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Reassessing the improbability of a muscular crinoid stem

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Muscular articulations in modern stalked crinoids are only present in the arms. Although it has been suggested that certain coiled-stemmed fossil taxa may have been functionally adapted to utilize muscles, evidence supporting this interpretation is lacking. Here, we use cathodoluminescence and SEM to reveal the skeletal microstructure of the enigmatic coiled-stemmed taxon *Ammonicrinus* (Flexibilia). Based on the well-established link between skeletal microstructure and the nature of infilling soft tissues in modern echinoderms, we reconstructed the palaeoanatomy of the Middle Devonian ammonicrinids. We show that their median columnals with elongated lateral columnal enclosure extensions (LCEE) have stereom microstructure unexpectedly resembling that in the crinoid muscular arm plates. In particular, large ligamentary facets, that are present on each side of a transverse ridge, are mainly comprised of fine galleried stereom that is indicative of the mutable collagenous tissues. In contrast, fine labyrinthic stereom, commonly associated with muscles, is situated in the periphery on each side of the surface of elongated LCEE. Our findings thus strongly suggest that the muscles may have also been present in the stem of ammonicrinids. These results reassess the previous hypotheses about evolution of muscles in crinoids and provide new insights into the mode of life of *Ammonicrinus*.

Living stalked crinoids (Crinoidea), commonly known as sea lilies, possess muscular articulations between opposing plates only in their arms¹. This type of articulation, which allows a high degree of relatively rapid arm movements, is believed to have first evolved during the Early Devonian². However, among many Devonian crinoid clades, only advanced cladids are known to have acquired muscular articulations in their arms³. It has been argued that the appearance and subsequent evolutionary success of this crinoid group and their post-Paleozoic descendants may be related to the presence of their muscular arms⁴. Indeed, acquisition of muscles is considered a major innovative step in crinoid evolution.

In contrast to crinoid arms which may bear muscular articulations, articulations between opposing plates in the crinoid stem are exclusively non-muscular¹. Any flexibility of the stem in modern crinoids is always under the control of the ligamentary mutable collagenous tissues (MCTs)⁵. Although it has been suggested that the stems of certain coiled-stemmed fossil crinoids might have been muscular⁶, evidence supporting this interpretation is virtually unknown^{7,8}.

The Devonian lecanocrinid crinoid *Ammonicrinus* (Flexibilia) is one of the most bizarre coiled-stemmed crinoids. This enigmatic crinoid genus has long attracted the attention of many palaeontologists because of its unusual morphology^{9–28}. It is characterized by a xenomorphic stem comprised of distal barrel-shaped columnals, and the median-proximal columnals have characteristic lateral columnal enclosure extensions that were planispirally coiled and displayed the ability to enclose the crown, which was equipped with short arms (Fig. 2a). Furthermore, the columnals of some ammonicrinid species have a number of other unique features, including their latera that, contrary to most crinoids, are covered by echinoid-like tubercles that may bear articulated spines indicating a possible protective function²⁸. Unsurprisingly, the mode of life of these crinoids has become the subject of a long running controversy. In contrast to the “normal”, erect feeding posture of most stalked crinoids, ammonicrinids were typically considered “plate-encased” crinoids feeding in low velocity horizontal currents¹⁹. However, a planktonic lifestyle for these crinoids was also suggested by some authors¹⁰. Most recently, on the basis of theoretical considerations about functional morphology and palaeoenvironmental analysis, it was concluded that ammonicrinids were soft-bottom dwellers, feeding in low-velocity currents, possibly through a self-produced water flow mediated by the contraction the stem delivered by non-muscular mutable collagenous tissues (MCT)²⁸. In particular, a self-produced water flow might have been generated in the interior of the enrolled proximal stem by partial opening and closing of the base of the central mass. This was likely facilitated by synarthrial articulation of the ammonicrinid mesistele characterized by the presence of the two ligamentary



