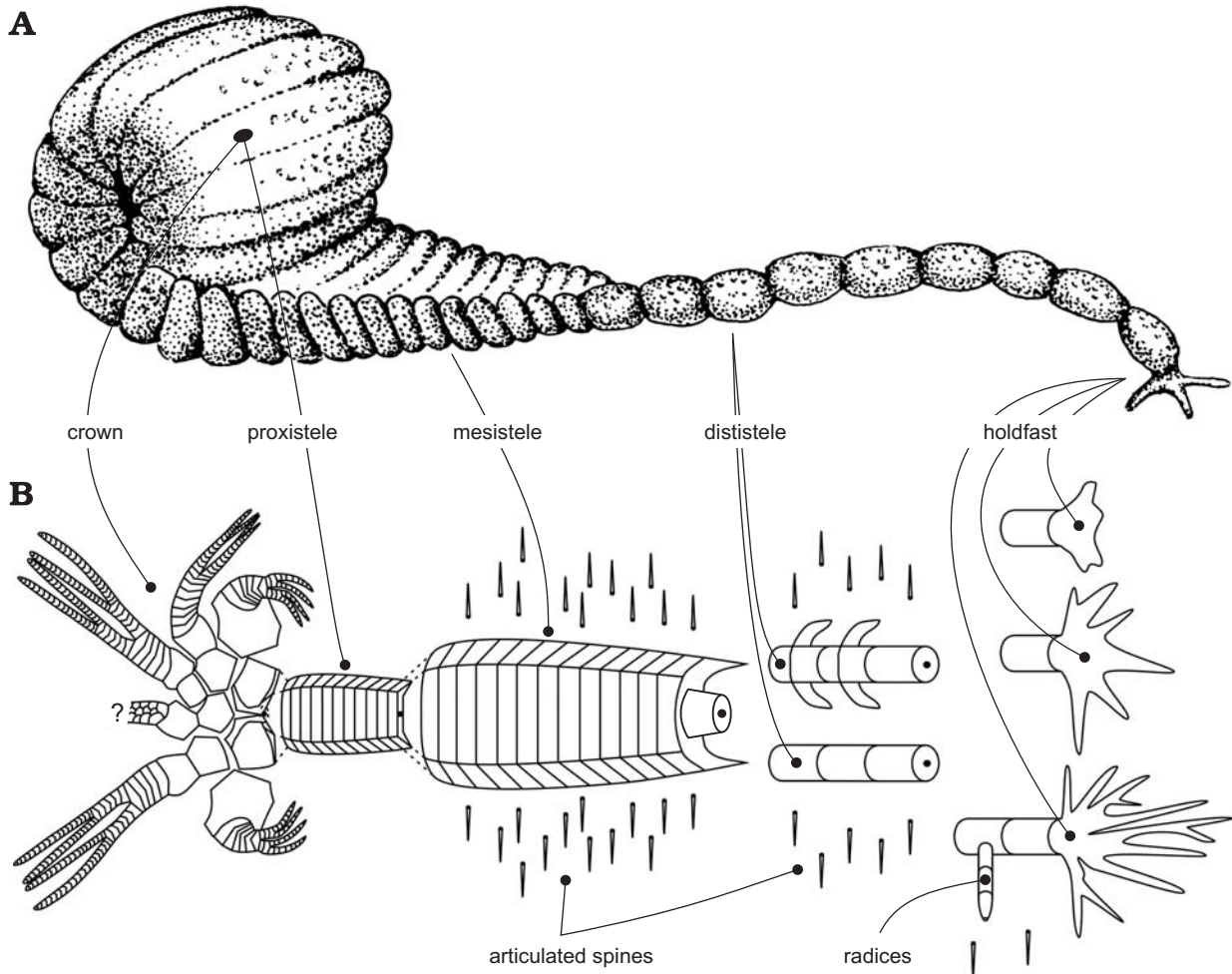
Fig. 1. **A**. Reconstruction of the *Ammonicrinus* life time position (modified after Piotrowski 1977: 208, fig. 2). **B**. *Ammonicrinus* plate diagram (not to scale).

Remarks

The privately published papers of Hauser (2005) and Hauser et al. (2009) discussing *Ammonicrinus* contained misinterpretations. Striking in this context is his reconstruction of "*A. wanneri*" from isolated mesistele columnals from different individuals as a "circular sphere" (2005: 34, 38–39, fig. 5a, b). They are given no further consideration herein (also see critical comments in Bohatý and Herbig 2007).

The isolated columnals described as "*A. bulbosus* sp. nov. (col.)" by Prokop (2009: 162) are very similar to the isolated Lower Devonian ossicle illustrated by Hotchkiss et al. (1999: 331, fig. 2.21). These elements could not be distinguished from juvenile ossicles of *A. sulcatus* and are in urgent need of further research based on more complete material in order to validate "*A. bulbosus*". Therefore, this species could not be considered further herein (Rudolf J. Prokop, personal communication 2009).

Institutional abbreviations.—GIK, Institut für Geologie und Mineralogie der Universität zu Köln, Germany; LPB, Laboratoire de Paléontologie de Brest (Université de Bretagne Occidentale), France; MBE, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany; MZ, Muzeum Ziemi, Warsaw, Poland; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; USNM, National Museum of Natural History (Smithsonian Institution), Washington DC, USA.

Other abbreviations.—A ray, lateral-anterior radial plate of cup; AE interray, anterior part of cup between the anterior radial plate (A) and left antero-lateral radial plate (E); CD interray, posterior part of cup between the right posterior radial plate (C) and the left posterior radial plate (D); LCEE, lateral columnal enclosure extensions.

Material and methods

Type specimens are deposited in the GIK, the Geowissenschaftliches Zentrum der Universität Göttingen, Germany (without repository numbers), the LPB, the MBE, the MZ, the SMF, and the USNM.

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 dis-

sected 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 follow Moore and Teichert (1978) with the following exception: measurement terms follow Webster and Jell (1999). The systematics of the mentioned cupressocrinitids follows Bohatý and Herbig (2010).

Crinoid localities and stratigraphy are given in the Appendix 1. The terms subformation and member are not synonymised sensu Steininger and Piller (1999); they are used hierarchically (Ulrich Jansen, personal communication 2005; also see Bohatý 2005a). The capitalisation of the Givetian subdivisions follows Becker (2005, 2007).

Historical background

The first report (Springer 1926) of *Ammonicrinus* dealt with crowns, enrolled within the mesi- and proxistele and several isolated columnals of the mesistele (Fig. 2A–D). *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 (1926) interpretation of this remarkable new genus was mainly based on comparison with other enrolled forms, like *Myelodactylus* or *Camptocrinus* (Springer 1926: 24). Springer (1926: 24) assigned his new genus to the Camerata and to the "Hexacrinidae" with its genus *Arthroacantha* Williams, 1883.

With the present, large collections, it is herein recognised that Springer (1926) figured three different species; (i) *A. wanneri* (1926: pl. 6: 4-4b; refigured in Fig. 2A, C of the present work), (ii) a species with wider a diameter coiled stem, herein described as *A. leunisseni* sp. nov. (1926: pl. 6: 5-5b; refigured in Fig. 2B, D of the present work) and (iii) two isolated columnals from the mesistele of *A.* cf. *sulcatus* (1926: pl. 6: 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 (1926) type material by its coiled, wide, barrel-shaped proxi- and mesistele (Fig. 2E). Krause (1927: 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). Another species, *A. doliiformis* Wolburg, 1938a (for 1937), from the Selscheider Formation of locality 11, was attached to brachiopod valves via an attachment disc, which, furthermore, has an attached dististele. This dististele is similar to a "normal" crinoid stem (Fig. 3A₁, A₂, B). Based on his discoveries, Wolburg (1938a: 238) correctly rejected
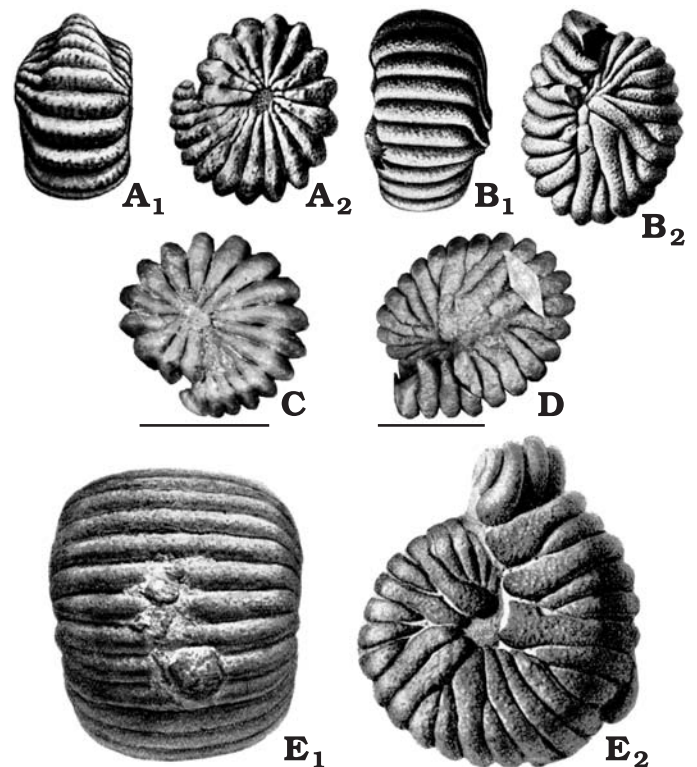

Fig. 2. The first figures of *Ammonicrinus* from Springer (1926) and Krause (1927). **A**. *Ammonicrinus wanneri* Springer, 1926 (from Springer 1926: pl. 6: 4a, b). A₁, view of the exteternal flanks of the coiled mesistele; A₂, coiled mesistele in lateral view. **B**. *Ammonicrinus leunisseni* sp. nov. (= "*A. wanneri*" in Springer 1926: pl. 6: 5, 5b). B₁, view of the exteternal flanks of the coiled mesistele; B₂, coiled mesistele in lateral view. **C**. Photograph of the holotype of *Ammonicrinus wanneri* Springer, 1926, USNM-S2115; lateral view of coiled mesistele; connection between mesi- and dististele, dististele and attachment missing (see fracture surface at distal mesistele). **D**. Photograph of USNM-S2115, the Springer (1926) original of "*Ammonicrinus wanneri*" (= *A. leunisseni* sp. nov. herein); lateral view of coiled mesistele; connection between mesi- and dististele, dististele and attachment missing (see fracture surface at distal mesistele). **E**. *Ammonicrinus doliiformis* Wolburg, 1938a (for 1937) (= "*A. wanneri*" in Krause 1927: pl. 8: 4, 2). E₁, view of the exteternal flanks of the coiled mesistele; E₂, coiled mesistele in lateral view. A–D from the Middle Devonian, Eifel Limestone; Prüm, Eifel, Germany (Springer 1926: 25); E from the Middle Devonian of Sötenich, Eifel (Krause 1927: 456). A, B, E not to scale; C, D scale bars 10 mm.

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. 3B).

By carefully excavating a preserved crown of "*A. wanneri*" from locality 8 (= *A. jankei* sp. nov.), 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 (Fig. 4B₂, B₆, B₇). As interpreted here, this applies solely to the stratigraphically younger ammonicrinids; but the oldest species, *Ammonicrinu kerdreoletensis*, is not covered entirely by the LCEE. That possibly implies feeding in the cur-
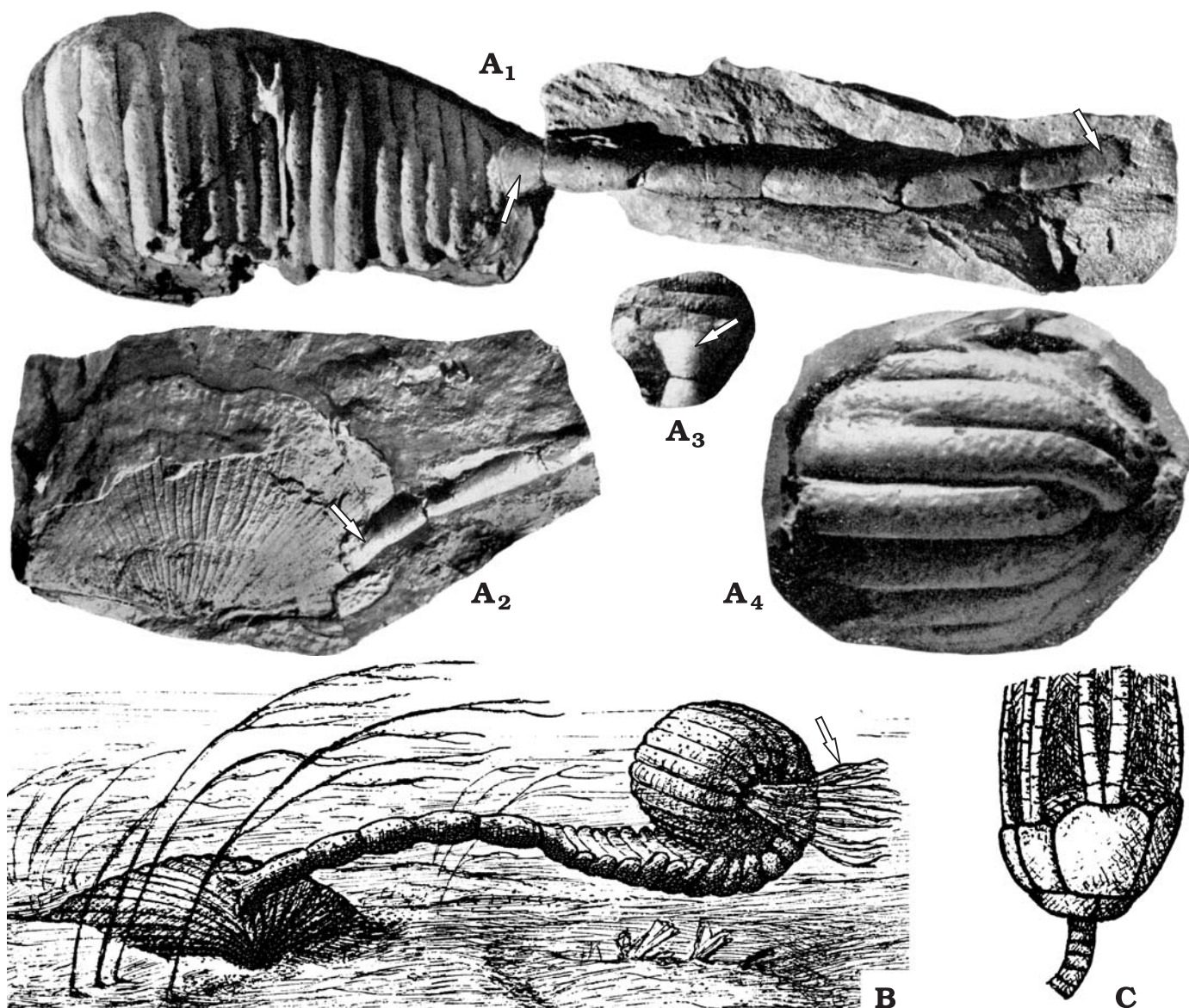
Fig. 3. The lecanocrinid species *Ammonicrinus doliiformis* Wolburg, 1938a (for 1937) from the Selscheid Formation of Ohle, Sauerland (Wolburg 1938a: 230). **A**. Casts of nearly complete specimen. Specimen attached to a brachiopod valve (right arrow) (A$_1$), showing the characteristic triangular connection between mesi- and dististele (left arrow) and slightly compressed mesistele (from Wolburg 1938a: pl. 17: 1); detail view of the attachment disc (arrow) (A$_2$), encrusting the brachiopod (from Wolburg 1938a: pl. 18: 8); detail view of the triangular connection between mesi- and dististele (arrow) (A$_3$) (from Wolburg 1938a: pl. 17: 6a); detail view of the coiled, slightly compressed mesistele (A$_4$) (from Wolburg 1938a: pl. 17: 4). **B**. Former assumed reconstruction of life mode, figured with a crown that protrudes toward the lateral-exterior (arrow) (from Wolburg 1938a: 240, fig. 5). **C**. Former assumed reconstruction of the crown (1938a: 233, fig. 4). Not to scale.