facets. In this model²⁸, partial opening might have been enabled by stiffening of the outer ligaments of the mutable collagenous tissues (MCT), whereas closing might have been controlled by stiffening of the inner ligaments of MCT. However, although MCTs have the special ability to change their mechanical properties²⁹, the tissue conversion from stiff to soft enabling the efficient contraction of the entire stem could have proceeded rather slowly. Indeed, according to Donovan⁷ the snap coiling under ligamentary control as hypothesized for some Paleozoic crinoids⁶ would not have been possible. This suggests another possibility: ammonicrinid stem might have contained muscles. To test this hypothesis, given the well-established relationship between the skeletal microstructure and the nature of the soft tissue in modern echinoderms^{30–32}, it is possible to reconstruct the soft tissue palaeoanatomy of ammonicrinids with microstructural characterization of their skeletons. However, diagenetic alteration commonly leads to a significant obliteration of the primary microstructural features of the echinoderm skeleton³³. Recently, Gorzelak and Zamora³⁴ introduced a promising technique, i.e., cathodoluminescence (CL), to reconstruct the original stereom microstructure in strongly recrystallized calcitic Cambrian echinoderms. Here, we use this powerful method supplemented by conventional SEM observations of well preserved specimens to characterize the skeletal microstructure of Devonian *Ammonicrinus*. This approach not only provides insights into the skeletal microarchitecture and palaeoanatomy of these enigmatic crinoids but also for a reassessment of the previous hypotheses about the mode of life of *Ammonicrinus* and evolution of muscles in crinoids.

Geological setting and materials

The crinoid material studied here comes from the Grzegorzowice–Skały section. This section is a Lower to Middle Devonian sequence situated in the eastern part of the Bodzentyn Syncline in the Łysogóry region of the Holy Cross Mountains. The Eifelian–Givetian part of the sequence, including the Skały Beds, is exposed on the eastern slope of the Dobruchna River valley in the neighborhood of Skały village (Fig. 1). The lithologically variable Skały Beds contain a rich and diverse fauna including crinoids^{35,36}.

The crinoid material was collected from the lower part of the Skały Beds, from the so-called brachiopod shales (=complex XIV³⁷) and

represents *Tortodus kockelianus* Zone of the upper Eifelian (~390 Ma)^{38,39}.

Among the preserved crinoid ossicles are disarticulated elements of the xenomorphic column of *Ammonicrinus sulcatus* Kongiel. The material includes mainly large and massive columnals with elongated (Fig. 2b) or reduced (Fig. 2g) lateral columnal enclosure extensions from the middle part of stem and barrel-like columnals from the distal part of the stem (Fig. 2l).

Results

Ammonicrinid columnals analysed in this study are infilled with cement that is precipitated in optical continuity to the stereom trabeculae (Fig. 3). Thus under polarizing microscopy, the entire plate behaves as a single calcite crystal, and the stereom microstructure is hardly visible (Fig. 3a,b). EDS spot elemental analyses from selected regions revealed that the chemical composition of the stereom and cement are similar (Fig. 4), i.e., both are preserved as calcium carbonate with slightly different concentrations of Mg and Fe (Fig. 4). In BSE mode, the contrast between chemical composition of calcitic stereom and ferroan calcitic cement is somewhat more distinct (Fig. 4) although it is not very clear.

The contact between the stereom and cement is best revealed by cathodoluminescence (CL) (Fig. 3, Fig. 5). Under CL, ammonicrinid specimens have orange luminescing stereom and nonluminescent ferroan calcite (Fig. 3c, Fig. 5). The CL emission spectra of the stereom revealed emission maximum at about 615 nm, which is indicative of Mn²⁺ activation in calcite (Fig. 3d). Clearly, the observed strong contrast between cement and the relic “ghost” microstructure is a consequence of the differences in concentrations of trace elements during diagenesis, i.e., Mn²⁺, that is the most significant activator element and Fe²⁺ that is the most important quencher element. This contrast, revealed by CL, allowed the primary stereom organization of investigated specimens to be reconstructed. The stereom in a few (less recrystallized) specimens was also revealed using conventional imaging in SEM (Fig. 6).

Stereom organization of median columnals. Five types of stereom can be distinguished in median columnals (Fig. 2). The articular facet on each side of a transverse ridge is mainly constructed of fine (trabeculae thickness: 2.5–6.9 μm) galleried stereom, in which pores (5.1–14.3 μm in diameter) are aligned in one direction, commonly perpendicular to the articular facet (Figs. 2d–f, i–k, Figs. 5e,h). In larger columnals, the inner, peripheral side of a well-developed facet is triangular in shape, and elongated lateral columnal enclosure extensions are covered by fine (4–7.7 μm thick) labyrinthic stereom, in which pores are irregular in size (4.1–8.8 μm) and have no alignment (Figs. 2c,f, Fig. 5a,f). However, the facets of smaller columnals with strongly reduced lateral columnal enclosure extensions contain only galleried stereom (Fig. 2h–k). Fine labyrinthic stereom is also recognized near the latera in the regions of the so-called echinoid-like tubercles (Figs. 2c–f, h–k; Figs. 5c,d,i). The outer morphology of these tubercles resembles the so-called “glassy tubercles” of echinoderms⁴⁰. However, internally they are composed of porous stereom, not compact, imperforated calcite as observed in the glassy tubercles. The latera of median columnals is usually constructed of a microperforated stereom layer with a mean thickness of ~20 μm (Figs. 2c–f, h–k, 5c). The interior of both larger and smaller columnals is mostly comprised of coarse (10–20 μm) galleried or rectilinear stereom radiating laterally (Figs. 2c–f, h–k; Figs. 5c,d,g,i). The inner side near the axial canal also contains coarse (8.1–22.7 μm) labyrinthic stereom (Figs. 2c–f, h; Figs. 5b,e,h).

Stereom organization of distal columnals. Distal columnals are made of two distinct stereom fields: the biconical zone of fine galleried stereom perpendicular to the articular facet, and a much

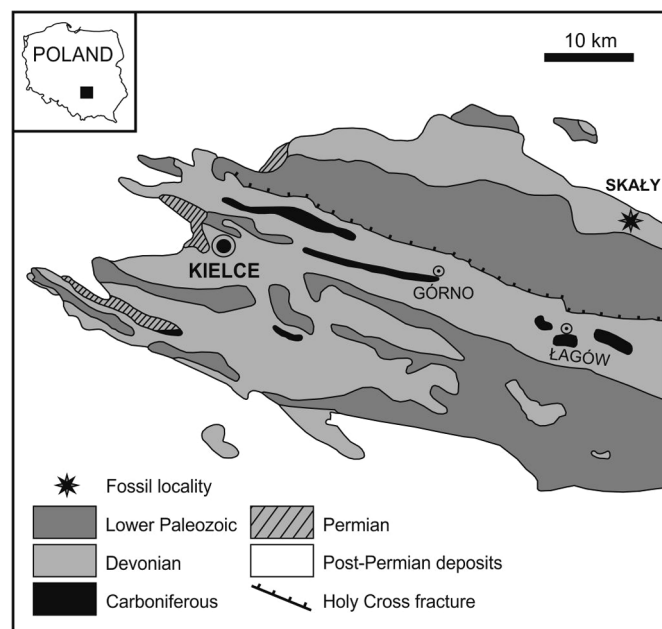


Figure 1 | Geological map of western part of the Holy Cross Mountains and location of study site. Modified from ref. 35.