rent. Ubaghs (1952) also proposed the plate diagram of the crown (Fig. 4B$_5$) and identified *Ammonicrinus* as a lecano-crinid flexibilian (1952: 204). It is confirmed herein that his second radianal plate (Ubaghs 1952: 205, fig. 1), or "supple-mentary plate" of Wanner (1954), is based on a frequent occuring anomaly, as already assumed by Wanner (1954: 235). This anomaly resembles the atypical gasterocomoid genera *Nanocrinus* Müller, 1856, *Trapezocrinus* Haude, 2007 and the rare *Lecythocrinus* Müller, 1858 that also show fre-quent occuring anomalies in the anal plate architecture (com-pare Bohatý 2006a).

Combining the concepts of Ubaghs (1952) with the most complete specimens from Wolburg (1938a), Piotrowski (1977: 208–209, figs. 2, 3) provided the best interpretation of the mode of life of *Ammonicrinus* (Fig. 5). Piotrowski (1977: 208) assumed that the high specialisation of the stem pro-vided a firm support in soft-bottom sediments and protection from water borne sediments. He (1977) 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 bot-tom. "The water carrying food was introduced into the cen-tral part of the stem through a furrow formed by distal parts
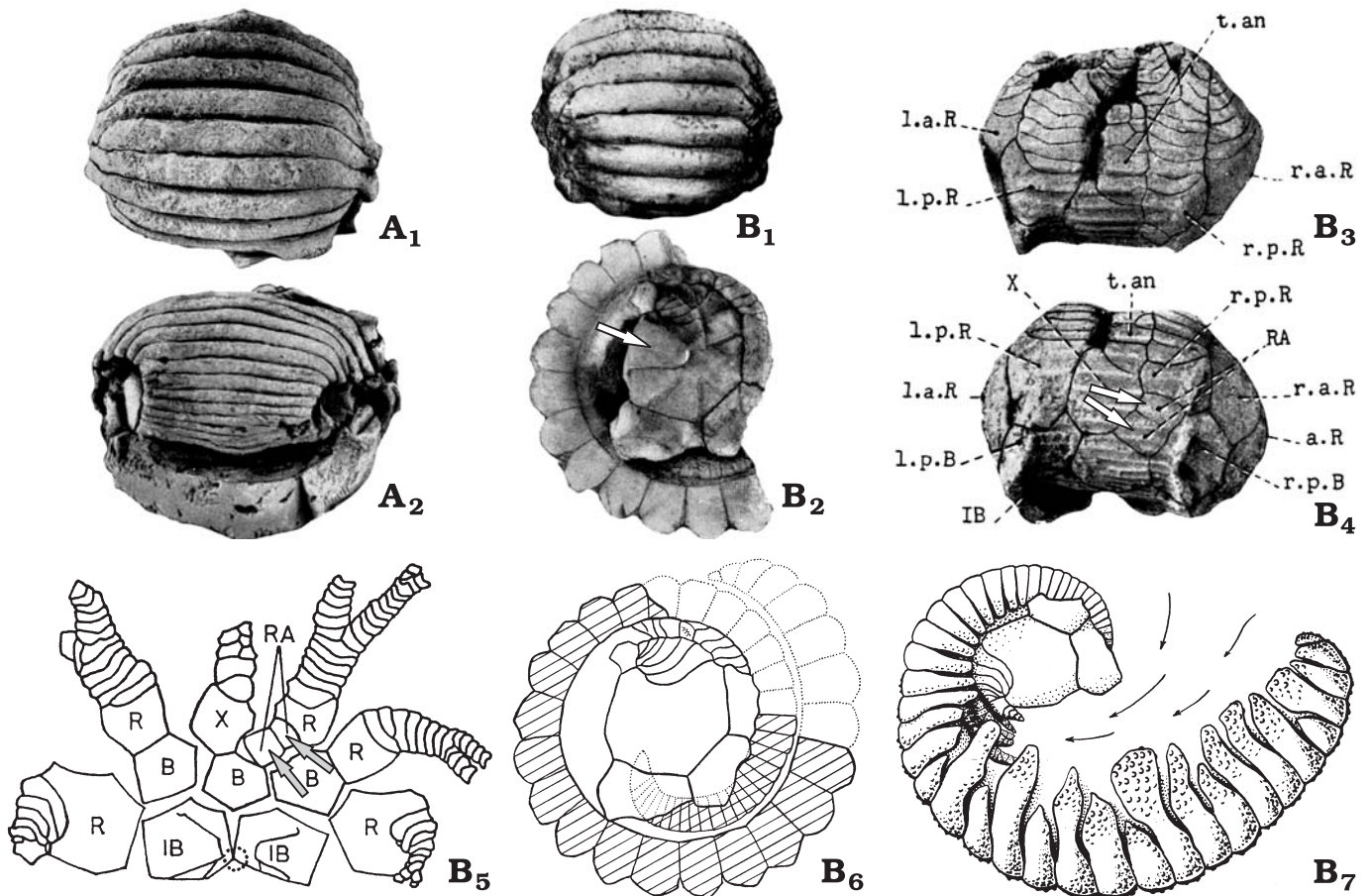
Fig. 4. First illustration of the actual plate diagram and definition of genus *Ammonicrinus* as a lecanocrinid Flexibilia by Ubaghs (1952). **A**. *Ammonicrinus doliiformis* Wolburg, 1938a (for 1937), SMF-XXIII-165a from the "Rommersheim Formation" of the Auburg, Gerolstein, Eifel, Germany (Ubaghs 1952: 220). View of coiled mesistele (A_1); view of exposed proxistele (A_2) (taken from Ubaghs 1952: pl. 3: 1, 3). **B**. Anomalous crown of "*Ammonicrinus wanneri*" from the "Rommersheim Formation" of the Steineberg, N of Kerpen, Eifel, Germany (Ubaghs 1952: 220) (= holotype of *A. jankei* sp. nov., no. SMF-XXIII-167a) coiled by the mesistele. View of the coiled mesistele (B_1) (Ubaghs 1952: pl. 1: 3); partly excavated crown (B_2), showing radiating ridges on radials and one slightly lobe-like enlarged appendage that possibly could support the lateral water respectively faecal-ejection (arrow) (Ubaghs 1952: pl. 1: 4); excavated crown in lateral view (B_3, B_4), the second "radianal plate" respectively "supplementary plate" (see arrows) is based on an anomaly (Ubaghs 1952: pl. 2: 3, 2); plate diagram (B_5), showing the two anomalous plates (arrows) (slightly modified after Ubaghs 1952: 205, fig. 1); schematic drawing of the coiled specimen (B_6); reconstruction of the assumed living feeding position (B_7) (Ubaghs 1952: 110, fig. 2; p. 223, fig. 5). Not to scale.

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" (Piotrowski 1977: 209). Piotrowski (1977: 209) compared *Ammonicrinus* with the mode of life of other crinoids (e.g., calceocrinids, Meek and Worthen 1869), which were adapted to filter food from horizontal bottom-water currents.

Carbonate microfacies analysis within several *Ammonicrinus*-localities of the Eifel (especially from locality 6) and the hydrodynamic interpretation of extremely fragile but perfectly preserved bryozoans (see Ernst 2008), lead to the recognition of low-intensity current water conditions close to the soft-bottoms, temporarily yielding a lack of the horizontal water currents assumed by Piotrowski (1977). Based on this interpretation, the exigencies of a feeding

method that supplemented Piotrowski's (1977) interpretation is proposed.

Morphological variability

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 Fig. 3 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:

The "exposed roller-type".—These specimens predominantly have the general skeletal morphology, as illustrated in Fig.
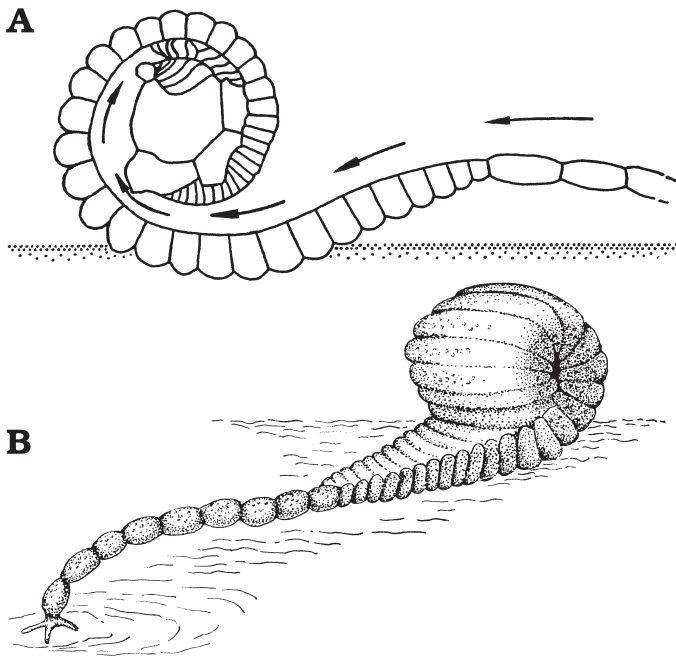
Fig. 5. Schematic illustrations of *Ammonicrinus sulcatus* Kongiel, 1958 after Piotrowski (1977). **A**. Lateral cross section through the feeding crinoid (Piotrowski 1977: 209, fig. 3). **B**. Former reconstruction of life time position (Piotrowski 1977: 208, fig. 2). Not to scale.

6. This form is herein classified as an exposed roller-type and is recognised only in the oldest known ammonicrinid, *Ammonicrinus kerdreoletensis*. This type, characterised by a laterally unprotected crown, would allow feeding in the current. The newly recovered material indicates that the stem of *A. kerdreoletensis* tapers as it approaches the crown, not in quite as many columnals perhaps but similar to that of camptocrinids, and their crown could be elevated up above the substrate. This elevation is not much but puts them above the sediment and into a possible low velocity current for feeding (Gary D. Webster, personal communication 2009). Similarly, unpublished myelodactylid specimens from the Eifelian strata of the Eifel Synclines had a similar mode of life and were also attached on hard objects, like brachiopods (unpublished data).