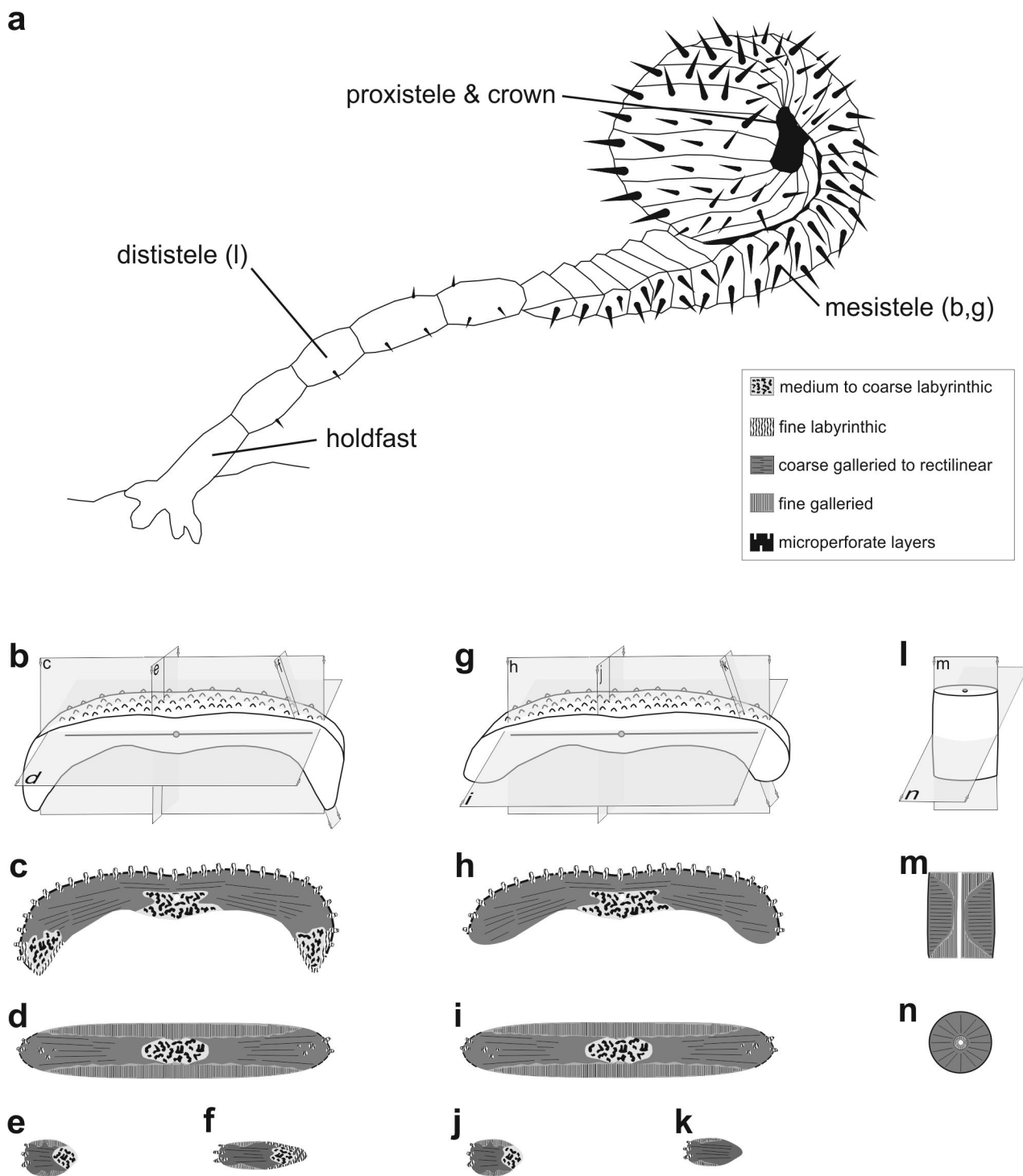


Figure 2 | Morphology and microstructure of *Ammonicrinus*. (a) Reconstruction of life time position (Modified from ref. 16). (b) Schematic draw of median columnal joint surface with elongated lateral columnal enclosure extension showing the orientation of investigated thin sections. (c) Distribution of stereom microstructure in transversal section. (d) Distribution of stereom microstructure in tangential section. (e) Distribution of stereom microstructure in longitudinal section. (f) Distribution of stereom microstructure in oblique-longitudinal section of the lateral columnal enclosure extension. (g) Schematic draw of median columnal joint surface with reduced lateral columnal enclosure extension showing the orientation of the investigated thin sections. (h) Distribution of stereom microstructure in transversal section. (i) Distribution of stereom microstructure in tangential section. (j) Distribution of stereom microstructure in longitudinal section. (k) Distribution of stereom microstructure in oblique-longitudinal section of the lateral columnal enclosure extension. (l) Schematic draw of distal columnal showing the orientation of the investigated thin sections. (m) Distribution of stereom microstructure in longitudinal section. (n) Distribution of stereom microstructure in transversal section.

coarser galleried to rectilinear stereom radiating laterally (Figs. 2m,n; Figs. 5j-l). The galleries extending from the facet are very long, especially near the axial canal (Fig. 2m; Figs. 5j,k) with the mean pore diameter of 7.1 μm and the mean trabecular thickness of

6.2 μm . The coarse stereom perpendicular to the latera with the mean pore diameter of 13.9 μm , and the mean trabecular thickness of 19 μm reaches to the outermost microperforated stereom layer with a mean thickness of 18 μm (Fig. 5l).