The "encased roller-type".—These specimens predominantly have the general skeletal morphology, as illustrated in Figs. 1A, 5, 7, 14A, C. This standard form is herein classified as encased roller-type and is recognised in all known ammonicrinids, except of *A. kerdreoletensis*. The specimens are more or less enrolled, 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 was attached to hard objects, such as brachiopod valves (Fig. 3A$_2$, B; also see Haude 1981: 200,
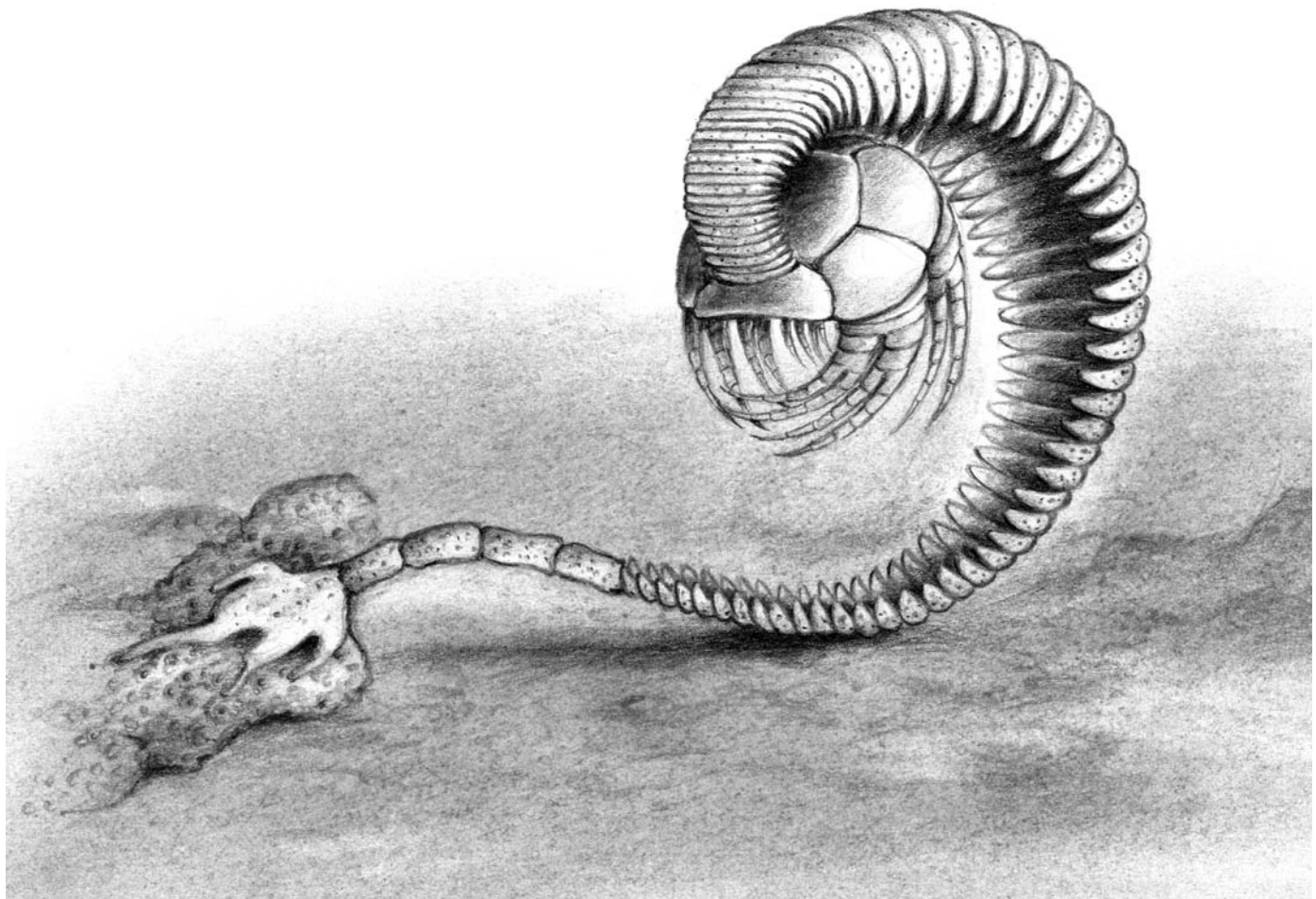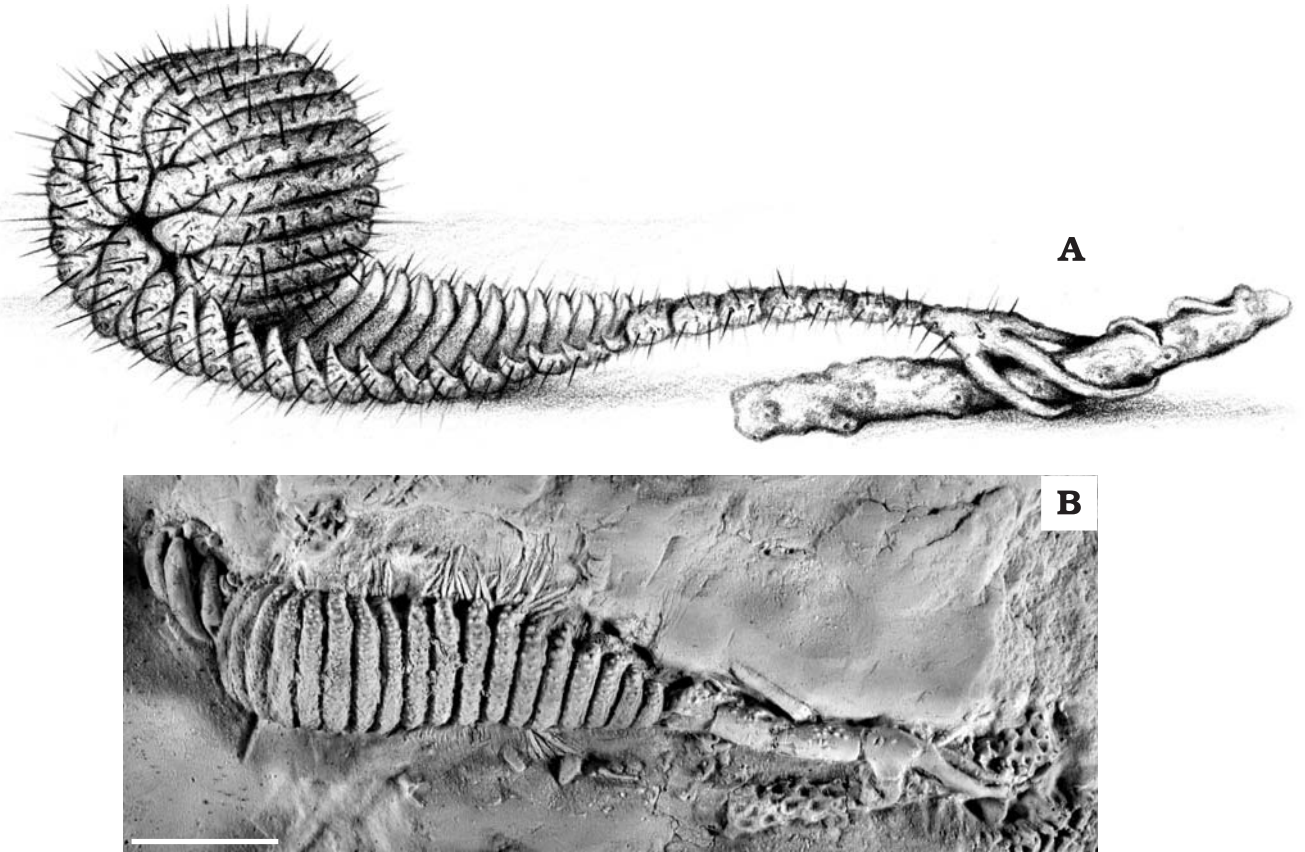
Fig. 7. *Ammonicrinus leunisseni* sp. nov. **A**. Reconstruction of a "encased runner-type" of *A. leunisseni* sp. nov. attached to a tabulate coral (model); the spined specimen dwelled enrolled on the muddy seafloor. **B**. The original (GIK-2102) from the Eifel (locality 6, Appendix 1), Germany, Lower Givetian (Middle Devonian); showing slightly compressed proximal mesistele. A not to scale, B scale bar 10 mm.

fig. 12A), tabulate corals (Fig. 7) or bryozoans (Figs. 9M, 12K$_1$, K$_2$). The hard object of attachment affected either the development of an attachment disc (Fig. 3A$_2$, B) or variously formed radices (see Figs. 7, 12K$_1$). Both modes of attachment were observed in one species.

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 (Fig. 8). These are attached primarily to empty brachiopod valves that laid on a soft-bottom. These ammonicrinids did not live partly enrolled on the seafloor with the column, as recognised in the roller-types. The proximal part of the crinoid larval stage settled on top of the hard object (Figs. 8, 12L). This form is herein classified as the rare settler-type and is recognised in *A. leunisseni* sp. nov., *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., *Halocrinites inflatus* [Schultze, 1866]; *H. sampelayoi* [Almela and Revilla, 1950]; *Arthroacantha* sp.) lifted their crowns for feeding. A question is why every *Ammonicrinus* did not adopt this form, because of presumed saving of skeletal material and the hydrodynamically advantageous feeding position above the muddy seafloor. Perhaps, this is due to the instability of the soft-bottom and the continuous input of fine sediment. Most brachiopod valves partially sank in or, respectively, became buried postmortem by sediment.

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. leunisseni* sp. nov.) 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 (Fig. 3A$_1$, A$_3$). 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.

← Fig. 6. Reconstruction of a feeding "exposed runner-type" of *Ammonicrinus kerdreoletensis* Le Menn and Jaouen, 2003, 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. Not to scale.
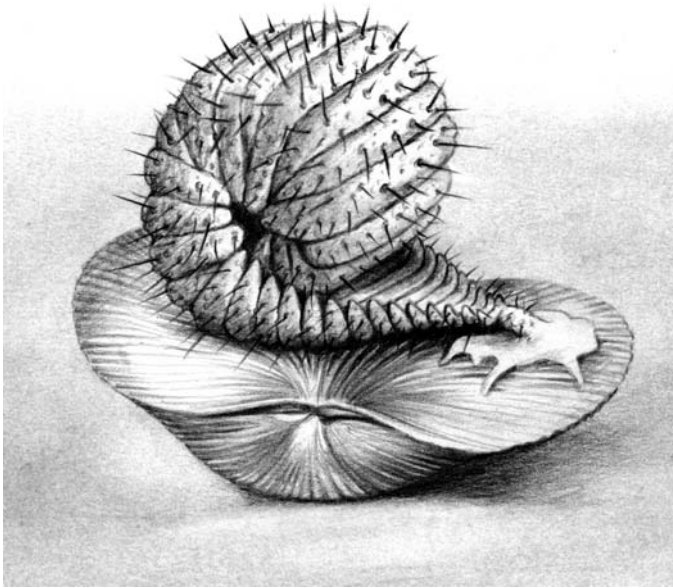
Fig. 8. Reconstruction of a spined "settler-type" of *Ammonicrinus leunisseni* sp. nov., attached to a brachiopod brachial valve (*Schizophoria* sp.); the original (GIK-2103) from locality 6 is figured in Fig. 12L. Not to scale.

In contrast, *A. sulcatus*, *A. wanneri*, and *A. leunisseni* sp. nov. 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 (Fig. 10G–I). However, this barrel-like appendage can also be duplicated and directed both, to the dististele and the mesistele (Fig. 10J, K), and 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. leunisseni* sp. nov.—all species with the ability to exhibit the encased roller- or the settler-type. That recognition affected Piotrowski's (1977: 214, table 3) 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. Therefore, and because of the recognised intraspecific variability of the ossicular sculpturing, "*A. kongieli*" is declared a subjective junior synonym of *A. sulcatus*.

Systematic palaeontology

Springer (1926: 23) originally classified *Ammonicrinus* with its type species *A. wanneri* as a possible member of the subclass Camerata Wachsmuth and Springer, 1885, family Hexacrinitidae Wachsmuth and Springer, 1885 ("Hexacrinidae" 1926: 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 and Laudon (1943), who placed *Ammonicrinus* in the "subclass Inadunata", family "Heterocrinidae" (Bassler 1938) or "Iocrinidae" (Moore and Laudon 1943). Ubaghs (1952), who first dissected an *A. wanneri* crown from the surrounding stem and, therefore, was the first to demonstrate that *Ammonicrinus* is a true member of class Crinoidea Miller, 1821 (see Wanner 1954: 231). Ubaghs (1952) assigned the genus to the subclass Flexibilia Zittel, 1895, order Sagenocrinida Springer, 1913 and "family Lecanocrinidae Springer, 1913", whereas Wanner (1954: 231) identified the exceptional position of *Ammonicrinus* within 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 and 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: T783–T784).

Class Crinoidea Miller, 1821
Subclass Flexibilia Zittel, 1895
Order Sagenocrinida Springer, 1913
Superfamily Lecanocrinoidea Springer, 1913
Family Calycocrinidae Moore and Strimple, 1973
Genus *Ammonicrinus* Springer, 1926

Type species: *Ammonicrinus wanneri* Springer, 1926.

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. kerdreoletensis*), partly visible in lateral respectively radial view (*A. doliiformis*), or completely covered by the mesistele (e.g., *A. leunisseni* sp. nov.); 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. kerdreoletensis*), sculptured with fine tubercles (*A. doliiformis*, *A. leunisseni* sp. nov., *A. sulcatus*, *A. wanneri*) or with radiating ridges on radials (*A. jankei* sp. nov.). A large anal X is positioned above CD basal and followed by several smaller plates of the anal tube. The arms are formed by wide, short and straight or laterally somewhat curved brachials, branching isotomously on primibrachials 5 to 8 with up to 10 secundibrachials in some branches, followed by 10–20 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 herein termed lateral columnal enclosure extensions (LCEE) covering the crown, and the proxistele with smaller lateral extensions on columnals; the dististele is either long and composed of numerous columnals ("exposed runner-type", observed in *A. kerdreoletensis*; "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. leunisseni* sp. nov., *A. sulcatus* and *A. wanneri*); the dististele can develop radices (rare, observed in *A. leunisseni* sp. nov.) 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 radices; the LCEE of the mesistele are either constantly equally developed (*A. kerdreoletensis*, *A. wanneri*), composed of regularly or irregularly arranged columnals with longer and shorter extensions (*A. jankei* sp. nov., *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. leunisseni* sp. nov.); 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. leunisseni* sp. nov., *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 angles or one lumen angle 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. leunisseni* sp. nov., *A. jankei* sp. nov.), or wide barrel-shaped (*A. doliiformis*, *A. sulcatus*). Mesi- and dististele are covered by echinoid-like tubercles, which bear articulated spines (recognised in *A. doliiformis*, *A. leunisseni* sp. nov., *A. sulcatus* and assumed in *A. kerdreoletensis*, *A. jankei* sp. nov.), mesistele sculptured by irregularly placed tubercles and additional spine-tubercles (*A. sulcatus*) or irregularly arranged ridges without tubercles on the exterior flanks (*A. wanneri*).

Stratigraphic and geographic range.—Devonian. Pragian (Lower Devonian) of the Czech Republic (see Hotchkiss et al. 1999: 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 (Harald

Prescher, personal communication 2008; material not figured herein).

Because "*Ammonicrinus*? *nordicus*" sensu Yakovlev and Ivanov (1956), from the Carboniferous of the Donetz Basin (Russia), is herein excluded from *Ammonicrinus* sensu Springer (1926), the genus is restricted to the Lower and Middle Devonian (Pragian–Givetian).

Ammonicrinus wanneri Springer, 1926

Figs. 2A, C, 9A–J, 15B.

pars 1926 *Ammonicrinus wanneri* Springer, 1926: 22–25, pl. 6: 4-4b, only.
non 1926 *Ammonicrinus wanneri* Springer, 1926: pl. 6: 5-5b = *A. leunisseni* sp. nov.
non 1926 *Ammonicrinus wanneri* Springer, 1926: pl. 6: 6 = *A*. cf. *sulcatus*.
1938a *Ammonicrinus wanneri*; Wolburg 1938a: pl. 18: 9.
non 1938a *Ammonicrinus wanneri*; Wolburg 1938a: pl. 18: 10 = *A. leunisseni* sp. nov.
non 1952 *Ammonicrinus wanneri*; Ubaghs 1952: 210, fig. 2, pl. 1: 1–7, pl. 2: 1–7 = *A. jankei* sp. nov.
non 1978 *Ammonicrinus wanneri*; Ubaghs 1978: T78, fig. 57: 6, 7 = *A. doliiformis*, 8 = *A. jankei* sp. nov.
pars 1978 *Ammonicrinus wanneri*; Moore 1978: T787, fig. 526: 5a–c, only.
non 1978 *Ammonicrinus wanneri*; Moore 1978: T787, fig. 526: 5d–e = *A. leunisseni* sp. nov.
pars 2003 *Ammonicrinus wanneri*; Webster 2003: GSA-webpage, *A. wanneri* Springer 1926, pl. 6: 4-4b, only.

Holotype: USNM-S2115 (Springer 1926: pl. 6: 4-4b, only) (Fig. 2A, C; also see colour photos of Springer's (1926) original on the webpage-search of the USNM Department of Paleobiology collection). The assumed type locality is "Prüm", within the Prüm Syncline, in the vicinity of locality 3 (Eifel, Rhenish Massif, Rhineland Palatinate, Germany); and the assumed stratigraphy is the uppermost Freilingen Formation (upper Eifelian) or superposed Ahbach Formation (Eifelian/ Givetian threshold, Middle Devonian).

Material.—Type material (Fig. 2A, C) and new material nos. GIK-2133–2142 (Fig. 9A–J).

Description.—*Ammonicrinus wanneri* has fine tubercles on the cup ossicles (Fig. 9B). The stem mainly distinguished by the characteristic mesistele, composed of columnals with long and relative regularly developed LCEE that protrude nearly orthogonally from both sides of the narrow columnals, forming a narrow discoidal coiled proximal column in closed position (Figs. 2A$_2$, C, 9A); mesistele composed of numerous columnals, which distally passes gradually into the dististele; several specimens have 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 radices; axial canal pentalobate; mesistele sculptured by irregularly positioned or oriented ridges, which, characteristically, run parallel to each other on the external flanks of the columnals (Fig. 9C, H); no spine-tubercles on the stem.
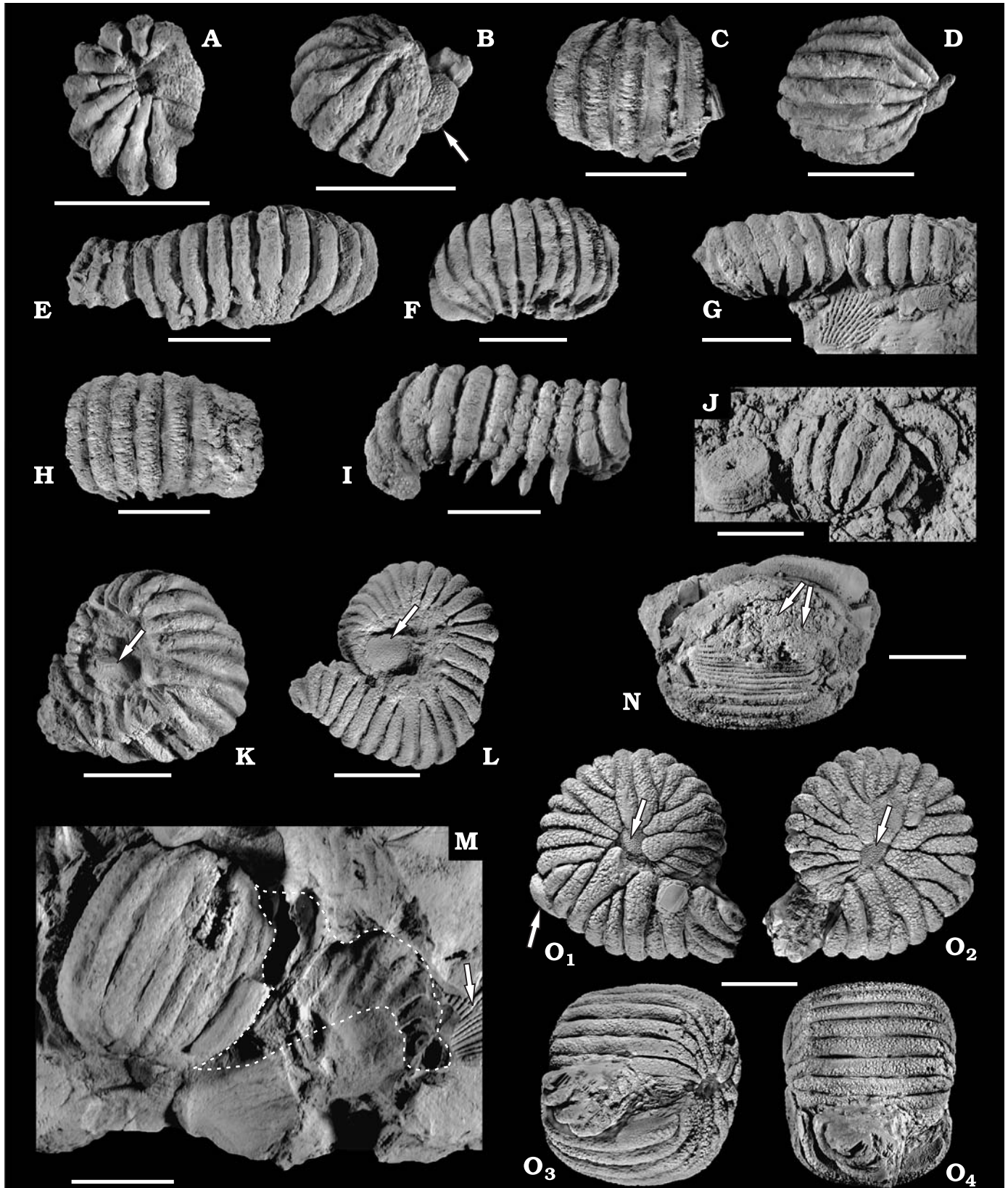
Fig. 9. Lecanocrinid *Ammonicrinus* species. **A–J**. *Ammonicrinus wanneri* Springer, 1926. **A–I**. From the Eifel (locality 3, Appendix 1), Germany, Lower Givetian (Middle Devonian). **J**. From the Eifel (locality 7, Appendix 1), Germany, Lower Givetian (Middle Devonian). **A**. Lateral view of a partly preserved specimen (GIK-2133) with coiled mesistele. **B**. Lateral view, respectively view of external columnal flanks of the coiled mesistele of a partly preserved specimen (GIK-2134) with one preserved, postulated cup ossicle (arrow). **C**. View of external columnal flanks of the mesistele of a partly preserved specimen (GIK-2135). **D**. Lateral view, respectively view of external columnal flanks of the coiled mesistele of a partly preserved specimen (GIK-2136), →

Discussion.—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. leunisseni* sp. nov. 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; 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. leunisseni* sp. nov. is a spined *Ammonicrinus*.

Stratigraphic and geographic range.—Upper Eifelian to Lower Givetian (Freilingen, Ahbach and Loogh formations) of the Eifel Synclines (Germany).

Ammonicrinus sulcatus Kongiel, 1958

Figs. 1A, 5A, B, 10, 13, 14A, 15C.

pars cf. 1926 *Ammonicrinus wanneri*; Springer 1926: pl. 6: 6 = *A*. cf. *sulcatus*.

1958 *Ammonicrinus sulcatus* Kongiel, 1958: 34–36, fig. 6a, b.

1977 *Ammonicrinus sulcatus* Kongiel, 1958; Piotrowski 1977: 208, 211–213, figs. 2, 4, 5B, 6, pl. 17: 1a–c, 2a–c, 3, 4, 5a, b, pl. 18: 4, 5a, b, 6–8, 10.

1977 *Ammonicrinus kongieli* Piotrowski, 1977: 213–215, pl. 18: 1a–c, 2, 3, 9, pl. 19: 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: 213]).

1978 *Ammonicrinus sulcatus* Kongiel, 1958; Ubaghs 1978: T78, fig. 57: 9.

2003 *Ammonicrinus sulcatus* Kongiel, 1958; Webster 2003: GSA-webpage.

2003 *Ammonicrinus sulcatus* Kongiel, 1958; Le Menn and Jaouen 2003: 208, fig. 1A.

Holotype: MZ-VIII-EP-1/1. The type locality is Grzegorzowice-Skały (Holy Cross Mountains, Poland); and the stratigraphy is Member XIV of the Givetian Skały beds (Middle Devonian) (see Piotrowski 1977: 213).

Material.—Type material and new material nos. GIK-2104–2120 (Fig. 10A–Q), GIK-2147–2155 (Fig. 13A–I).

Description.—*Ammonicrinus sulcatus* is distinguished by the fine tubercles on the cup ossicles (Fig. 10Q_1). 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 articulated spines, or distinguished by additional, irregularly arranged, sometimes slightly meandering nodular tubercles bearing the spine-tubercles (Fig. 10A–G); columnals of the juvenile mesistele with strongly tuberculated extensions and external flanks (Fig. 10L–O); dististele either medium long and composed of numerous columnals ("encased runner-type") 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 (Fig. 10J, K) 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.

Discussion.—*Ammonicrinus sulcatus* is similar to *A. leunisseni* sp. nov. and, especially, to *A. jankei* sp. nov. *A. sulcatus* developed characteristic and nearly linear external flanks of the mesistele, with short LCEE in contrast to the longer extensions of *A. leunisseni* sp. nov. Several cup ossicles of *A. sulcatus* have rudimentary radiating ridges that are not known in *A. leunisseni* sp. nov. but developed much stronger in *A. jankei* sp. nov. Because of the longer extensions of the mesistele of *A. jankei* sp. nov., the shape of the coiled stem is oblate spheroidal, rather than wide and barrel-shaped in *A. sulcatus*.

Stratigraphic and geographic range.—Givetian (Member XIV of the Givetian Skały beds) of Grzegorzowice-Skały, Holy Cross Mountains (Poland) and upper Eifelian (Bohnert Member of the Freilingen Formation) of Kerpen and Nollenbach within the Hillesheim Syncline (Eifel, Germany).

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showing typical LCEE. **E**. View of external columnal flanks of a nearly uncoiled mesistele ("runner-type") (GIK-2137). **F**. View of external columnal flanks and LCEE of a slightly compressed, coiled mesistele (GIK-2138). **G**. View of external columnal flanks of a nearly uncoiled mesistele ("runner-type") (GIK-2139). **H**. View of external columnal flanks of the mesistele of a partly preserved specimen (GIK-2140). **I**. View of external columnal flanks of a nearly uncoiled mesistele ("runner-type") (GIK-2141). **J**. View of external columnal flanks of the coiled mesistele of a weathered specimen (GIK-2142) on matrix. **K–O**. *Ammonicrinus doliiformis* Wolburg 1938a (for 1937). **K, L**. From the Eifel (locality 9, Appendix 1), Germany, upper Eifelian (Middle Devonian). **M**. From the Bergisches Land (locality 10, Appendix 1), Germany, Eifelian/Givetian threshold (Middle Devonian). **N**. From the Eifel (locality 4, Appendix 1), Germany, upper Eifelian (Middle Devonian). **O**. From the Eifel (locality 5, Appendix 1), Germany, upper Eifelian (Middle Devonian). **K**. Lateral view of a coiled specimen (GIK-2143) with lost dististele and cracked LCEE of the mesistele, exposing the coiled proxistele and several cup ossicles (arrow). **L**. Lateral view of a nearly completely coiled specimen (GIK-2144) with lost dististele and cracked LCEE of the mesistele, exposing distal-most part of the coiled proxistele and several cup ossicles (arrow). **M**. View of external columnal flanks of a preserved, coiled mesistele (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. **N**. Facet view of a coiled, adult specimen (GIK-2146) with exposed distal part of the proxistele and disarticulated remains of the arms (arrows). **O**. Perfect, three dimensionally preserved, adult specimen (MB.E.-287, original of Krause 1927). Coiled mesistele in lateral view (O_1), dististele, attachment and spines missing, centres of tuberculated radials partly visible (arrow); the specimen is infested by a (?)craniid brachiopod (arrow on the left); opposite lateral view (O_2), centres of radials partly visible (arrow); oblique lateral view (O_3); view of the external flanks of the mesistele (O_4) (centre and upper part of the figure) and of the facet area of distal mesistele (below), showing wide barrel-shaped outline. Scale bars 10 mm.
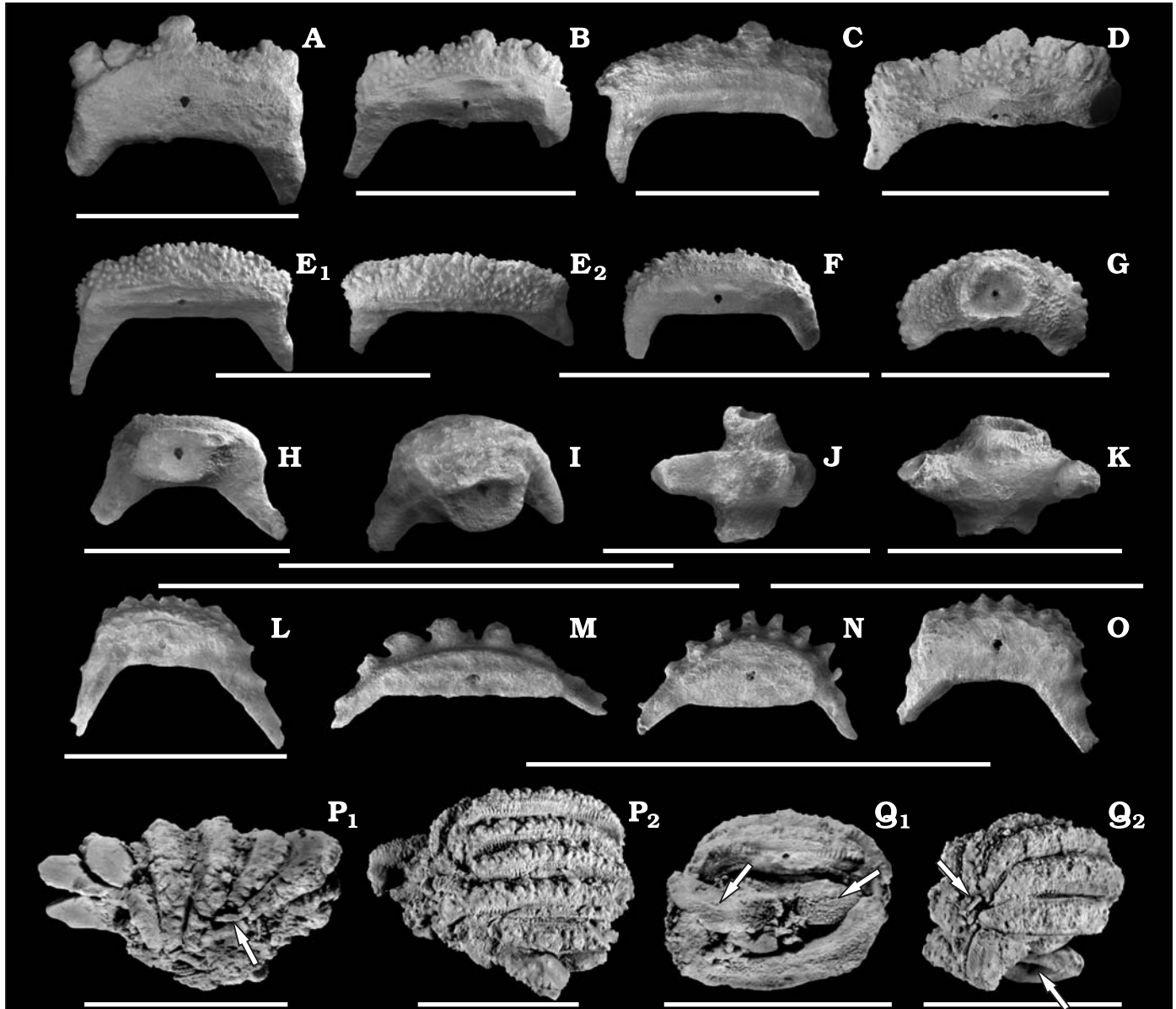
Fig. 10. The lecanocrinid species *Ammonicrinus sulcatus* from locality 1 (A–G, I–Q) and 2 (H) (see Appendix 1). **A–D**. Facet views of GIK-2104–2107, showing nodular tubercles and spine-tubercles on exterior flanks of the columnals of the mesistele. **E**. Facet view (E_1) and view of the exterior flank of a specimen (E_2) (GIK-2108), showing tubercles and spine-tubercles on exterior flank of the columnal of the mesistele. **F**. Facet view of a specimen (GIK-2109), showing tubercles and spine-tubercles on exterior flank of the columnal of the mesistele. **G**. Facet view of a strongly sculptured columnal (GIK-2110) of the distal-most mesistele, showing connection to the dististele. **H**. Facet view of a columnal of the distal-most mesistele (GIK-2111), showing long LCEE and connection to the dististele. **I**. Facet view of a columnal of the distal-most mesistele (GIK-2112), showing relatively long LCEE and connection to the dististele. **J**. Interior view of a distal-most, barrel-like columnal of the mesistele (GIK-2113) with LCEE. **K**. Interior view of a distal-most, barrel-like columnal of the mesistele (GIK-2114), with partly preserved LCEE. **L**. Facet view of a juvenile distal columnal of the mesistele (GIK-2115) with nodular tubercles on exterior flank and on LCEE. **M–N**. Juvenile columnals of the proximal mesistele in facet views, showing well developed nodes on exterior flanks. **M**. GIK-2116. **N**. GIK-2117. **O**. Facet view of a juvenile distal columnal of the mesistele (GIK-2118) with nodular tubercles on exterior flank and on LCEE. **P**. Lateral view (P_1) and view of the exterior flank (P_2) of the partly preserved mesistele (GIK-2119); the specimen shows nodular tubercles, spine-tubercles and a few partly preserved spines (arrow). **Q**. Facet view (Q_1) and lateral view (Q_2) of a cracked, coiled mesistele (GIK-2120), showing several tuberculated and concave ossicles of the cup (arrows). Scale bars 10 mm.