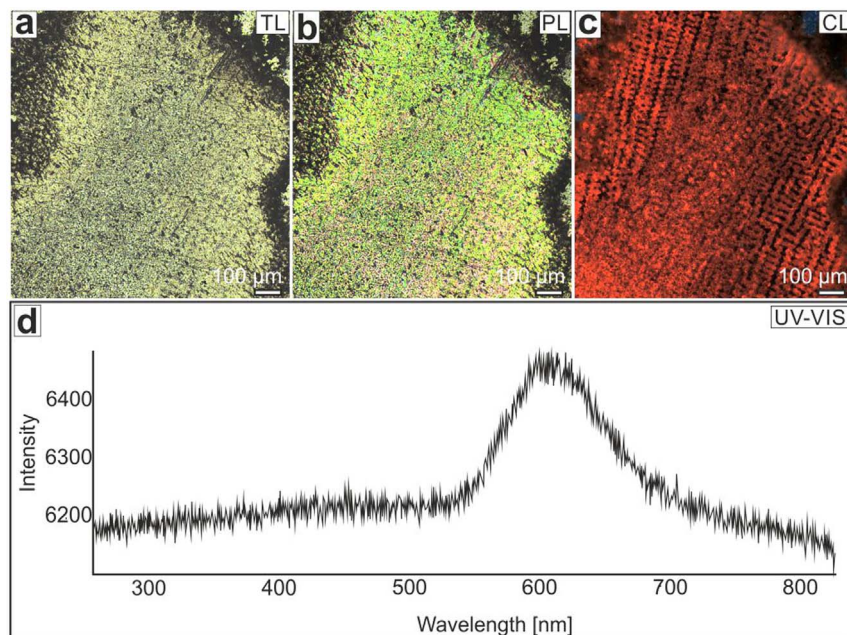


Figure 3 | Photomicrographs of median columnal of *Ammonicrinus* (tangential section). (a) Optical (TL), (b) Polarizing (PL) and (c) Cathodoluminescence (CL) views. (d) CL-activated UV-VIS spectrum of the intense orange-red luminescent ammoniacrinid columnal showing Mn^{2+} emission maximum at ~ 615 nm. Note that the stereom microstructure is greatly enhanced under cathodoluminescence.

Discussion

Among traditional proxies for identifying muscles in echinoderms, facet morphology was invoked^{2,7}, and some studies have argued that the presence of a transverse ridge in brachials is sufficient to state that articulations are muscular. Although a similar ridge occurs on ammoniacrinid columnal facets, caution is needed in such interpretations because the stem of extant bourgueticrinids, which also yields synarthrially articulating column, does not possess muscles⁵. Similarly, certain Paleozoic forms (such as *Camptocrinus*, *Platycrinites*, *Pisocrinus*), despite the presence of the transverse ridge in their brachials and/or columnals, are regarded as having had exclusively ligamentary articulations⁷.

It has been argued that the stereom microstructure is a much more reliable proxy for identifying the nature of the investing soft tissues than the overall morphology of the articular facet³². Indeed, as demonstrated by Macurda and Meyer⁴¹ and Smith³⁰, there is a strong link between skeletal microstructure and the nature of infilling soft tissues in echinoderms. For example, fine galleried stereom is always indicative of through-going ligamentary collagenous fibers, whereas

fine labyrinthic stereom is usually associated with the muscle fiber attachment. Following this approach, Lane and Macurda⁴² identified muscular articulations in Pennsylvanian crinoid brachial plates. Other microstructural studies on Paleozoic crinoid stems from different clades (*Pisocrinus*, *Barycrinus*, *Gilbertocrinus*, *Myelodactylid*) revealed that they are comprised of a stereom exclusively associated with collagenous ligamentation, not musculature^{43–46}. More recently, using an extensive compilation of stereom data obtained from modern echinoderms, Clausen and Smith³² reconstructed the soft tissue palaeoanatomy of Cambrian echinoderms. Following the same microstructural approach, we also inferred the soft tissue palaeoanatomy of *Ammonicrinus* (Figs. 7, 8).

The facets of distal and median ammoniacrinid columnals with short LCEE, as in the stem of modern crinoids, are made up almost entirely of galleried stereom that is indicative of collagen fibres binding adjacent columnals (Fig. 7). In contrast, median columnals with elongated LCEE also have fine labyrinthic stereom that coats the innermost (peripheral) surface of LCEE. In many species of recent crinoids, this stereom type is characteristic for muscle attachment