Ammonicrinus doliiformis Wolburg, 1938a (for 1937)

Figs. 2E, 3, 4A, 9K–O, 15D.

1938a (for 1937) *Ammonicrinus doliiformis* Wolburg, 1938a: 230–241, figs. 1–5, pl. 17: 1–5, 6a, b, 7, pl. 18: 1(?), 2a, b, 3, 4, 5–7(?), 8.
1927 *Ammonicrinus wanneri* Springer, 1926; Krause 1927: pl. 8: 1–6.

1952 *Ammonicrinus doliiformis* Wolburg, 1938a; Ubaghs 1952: 216–218, pl. 3: 1–5.
1978 *Ammonicrinus doliiformis* Wolburg, 1938a; Ubaghs 1978: T64, fig. 44: 3.
1978 *Ammonicrinus wanneri* Springer, 1926; Ubaghs 1978: T78, fig. 57: 6, 7.

2003 *Ammonicrinus doliiformis* Wolburg, 1938a; Webster 2003: GSA-webpage.

2005 "*Ammonicrinus wachtbergensis*" sp. nov.; Hauser 2005: 4, 23–25, figs. 1, 15a, b, second unnumbered fig. below on p. 34, pl. 1: 3a–c, front and backside covers of private publication.

Holotype: Due to world war damages, only one cast of the dististele of Wolburg's (1938a) type material is still preserved in the Geowissenschaftliches Zentrum der Universität Göttingen, Germany (without repository-number) (Reimund Haude, personal communication 2009). The type locality is Plettenberg-Ohle at the Lenne River (SE of Werdohl, Märkischer Kreis, Sauerland; UTM unknown); and the stratigraphy is "Selscheider Formation" sensu Wolburg (1938a: 230); more probable, the type material came from the Odershäuser Formation of the Eifelian/Givetian threshold (Middle Devonian) (Martin Basse, personal communication 2009).

Material.—Type material (Figs. 2E, 9O), originals of Wolburg (1938a) (Fig. 3A–C) and Ubaghs (1952) (no. SMF-XXIII-165a; Fig. 4A) and new material nos. GIK-2143–2146 (Fig. 9K–N).

Description.—*Ammonicrinus doliiformis* is distinguished by fine tubercles on the surface of the cup ossicles (Fig. 9K, L, O_1, O_2). The arms are relatively long and formed by medium wide, short and straight or laterally somewhat curved brachials. The dististele (Fig. $3A_1$, A_2) 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 (Fig. $3A_1$, A_2); 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 (Figs. $9O_1$, O_2, 15D); connection between disti- and mesistele distinguished by a triangular columnal without extensions (Fig. $3A_1$, A_3); columnals of the mesistele with long, less curved external flanks with relatively thin cross sections; shape of coiled stem wide barrel-shaped (Fig. $9O_3$, O_4); the cup is partly visible in lateral radial view (Fig. $9O_1$, O_2); mesi- and dististele covered by echinoid-like spine-tubercles, which bear articulated spines.

Discussion.—*Ammonicrinus doliiformis* is similar to *A. leunisseni* sp. nov. Wolburg's (1938a) 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. leunisseni* sp. nov.

After studying the holotype of "*Ammonicrinus wachtbergensis* Hauser, 2005" (= original of Krause 1927, figured as *A. wanneri*), it is clearly evident that the specimen is a typical adult that is a 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, 2005" is declared a subjective junior synonym of *A. doliiformis*.

Stratigraphic and geographic range.—Eifelian (Selscheid Formation) of Ohle, Sauerland (Germany), Eifelian (Oderhäuser Formation) of Lindlar-Hartegasse (Germany), Eifelian (Eilenberg Member of the Freilingen Formation) of Sötenich (Sötenich Syncline, Eifel), Gondelsheim (Prüm Syncline, Eifel), Niederehe (Hillesheim Syncline, Eifel) and "Rommersheim Formation" of the "Auburg" near Gerolstein (Gerolstein Syncline, Eifel) (Germany).

Ammonicrinus kerdreoletensis Le Menn and Jaouen, 2003

Figs. 6, 11, 15A.

2003 *Ammonicrinus kerdreoletensis* Le Menn and Jaouen, 2003: 207, 210–211, fig. 4A–C.

Holotype: LPB-1073. The type locality is Coupe de Kerdréolet, niveau K2, L'Hôpital-Camfrout, Département Finistère (Brittany, France); and the stratigraphy is Kerdréolet Formation, Emsian (Lower Devonian).

Material.—Type material and new material no. GIK-2121 (Fig. 11).

Fig. 11. The lecanocrinid species *Ammonicrinus kerdreoletensis* Le Menn and Jaouen, 2003 (GIK-2121) from Vireux-Molhain (locality 12, Appendix 1), France, lower Eifelian (Middle Devonian); lateral view of long mesistele, proxistele and huge cup (arrow) on matrix. Scale bar 10 mm.

Description.—*Ammonicrinus kerdreoletensis* has 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 clearly visible in lateral view (Fig. 11); the cup ossicles 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 (Fig. 11), LCEE of the mesistele regularly arranged and very short (Fig. 15A), 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 articulated spines (not preserved).

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

As stated above, the cup of *A. kerdreoletensis* is laterally not covered by the LCEE. That possibly implies feeding in the current (Fig. 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. kerdreoletensis* tapers toward the crown, which was obviously elevated up from the substrate into a possible low velocity current for feeding. Therefore, *A. kerdreoletensis* can be designated a morphological progenitor of the younger and encased ammonicrinids.

Stratigraphic and geographic range.—Emsian (Kerdréolet Formation) of the Coupe de Kerdréolet, niveau K2, L'Hôpital-Camfrout, Département Finistère (Brittany, France) and lower Eifelian of Vireux-Molhain (southern Ardennes, northern France).

Ammonicrinus leunisseni sp. nov.

Figs. 2B, D, 7, 8, 12, 14C.

1926 *Ammonicrinus wanneri* Springer, 1926: 22–25, pl. 6: 5-5b.
1938a *Ammonicrinus wanneri* Springer, 1926; Wolburg 1938a: pl. 18, fig. 10.

1978 *Ammonicrinus wanneri* Springer, 1926; Moore 1978: T787, fig. 526: 5d, e.
pars 2003 *Ammonicrinus wanneri* Springer, 1926; Webster 2003: GSA-webpage, *A. wanneri* Springer 1926, pl. 6: 5-5b, only.

Etymology: After Robert Leunissen (Nideggen-Wollersheim), for his tremendous help in sampling of material for the present publication.

Type material.—Holotype: USNM-S2115 (Springer 1926: 105, pl. 6: 5-5b, only) (Fig. 2B, D); also see colour photos of the Springer-original on the webpage-search of the USNM Department of Paleobiology collection.

Type locality (assumed): "Prüm", within the Prüm Syncline, in the surrounding of locality 3 (Eifel, Rhenish Massif, Rhineland Palatinate, Germany).

Type horizon (assumed): Uppermost part of the Freilingen Formation (upper Eifelian) or, more probable, superposed Ahbach Formation (Eifelian/Givetian threshold, Middle Devonian).

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 radices, 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 (Fig. 12F). 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 movable, articulated spines (Figs. 7, 8, 12I, J_1, L, 14C) 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 (Fig. 2D). Columnals of the mesistele

Fig. 12. The lecanocrinid species *Ammonicrinus leunisseni* sp. nov. **A–E, I, J, L**. From the Eifel (locality 6, Appendix 1), Germany, Lower Givetian (Middle Devonian). **F, G, K**. From the Eifel (locality 3, Appendix 1), Germany, Lower Givetian (Middle Devonian). **H**. From the Eifel (locality 9, Appendix 1), Germany, upper Eifelian (Middle Devonian). **A**. Lateral view of a specimen (GIK-2122) with lost spines, showing complete coiled mesistele and one preserved columnal of the dististele (arrow). **B**. Lateral-facet view of a specimen with lost spines (GIK-2123), showing coiled mesistele and proxistele. **C**. View of the exterior columnal flanks of a slightly compressed specimen (GIK-2124) with lost spines, showing proxistele and mesistele with one distal-most, barrel-shaped columnal with LCEE (arrow). **D**. View of the exterior columnal flanks of a weathered and compressed specimen (GIK-2125) with lost spines, showing part of the mesistele and proxistele and rest of disarticulated ossicles of the cup preserved. **E**. Lateral view of a partly preserved specimen (GIK-2126) with lost spines and well preserved spine-tubercles on the coiled mesistele. **F**. View of the exterior columnal flanks of a partly preserved, coiled mesistele (GIK-2127) with lost spines and one radial plate preserved (arrow). **G**. View of the exterior columnal flanks of a partly preserved, uncoiled mesistele (GIK-2128) with lost spines. **H**. Interior view of a partly preserved, coiled specimen (GIK-2129), showing rest of cup and impressions of the lost arms (arrow). **I**. 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 radices on columnals of the dististele (arrow). **J**. A specimen on matrix with well preserved spines (GIK-2131). View of the exterior columnal flanks (J_1) with coiled proximal-most mesistele and proxistele and uncoiled distal column ("runner-type") with →
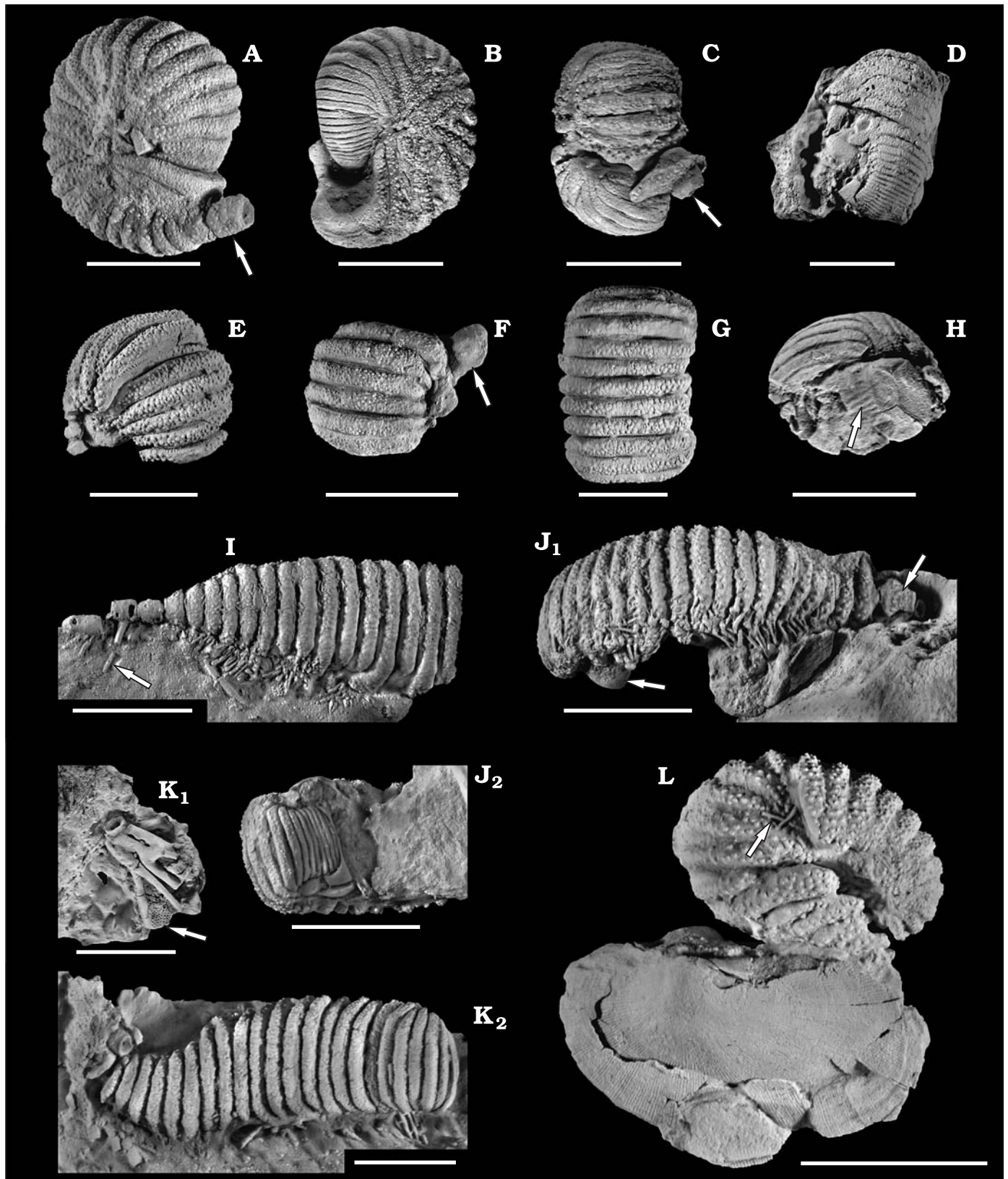
one barrel-shaped columnal showing short LCEE (arrow on the right); the specimen shows numerous preserved spines on the mesistele; one radial plate is visible (arrow on the left); aboral view of proxistele and base of cup (J_2). **K**. Specimen GIK-2132. Isolated holdfast (K_1) attached to a fenestrate bryozoan (arrow); view of the exterior columnal flanks of uncoiled mesistele (K_2) on matrix ("runner-type"). **L**. Coiled specimen (GIK-2103), attached on a brachiopod brachial valve (*Schizophoria* sp.) (compare to reconstruction, figured in Fig. 8); the specimen strongly reduced the dististele and settled with an attachment disc on the brachiopod ("settler-type"). Scale bars 10 mm.

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 (compare Fig. 12A and 12C) 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" (Figs. 7, 14C), or short and composed of only few or nearly reduced columnals, characterizing the "settler-type" (Figs. 8, 12L). Several examples with developed radices on the columnals of the dististele are known (Figs. 7B, 12I). The distal-most dististele is connected with an attachment disc (rare) or, typically, with a variously formed holdfast composed of radices (Figs. 7B, 12K$_1$). 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 (Figs. 2D, 12A, B).

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

Differential diagnosis.—*Ammonicrinus leunisseni* sp. nov. 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. leunisseni* sp. nov. 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. leunisseni* sp. nov.

Stratigraphic and geographic range.—Freilingen Formation (Eifelian) to Loogh Formation (lowermost Lower Givetian) of the Prüm and Hillesheim and (?)Gerolstein synclines (Eifel, Rhenish Massif, Rhineland Palatinate, Germany). The species has its maximum distribution within the Olifant and Zerberus members of the Müllert Subformation (Ahbach Formation, lowermost Lower Givetian).

Ammonicrinus jankei sp. nov.

Figs. 4B, 14B, 15C.

1952 *Ammonicrinus wanneri* Springer, 1926; Ubaghs 1952: 210, fig. 2, pl. 1: 1–7, pl. 2: 1–7.

1978 *Ammonicrinus wanneri* Springer, 1926; Ubaghs 1978: T78, fig. 57: 8.

pars 2003 *Ammonicrinus wanneri* Springer, 1926; Webster 2003: GSAwebpage, *A. wanneri* Springer, 1926, Ubaghs 1952: 210, fig. 2, pl. 1: 1–7, pl. 2: 1–7 and Ubaghs 1978: T78, fig. 57: 8, only.

Etymology: After Eberhard Janke (Elsdorf), for his help in sampling of material, especially from time-consuming washings, for the present publication.

Type material: Holotype: SMF-XXIII.167a.

Type locality: Locality 8: Hill range near the "Steineberg", N of Kerpen, S of Flesten within the Hillesheim Syncline (Eifel, Rhenish Massif, Rhineland Palatinate, Germany).

Type horizon: "Rommersheim Formation" (Ubaghs 1952: 206). My

studies at the type locality suggest that the species came from the Freilingen Formation (upper Eifelian, Middle Devonian).

Diagnosis.—An *Ammonicrinus*, distinguished by a crown with a rhombic outline, smooth 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.

Ammonicrinus jankei sp. nov. 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* sp. nov. 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* sp. nov. are thinner in cross section than those of *A. sulcatus* and have 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 contrast, the shape of the coiled stem that covers the crown of *A. jankei* sp. nov. is oblate spheroidal.

Description.—The crown is mainly distinguished by its shape that shows a characteristic rhombic outline in lateral-anal view (Fig. 4B$_3$, B$_4$), which is caused by the radials, which are convex, conical, and extending 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 (Figs. 4B$_2$, 14B). The lateral-most radials have a slightly lobe-like enlarged appendage that could possibly support the lateral water faecal-ejection (Figs. 4B$_2$, 14B). 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 presumably 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 (Fig. 4B$_4$). 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 (Fig. 4B$_1$). 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.

Stratigraphic and geographic range.—(?)Junkerberg and Freilingen formations (Eifelian) to lower (?)Ahbach Formation (uppermost upper Eifelian) of the Hillesheim Syncline (Eifel, Rhenish Massif, Rhineland Palatinate, Germany). The species has its maximum distribution within the Freilingen Formation.

Postmortem epizonal encrusting

Articulated and 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:

Brachiopoda.—The specimen of *A. doliiformis* in Krause (1927; refigured in Figs. 2E, 9O of the present work) was infested by a (?)craniid brachiopod (Fig. 9O$_1$). 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.

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

Trepostomata: One pluricolumnal and one isolated columnal of the mesistele (GIK-2147, Fig. 13A and GIK-2149, Fig. 13C) were encrusted postmortem by the trepostome bryozoan *Leptotrypella* Vinassa de Regny, 1921. An additional pluricolumnal of the mesistele (GIK-2150, Fig. 13D) was also encrusted postmortem by the trepostomate bryozoan, *Eostenopora* Duncan, 1939. Trepostome bryozoans were also reported attached to the crown ossicles of the cladid crinoid family Cupressocrinitidae Roemer, 1854 (compare to Bohatý 2009). One brachial of a completely preserved *Halocrinites nodosus* crown (Sandberger and Sandberger, 1856) (Bohatý 2009: fig. 2.8), one cup of an also entire *H. schreueri* crown (Bohatý, 2006b) (see Bohatý 2009: fig. 11.4) and one theca of *Procupressocrinus gracilis* (Goldfuss, 1831) (Bohatý 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. (Bohatý 2009: figs. 6.3, 7.2).

Cystoporata: The erect pluricolumnal of the distal mesistele (GIK-2148, Fig. 13B) 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 bryo-

zoan, *Cyclotrypa* Ulrich, 1896, is recognised on one columnal (GIK-2152, Fig. 13F) and one pluricolumnal (GIK-2153, Fig. 13G) of the mesistele.

Fenestrata: One isolated mesistele columnal (GIK-2155, Fig. 13I) was encrusted postmortem by a holdfast of an undetermined fenestrate bryozoan. Bohatý (2009: fig. 11.1) reported stems of *Halocrinites geminatus* (Bohatý, 2005b) 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 2005b: fig. 3B). In contrast, some shorter stem fragments or other disarticulated cupressocrinid ossicles (see Bohatý 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: fig. 3A, B). Głuchowski (2005) 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: fig. 11.16–18). The example is encrusted by the holdfast of a fenestrate bryozoan (*Cyclopelta* sp.) that grew 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.

Microconchida.—One isolated columnal of the mesistele of *A. sulcatus* (GIK-2155, Fig. 13H) 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 (2005b, 2006b, 2009). It is remarkable that larger individuals are rare and isolated (compare to Bohatý 2006b: pl. 5: 8), whereas numerous smaller microconchids encrusted the crinoids (see Bohatý 2009: figs. 2.6, 11.7, 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: 323, fig. 5I–L).

Crinoidea.—The pluricolumnal of *A. sulcatus* (GIK-2151, Fig. 13E) was encrusted postmortem by a crinoid holdfast, which settled on several tubercles with lost spines. Another *A. sulcatus* pluricolumnal (GIK-2150, Fig. 13D) was encrusted postmortem by a trepostomate bryozoan that was then infested by a small crinoid attachment disc. Głuchowski (2005: 322) documented the postmortem encrustation 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 and 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 Franzen (1977) and Peters and Bork (1998). Furthermore, Bohatý (2009) reported crinoid holdfasts attached to the crown ossicles of different cupressocrinids. One cup of *Halocrinites schlotheimii schlotheimii* Steininger, 1831 (Bohatý 2009: fig. 11.9) and one isolated radial and arm plate of *H. geminatus* were encrusted by the holdfasts of other cladid crinoids (?*Procupressocrinus gracilis*).

Chaetitida.—One weathered pluricolumnal of *A. sulcatus* was encrusted by Chaetitida indet. (unfigured material). The encrustation occurred postmortem, because the chaetitid settled on the external and internal regions of the ossicles. Bohatý (2009) mentioned *H. s. schlotheimii* cups, which were completely encrusted by indeterminable stromatoporoids. These encrustations were settled again by chaetetids.

Palaeoecological hypothesis

Ammonicrinus—a spined soft-bottom dweller

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 ossicle 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, articulated spines (Figs. 7, 8, 12I, J$_1$, L, 14C). 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. These elements were mentioned initially by Haude (1981: 199). Several complete ammonicrinid skeletons, embedded in fine homogenous argillaceous limestone rocks, were prepared using fine micro sand-streaming methods. Uncoiled individuals and numerous enrolled ammonicrinids were preserved with articulated spines. A protective function against "predatory" influences like platyceratid gastropods, arthropods, echinoids or the epizonal encrustation of bryozoans, tabulate corals, chaetitids or microconchids (see Fig. 13) is possible.

The spines may have functioned to stabilise the crown into an effective living position. Concordant with this theory, the longest articulated spines are laterally positioned, directed toward the soft-bottom and could have stabilised the individual in a lateral direction and may have also helped keep the body from sinking into the soft substrate.

The most studied and completely preserved ammonicrinids from the German Devonian were preserved as autochthonous embedded endoskeletons. The total skeletal surface is covered by spine-tubercles, previously considered as tubercled plate sculpturing (e.g., Springer 1926; Piotrowski 1977). The holdfast only bears a few articulated spines, and spine density increases proximally. 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 through the ontogenetic stages. The spines are clearly movable because several individuals were preserved with completely preserved mesisteles with spines preserved in all directions toward the exterior. The laterally positioned spines are the longest and contrast to the elements at the top in the centre of the columnal, which are the finest and shortest of the individual.

It is important to note that the development of the spines is an ecophenotypic trait and is recognised herein as 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 radices). Therefore, the development of articulated 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. leunisseni* sp. nov. 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, or spine-tubercles, differs. Furthermore, the feature either composes the only, evenly distributed "ossicular adornment", (compate to Fig. 10E) or the spine-tubercles are unequally spaced on additional, "real plate sculpturings", like unshaped nodes (compare to Fig. 10A–D).

Two interpretations of the spinose endoskeleton

Exterior protection.—The distribution of the articulated spines on the skeleton could indicate the need for protection from vagile benthic "predators". For example, numerous platyceratid gastropod conchs are preserved in associated faunas. Moreover, syn-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.