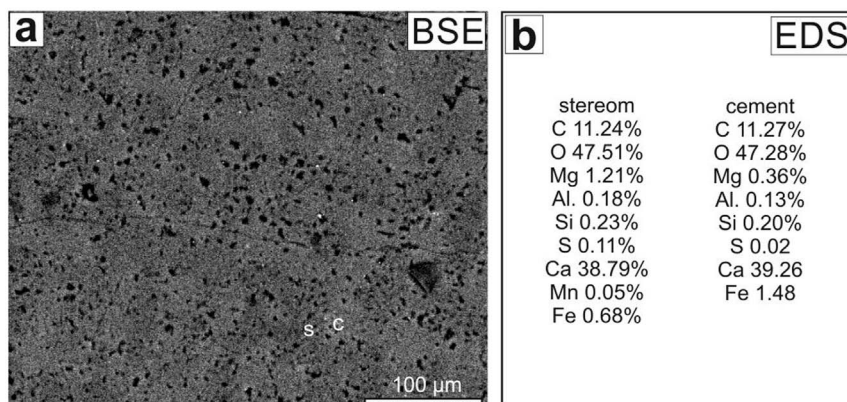


Figure 4 | Results of geochemical analyses of *Ammonicrinus*. (a) SEM back-scattered electron (BSE) image of the polished ammoniacrinid columnal showing the contrast between materials of lower (darker areas = stereom) versus higher atomic number (lighter areas = cement). (b) Results of EDS analyses of the stereom (s) and cement (c).