Interior protection.—The spinose pattern could also have protected the crown, when exposed by partial opening of the enrolled proximal stem. Fine articulated spines served as a skeletal micromesh or "bow net" sensu Haude (1981: 199, 200, fig. 12B). Nutrient particles could pass to the arms, 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: (i) tolerance against sedimentary material, clogging the filtration fan; (ii) the question of the feeding mode under low-intensity current water conditions.
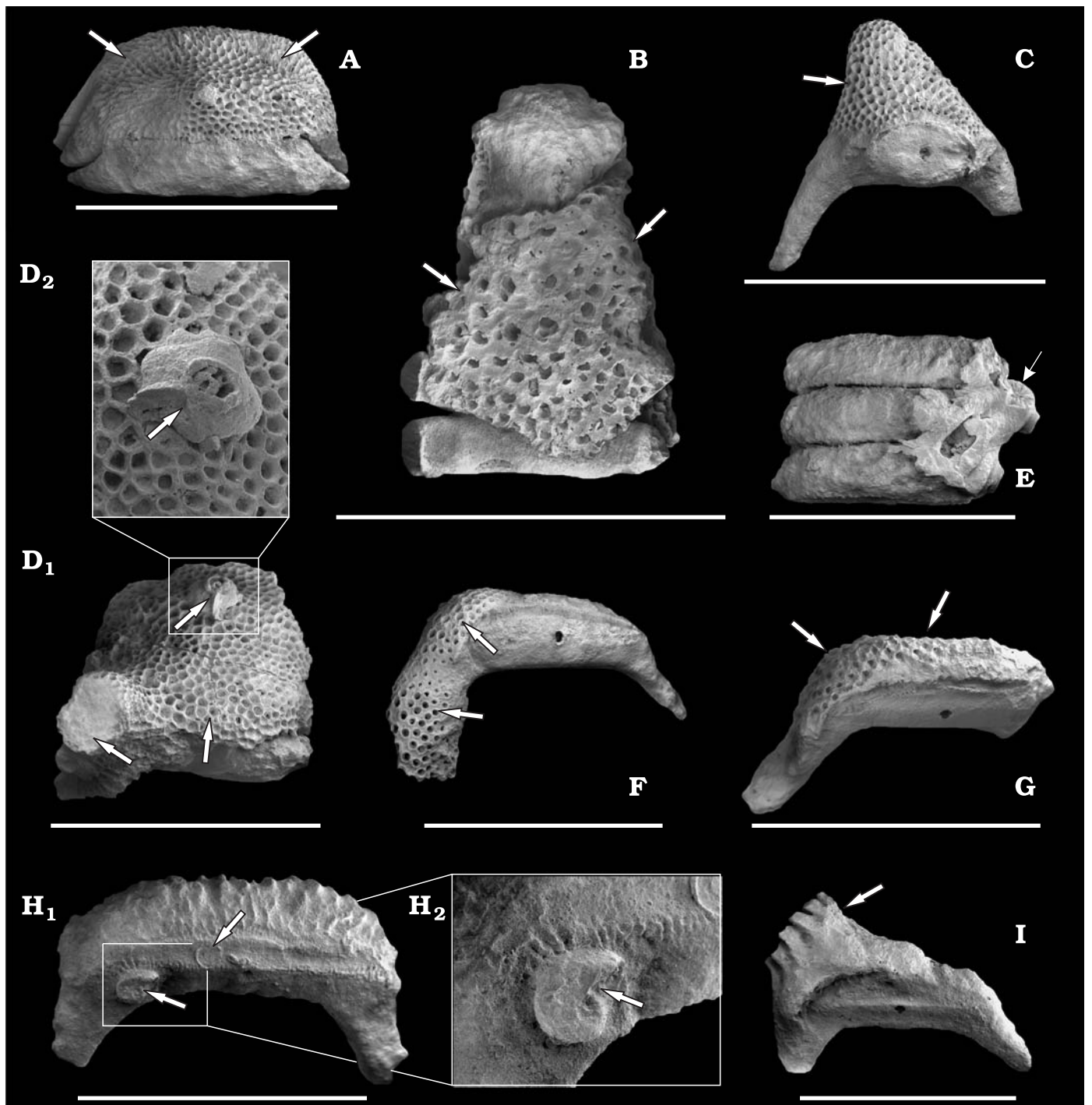
Fig. 13. Postmortem epizoan encrusting on disarticulated columnals of the lecanocrinid crinoid species *Ammonicrinus sulcatus* Kongiel, 1958. **A–G.** From the Eifel (locality 1, Appendix 1), Germany, upper Eifelian (Middle Devonian). **H, I.** From the Eifel (locality 2, Appendix 1), Germany, upper Eifelian (Middle Dvonian). **A.** View of external flanks of a pluricolumnal of the mesistele (GIK-2147), encrusted by a trepostomate bryozoan (*Leptrotrypella*(?) sp.) (arrows). **B.** Internal view of a pluricolumnal of the distal-most mesistele (GIK-2148), encrusted by a cystoporate bryozoan (*Eridopora*(?) sp.) (arrows). **C.** Facet view of an isolated, distal-most columnal of the mesistele (GIK-2149), encrusted by a trepostomate bryozoan [*Leptrotrypella*(?) sp.] (arrows). **D.** External flanks of a pluricolumnal of the mesistele (GIK-2150), encrusted by a trepostomate bryozoan (*Eostenopora*(?) sp.) (see arrows below); the bryozoan is infested by a crinoid attachment disc (arrows in D_2); general view (D_1), detail view (D_2). **E.** View of external flanks of a pluricolumnal of the mesistele (GIK-2151), encrusted by a crinoid holdfast (arrow). **F.** Facet view of an isolated columnal of the mesistele (GIK-2152), encrusted by a cystoporate bryozoan (*Cyclotrypa*(?) sp.) (arrows). **G.** Facet view of a pluricolumnal of the mesistele (GIK-2153), encrusted by a cystoporate bryozoan (*Cyclotrypa*(?) sp.) (arrows). **H.** Facet view of an isolated columnal of the mesistele (GIK-2154) (H_1), encrusted by microconchid valves (see arrows in detail view (H_2). **I.** Facet view of an isolated columnal of the mesistele (GIK-2155), encrusted by a holdfast of a fenestrate bryozoan (arrow). Scale bars 10 mm.
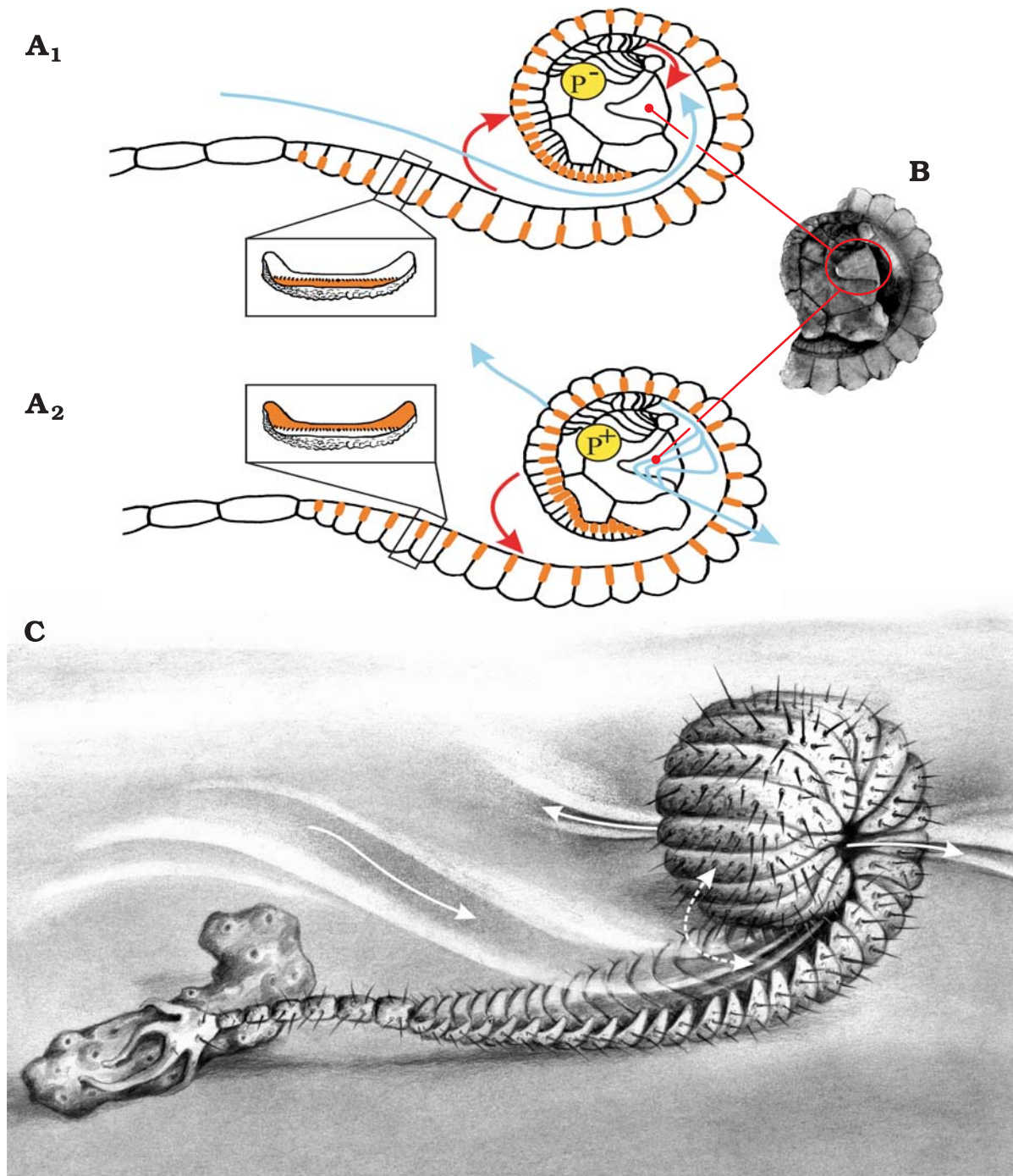
Fig. 14. **A**. Schematic reconstruction of *Ammonicrinus* (strongly modified after Piotrowski 1977: 209, fig. 3) of a feeding *Ammonicrinus* within low-intensity current water. Alternating water pressure was possibly generated in the interior of the enrolled proximal stem by slow, bellow-like partial opening and closing (red arrows) of the base of the central mass; due to the synarthrial (bifacial) articulation of the ammonicrinid mesistele that developed two huge ligamentary facets (orange), separated by the fulcrum, bellow-like partial opening could possibly enabled by stiffening of the outer ligaments (see orange bars in A$_1$); closing could be controlled by stiffening of the inner ligaments (see orange bars in A$_2$). A$_1$, suction during opening may result from low-pressure (P$^-$) and create an ingesting water flow (blue arrow); A$_2$, ejection during closure (red arrow) resulted from overpressure (P$^+$); to minimise faecal recycling, the water ejection may have occurred laterally (blue arrows), feasibly at both lateral centres, which have "openings". **B**. Lobe-like enlarged appendages (framed in red) could possibly support the lateral water faecal-ejection (modified from Ubaghs 1952: pl. 1: 4). **C**. Reconstruction of a feeding "encased runner-type" of *A. leunisseni* sp. nov., attached to a tabulate coral (model); the spined specimen dwelled enrolled on the muddy seafloor; alternating water pressure was obviously generated in the interior of the enrolled proximal stem globe by non-muscular, probably MCT-controlled, slow, bellow-like partial opening and closing of the oblate sphere at its bottom (dashed arrow); 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; 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). Not to scale.

Proposed life interpretation

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* presumably escaped from food competition with other crinoids 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 constraints were: (i) The direct contact with predaceous faunal elements of the vagile benthos; (ii) heightened tolerance for turbidity; (iii) Nutriment filtering within low-intensity current water, which possibly requires a self-generated water flow to bring material from the flocculent layer of organic debris along the bottom into the crinoid filtration fan.

Alternative feeding interpretations

Except for the oldest known ammonicrinid, *Ammonicrinus kerdreoletensis*, which has a laterally exposed cup implying a non-enrolled feeding position in the current (Fig. 6), the younger ammonicrinids (*A. doliiformis*, *A. jankei* sp. nov., *A. leunisseni* sp. nov., *A. sulcatus*, and *A. wanneri*) presumably lived enrolled on the muddy seafloor. Therefore, the infiltration of sediment was a concern. 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 low-intensity current water presumably calls for the generation of a biologically generated water flow and may suggest the hypothesis of a slow, pumping mechanism. Alternating water pressure was possibly generated in the interior of the enrolled proximal stem by bellow-like partial opening and closing of the base of the central mass. Suction during opening may create an ingesting water flow that could be funnelled in the "canal", formed by the unspined interior of the proximal columnals, whose U-shaped flanks were constructed by the LCEE. Ejection during closure may result from overpressure. To minimise faecal recycling, the water ejection most probably have occurred laterally, feasibly at both lateral centres, which have "openings" ("umbilical openings" sensu Piotrowski 1977: 209; Fig. 14C). The lateral-most radials of several species (e.g., *A. jankei* sp. nov.) have a slightly lobe-like enlarged appendage that could possibly support the lateral water faecal-ejection (Figs. 4B₂, 14A, B). Following this hypothesis, 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 could only be done very slowly (William I. Ausich, personal communication 2009), but within the water medium the generated maelstrom could be sufficient. 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 and Motokawa 1994, 1995, 1996; Birenheide et al. 2000; Motokawa et al. 2004) and was also reported within crinoid stalks (Wilkie et al. 1993, 2004). Recently, Hollis and 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 (Hollis and Ausich 2008: 138).

Due to the synarthrial (bifacial) articulation of the ammonicrinid mesistele that developed two huge ligamentary facets, separated by the fulcrum, bellow-like partial opening could possibly enabled by stiffening of the outer ligaments; closing could be controlled by stiffening of the inner ligaments, as illustrated in Fig. 14.

Conclusions

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-dwellers on more or less 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. Radices, observed in a few ammonicrinids, could additionally stabilise the individuals.

The younger ammonicrinids from the Rhenish Massif, the presumed soft-bottom dwellers, especially in in low-intensity current water, requires two main conditions: (i) It is apparently necessary to protect the crown by encasing it by the proximal mesistele. Furthermore, attacks from vagile benthic organisms presumably were anticipated with articulated spines. (ii) The hypothesis of a slow "stem pumping mechanism" could have possibly 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. Fossil indications for this hypothesis are: (i) the crown remained enclosed within the stem and did not protrude toward the lateral exterior; (ii) the interior of the columnals of the mesistele, whose U-shaped LCEE additionally formed a protection against immersive sediment, formed a "canal" for the in-
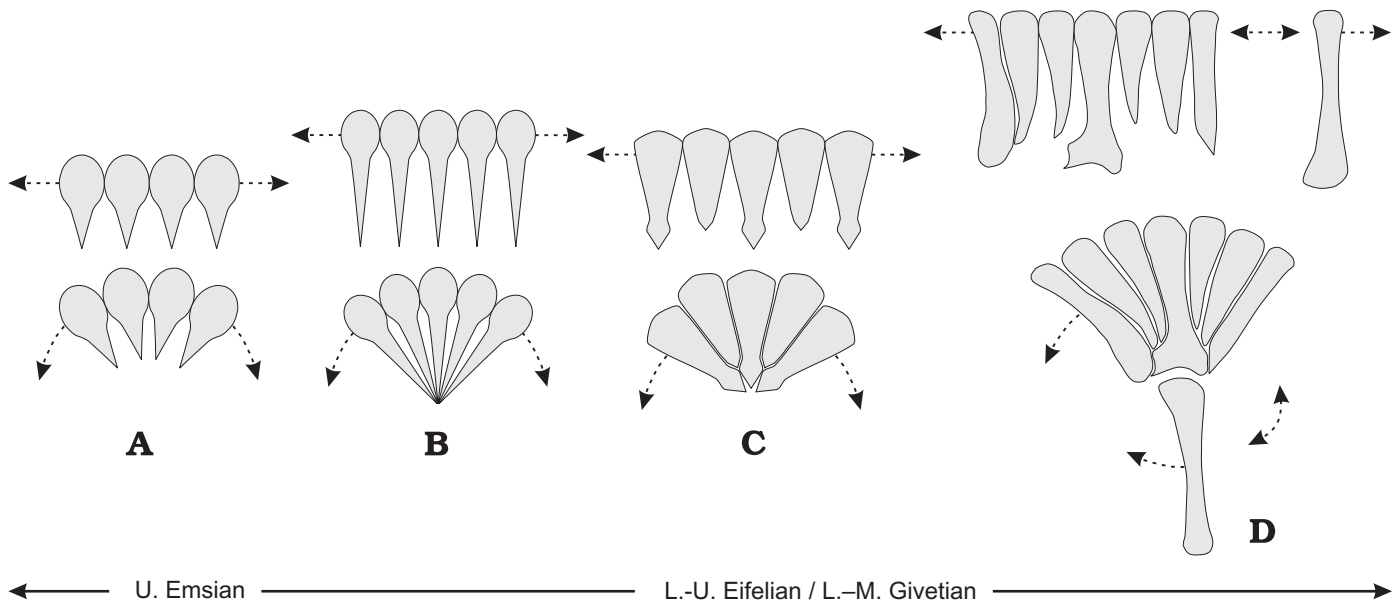
Fig. 15. Schematic sketches of different LCEE of the mesistele in uncoiled (above) and coiled positions (below), indicating evolution of perfecting the crown-encasing in coiled position by modifying the extensions form Emsian to Givetian. **A**. Lateral view of *Ammonicrinus kerdreoletensis* Le Menn and Jaouen, 2003, showing similar shaped columnals with very short LCEE; thus, the crown is laterally nearly unprotected in coiled position. **B**. Lateral view of *Ammonicrinus wanneri* Springer, 1926, with lengthened LCEE of the similar shaped columnals, which lattice-like guarded the crown in coiled position. **C**. Lateral view of *Ammonicrinus sulcatus* Kongiel, 1958, showing smaller columnals of the mesistele, which are interconnected with longer ones and afford lateral density of the coiled stem. **D**. Lateral view of *Ammonicrinus doliiformis* Wolburg, 1938a (for 1937), 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.

current water flow; (iii) the lateral-most radials of several species have a lobe-like enlarged appendage that could possibly support the lateral water faecal-ejection; and, (iv), the mesistele developed two huge ligamentary facets, which are separated by the fulcrum. However, it is important to note that this assumed ability does not 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 form, *A. kerdreoletensis*, has a relative huge crown in relation to the narrow mesistele, which is composed of narrow, similarly shaped columnals with very short extensions (Fig. 15A). 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 (Fig. 15B). 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* (Fig. 15C). 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 (Fig. 15D). 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 and Baumiller 2003 for Middle Devonian crinoid/platyceratid interactions). The necessity to increase the ammonicrinid crown protection could speculatively be linked to this ecological circumstance.