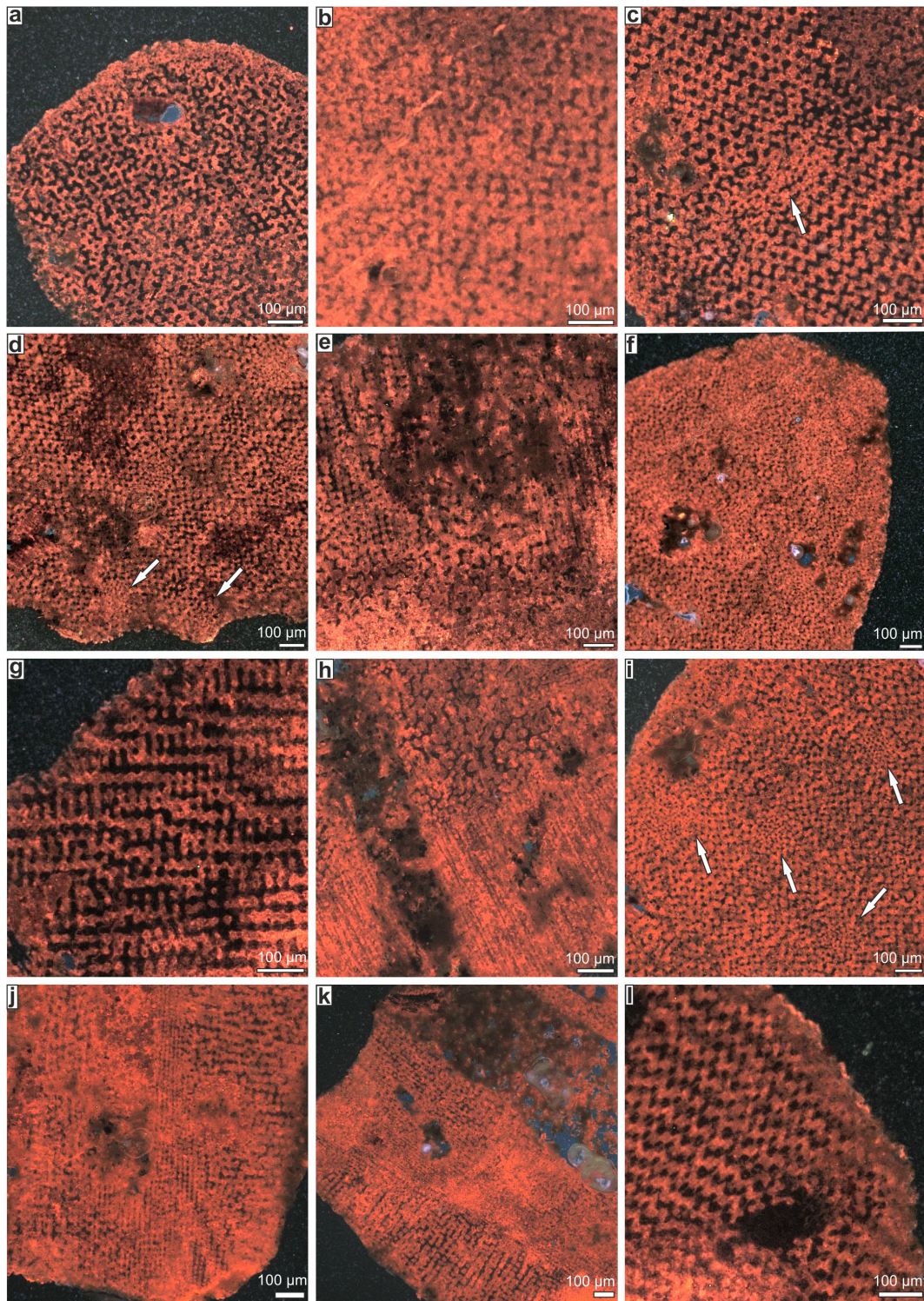


Figure 5 | Cathodoluminescence (CL) photomicrographs of median (a-i) and distal (j-l) columnals of *Ammoniacrinus*. (a) Transversal section showing medium to fine labyrinthine stereom near the periphery of the plate margin (region of the lateral columnal enclosure extension). (b) Transversal section showing the medium to coarse labyrinthine stereom in the centre of the section. (c) Transversal section showing coarse rectilinear and fine labyrinthine stereom (arrow) in the periphery of the plate margin (region close to the centre of the articular surface). (d) Longitudinal section close to the lateral columnal enclosure extension showing coarse rectilinear and/or galleried stereom and fine labyrinthine stereom (arrows) near the echinoid-like tubercles in the periphery of the plate margin. (e) Longitudinal section of the articular surface showing fine galleried stereom underlain by coarse labyrinthine stereom. (f) Oblique-longitudinal section of the lateral columnal enclosure extension showing medium to fine labyrinthine stereom. (g) Tangential section showing coarse rectilinear stereom in the periphery of the plate margin. (h) Tangential section showing coarse labyrinthine stereom underlain by fine galleried stereom near the axial canal. (i) Tangential section showing coarse labyrinthine to rectilinear stereom and fine labyrinthine stereom (arrows). (j) Longitudinal section showing fine galleried stereom (lower left) and coarse galleried to rectilinear stereom (upper right). (k) Longitudinal section showing fine galleried stereom near the lumen and perpendicular coarse galleried to rectilinear stereom near the periphery of the plate margin. (l) Longitudinal section showing coarse galleried to rectilinear stereom and microperforate layers in the periphery of the plate margin.