Acknowledgements

References

Almela, A. and Revilla, J. 1950. Especies fósiles nuevas del Devoniano de León. *Notas y Communicaciones del Instituto Geológico y Minero de España* 20: 45–60.

Bassler, R.S. 1938. Pelmatozoa Palaeozoica. *In*: W. Quenstedt (ed.), *Fossilium Catalogus, I: Animalia. Part 83*. 194 pp. W. Junk, s'Gravenhage.

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.

Becker, R.T. 2007. Correlation of the proposed Middle Givetian Substage with the global ammonoid record. *Subcommission on Devonian Stratigraphy, Newsletter* 22: 17–23.

Birenheide, R. and Motokawa, T. 1994. Morphological basis and mechanics of arm movement in the stalked crinoid *Metacrinus rotundus* (Echinodermata, Crinoidea). *Marine Biology* 121: 273–283.

Birenheide, R. and Motokawa, T. 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.

Birenheide, R. and Motokawa, T. 1996. Contractile connective tissue in crinoids. *Biological Bulletin* 191 (1): 1–4.

Birenheide, R., Yokoyama, K., and 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: 7–16.

Bohatý, J. 2005a. *Bactrocrinites* (Crinoidea) aus den Mittel-Devon der Eifel (linksrheinisches Schiefergebirge, Deutschland)—Taxonomie, Biostratigraphie und Fazieskontrolle. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 235: 381–410.

Bohatý, J. 2005b. Doppellagige Kronenplatten: Ein neues anatomisches Merkmal paläozoischer Crinoiden und Revision der Familie Cupressocrinitidae (Devon). *Paläontologische Zeitschrift* 79: 201–225.

Bohatý, J. 2006a. Seltene Gasterocomidae (Crinoidea) aus dem Mittel-Devon der Eifel (linksrheinisches Schiefergebirge, Deutschland). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 239: 399–443.

Bohatý, J. 2006b. Neue Cupressocrinitidae (Crinoidea) aus den mittel-

devonischen Kalkmulden der Eifel (linksrheinisches Schiefergebirge, Deutschland). *Senckenbergiana lethaea* 86 (2): 1–39.

Bohatý, J. 2009. Pre- and postmortem skeletal modifications of the Cupressocrinitidae (Crinoidea, Cladida). *Journal of Paleontology* 83: 45–62.

Bohatý, J. and Herbig, H.-G. 2007. The validity of the Middle Devonian camerate crinoid species *Hexacrinites hieroglyphicus* (Goldfuss, 1839) and *H. marginatus* (Schultze, 1866). *Geobios* 40: 731–736.

Bohatý, J. and Herbig, H.-G. 2010. Middle Givetian echinoderms from the Schlade Valley (Rhenish Massif, Germany)—habitats, taxonomy and ecostratigraphy. *Paläontologische Zeitschrift* 84: 365–385.

Dubatolova, Yu.A. [Dubatolova, Û.A.]1975. Devonian crinoids of the Minusin Basin [in Russian]. *Trudy Instituta Geologii i Geofiziki AN SSSR, Sibirskoe Otdelenie* 272: 1–58.

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. *Paleobiologica* 7: 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: 313–379.

Franzen, C. 1977. Crinoid holdfasts from the Silurian of Gotland. *Lethaia* 10: 219–234.

Gahn, F.J. and 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: 71–82.

Głuchowski, E. 1993. Crinoid assemblages in the Polish Givetian and Frasnian. *Acta Palaeontologica Polonica* 38: 35–92.

Głuchowski, E. 2005. Epibionts on upper Eifelian crinoid columnals from the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* 50: 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 illustrata (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*, 115–221, Arnz and Co., Düsseldorf.

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* 6: 1–362.

Haude, R. 1981. Mechanik, Morphogenese und Palökologische Bedeutung der "Pelmatozoen"-Stiele. *In*: W.-E. Rief (ed.), *Paläontologische Kursbücher, 1: Funktionsmorphologie*, 187–203. Paläontologische Gesellschaft, München.

Haude, R. 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.

Hauser, J. 2005. *Ammonicrinus (Crinoidea, Flexibilia) aus dem Paläozoikum von Deutschland (Eifel, Sauerland) und dem Heilig-Kreuz-Gebirge (Polen)*. 52 pp. Privately published by the author, Bonn.

Hauser, J., Landeta, F.G., and Savill, J.J. 2009. *Ammonicrinus wanneri* SPRINGER, 1926 (Crinoidea, Flexibilia) from the Portilla Formation, Givetian (Cantabrian Mountains, Province Leon, Northern Spain). *In*: J. Hauser and F.G. Landeta (eds.), *Crinoiden aus dem Unter- und Mitteldevon von Asturien und Leon (Nordspanien)*, 54–58. Privately published by the authors, Bonn [pre-published in 2008 on private web-page: <http://www.devon-crinoiden.de/ammonicrinusportilla.pdf >; does not meet ICZN regulations, J.B.].

Hess, H., Ausich, W.I., Brett, C.E., and Simms, M.J. 1999. *Fossil Crinoids*. 273 pp. Cambridge University Press, Cambridge.

Hollis, K.A. and Ausich, W.I. 2008. The Holdfast of *Gilbertsocrinus tuberosus* (Mississippian, Crinoidea). *Canadian Journal of Earth Sciences* 45: 135–140.

Hotchkiss, F.H.C., Prokop, R.J., and 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: 329–333.

Kongiel, R. 1958. Nowy gatunek *Ammonicrinus* i jego występowanie w Polsce [with French summary]. *Prace Muzeum Ziemi* 2: 31–40.

Krause, P.G. 1927. Über *Ammonicrinus* aus dem Mitteldevon der Eifel. *Zeitschrift der Deutschen Geologischen Gesellschaft* 79: 448–456.

Le Menn, J. 1985. Les Crinoïdes du Dévonien inférieur et moyen du Massif armoricain. *Mémoires de la Société géologique et minéralogique de Bretagne* 30: 1–268.

Le Menn, J. and Jaouen, P.A. 2003. Nouvelles espèces d'*Ancyrocrinus* et d'*Ammonicrinus*, crinoïdes à pédoncule spécialisé du Dévonien armoricain (Brest, France). *Comptes Rendus Palevol* 2: 205–212.

Meek, F.B. and 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. and Ausich, W.I. 1983. Biotic interactions among recent and among fossil crinoids. *In*: M.J.S. Tevesz and P.L. McCall (eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*, 377–427. Plenum Press, New York.

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 pp. Bryan and Co. Bristol, England.

Moore, R.C. 1978. Flexibilia. *In*: R.C. Moore and C. Teichert (eds.), *Treatise on Invertebrate Paleontology. Part T, Echinodermata 2, vols. 1–3*, T759–T812. The Geological Society of America and The University of Kansas, Boulder.

Moore, R.C. and Laudon, L.R. 1943. Evolution and classification of Paleozoic crinoids. *Geological Society of America Special Paper* 46: 1–153.

Moore, R.C. and Strimple, H.L. 1973. Lower Pennsylvanian (Morrowan) crinoids from Arkansas, Oklahoma and Texas. *University of Kansas Paleontological Contributions* 60 (Echinodermata 12): 84.

Moore, R.C. and Teichert, C. 1978. *Treatise on Invertebrate Paleontology. Part T, Echinodermata 2, vols. 1–3*. i–xxxviii + T1–T1027. The Geological Society of America and The University of Kansas, Boulder.

Motokawa, T., Shintani, O., and Birenheide, R. 2004. Contraction and stiffness changes in collagenous arm ligaments of the stalked crinoid *Metacrinus rotundus* (Echinodermata). *Biological Bulletin* 206: 4–12.

Müller, J. 1856. Über neue Crinoiden aus dem Eifeler Kalk. *Verhandlungen der Königlichen Akademie der Wissenschaften (Monatsberichte)* 1856: 353–356.

Müller, J. 1859 (1858). Über einige Echinodermen der rheinischen Grauwacke und des Eifeler Kalkes. *Königliche Akademie der Wissenschaften; Monatsberichte* 1859: 185–198 (pre-released 1858: 1–13).

Peters, S.E. and 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*, 203–208. John Murray, London.

Piotrowski, A. 1977. Genus *Ammonicrinus* Crinoidea, from the Middle Devonian of the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonia* 22: 205–219.

Roemer, C.F. 1852–1854. Erste Periode, Kohlen-Gebirge. *In*: H.G. Bronn (ed.), *Lethaea Geognostica* 3 (2): 1–788.

Prokop, R.J. 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: 161–164.

Sandberger, G. and Sandberger, F. 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 pp., 41 pls. (sep. atlas). Kreidel und Niedner, Wiesbaden.

Schultze, L.J.Th. 1866. *Monographie der Echinodermen des Eifler Kalkes*. 118 pp. Carl Gerolds Sohn, Wien.

Springer, F. 1913. Crinoidea. *In*: K.A. von Zittel (ed.), *Textbook of Paleontology, 2nd edition, vol. 1.*, 173–243. Macmillan and Co., London.

Springer, F. 1926. Unusual forms of fossil crinoids. *Proceedings of the U.S. National Museum* 67 (9): 1–137.

Steininger, J. 1831. *Bemerkungen über die Versteinerungen, welche in dem Übergangskalkgebirge der Eifel gefunden werden*, 1–44. Lints, Trier.

Steininger, F.F. and Piller, W.E. 1999. Empfehlungen (Richtlinien) zur Handhabung der stratigraphischen Nomenklatur. *Courier Forschungsinstitut Senckenberg* 209: 1–19.

Ubaghs, G. 1952. *Ammonicrinus* Springer, Crinoidea Flexibilia du Dévonien moyen d'Allemagne. *Senckenbergiana* 33: 203–226.

Ubaghs, G. 1978. Skeletal morphology of fossil crinoids. *In*: R.C. Moore and C. Teichert (eds.), *Treatise on Invertebrate Paleontology. Part T, Echinodermata 2, vols. 1–3*, T58–T216. The Geological Society of America and The University of Kansas, Boulder.

Ulrich, E.O. 1882. American Palaeozoic Bryozoa. *The Journal of the Cincinnati Society of Natural History* 5: 121–175, 233–257.

Ulrich, E.O. 1896. Bryozoa. *In*: C. Eastman (ed.), *Zittel's Textbook of Palaeontology, vol. 1*, 257–291. Macmillan, London.

Vinassa de Regny, P. 1921. Sulla classificazione die trepostomidi. *Societa Italiana di Scienze Naturali Atti* 59: 212–231.

Wachsmuth, C. and Springer, F. 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.

Wachsmuth, C. and Springer, F. 1897. The North American Crinoidea Camerata. *Harvard College Museum of Comparative Zoology, Memoir* 20: 1–359, 21: 360–897.

Wanner, J. 1943. Die Krinoiden des Rheinischen Devons. *Rheinische Heimatpflege* 13 (for 1941): 27–38.

Wanner, J. 1954. Die Analstruktur von *Ammonicrinus* Springer nebst Bemerkungen über Aberranzen und Anomalien bei Krinoiden. *Neues Jahrbuch für Geologie und Paläontologie, Monatschafte* 1954 (5): 231–236.

Webster, G.D. 2003. *Bibliography and Index of Paleozoic Crinoids, Coronates and Hemistreptocrinoids 1758–1999, Index of the Crinoid Crowns and Parts of Crowns*. Geological Society of America, Boulder. GSA Website: http://crinoid.gsajournals.org/crinoidmod.

Webster, G.D. and Jell, P.A. 1999. New Carboniferous crinoids from eastern Australia. *Memoirs of the Queensland Museum* 43: 237–278.

Wilkie, I.C. 1984. Variable tensility in echinoderm collagenous tissues—a review. *Marine Behavior and Physiology* 11: 1–34.

Wilkie, I.C., Emson, R.H., and Young, C.M. 1993. Smart collagen in sea lilies. *Nature* 366: 519–520.

Wilkie, I.C., Candia Carnevali, M.D., and Trotter, J.A. 2004. Mutable collagenous tissue: recent progress and an evolutionary perspective. *In*: T. Heinzeller and J.H. Nebelsick (eds.), *Echinoderms München*, 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.

Wolburg, J. 1938a for 1937. Bau und Biologie von *Ammonicrinus doliiformis* sp. nov. *Jahrbuch der preußischen geologischen Landesanstalt* 58: 230–241.

Wolburg, J. 1938b. Zur Frage der Lebensweise der eingerollten Crinoiden. *Zentralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B* 7: 254–261.

Yakovlev, N.N. and Ivanov, A.P. 1956. Marine crinoids and blastoids of the Carboniferous and Permian deposits of Russia [in Russian]. *Trudy Vsesoûznogo Naučno-Issledovatel'skogo Geologičeskogo Instituta* 11: 1–142.

Zittel, K.A. von 1895. *Grundzüge der Paläontologie (Paläozoologie), 1st edition*. 971 pp. R. Oldenbourg, München.

Appendix 1

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: 230); more probable, the ammonicrinids came from the Odershäuser Formation of the Eifelian/Givetian threshold (Middle Devonian) (Martin Basse, personal communication 2009).

Locality 12 (Vireux-Molhain, France)

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