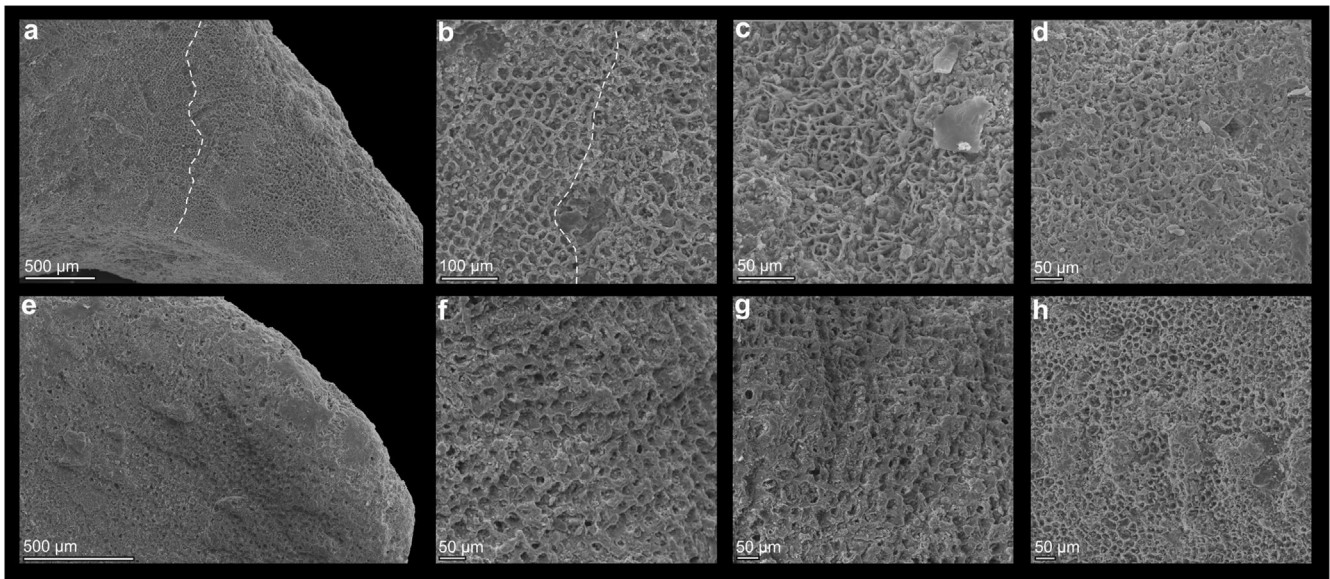


Figure 6 | Microstructural organization of the facet surface of median ammoniacrinid columnals with elongated (a-d) and reduced (e-h) lateral columnal enclosure extensions in SEM. (a) Boundary (dotted line) between fine galleried (left) and fine labyrinthic (right) stereom. (b) Higher magnification of (a). (c, d) Higher magnification of fine labyrinthic stereom. (e) Medium galleried stereom. (f, g) Higher magnification of (e). (h) Fine galleried stereom of the articular surface.

(Fig. 7). Only very rarely, ligaments are known to be also associated with labyrinthic stereom⁴⁷.

The fine labyrinthic stereom indicative of muscles is also present in the regions close to the so-called echinoid-like tubercles that may bear articulated spines. This implies that the spines of *Ammoniacrinus* could have been highly movable and were under the control of muscles. The other skeletal areas of both median and distal columnals (the interior and latera) are almost entirely composed of coarser, clearly structural (Fig. 7), galleried to rectilinear, labyrinthic and microperforate stereom.

Apart from morphological/microstructural criteria for recognizing soft tissues in echinoderms, taphonomic methods were also proposed⁴. These methods rely on the fact that the muscular articulations are taphonomically less resistant to disarticulation than exclusively ligamentary articulations. Difference in the disarticulation style is evident in the present material. In particular, ammoniacrinid columnals were found exclusively as isolated plates, whereas all other crinoids (camerates and inadunates) – traditionally regarding as having had exclusively ligamentary symplexial articulations between columnals, are commonly preserved as pluricolunans, i.e. fragments of articulated stems¹⁹. Thus, the observed disarticulation gradient is consistent with microstructural data suggesting the presence of muscles in some median columnals of *Ammoniacrinus*. The flexure of ammoniacrinid stem commonly observed in complete specimens from other Devonian localities may be also indicative of muscles. Indeed, according to Ausich and Baumiller⁴ crinoids bearing muscles are expected to have post-mortem flexure, whereas crinoids bearing ligaments are normally preserved straight.

Taken together, all of the traditional proxies (including the morphology of the facet, the stereom microstructure and taphonomy) imply the presence of muscles in some of the median ammoniacrinid columnals. On the basis of this new evidence, it is possible to evaluate critically the current hypothesis about the “stem-pumping” mode of life of *Ammoniacrinus*.

In *Ammoniacrinus sulcatus* analyzed in this study, the smaller columnals of the mesistele are interconnected with longer ones, which according to the new microstructural data might have contained muscles (Fig. 8). Following this hypothesis, at least the rapid contraction/closing of the stem could have been indeed possible, but

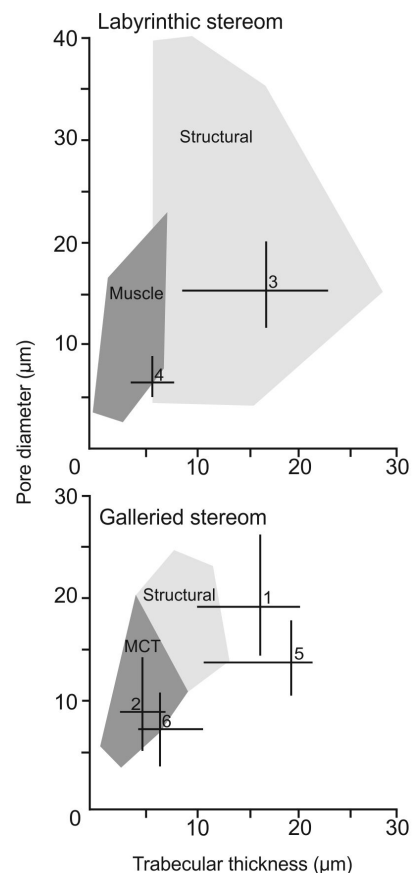


Figure 7 | Stereom fields in recent echinoderms. Taken from ref. 32. Dark shaded areas correspond to the stereom fields indicative of muscles and mutable collagenous tissues (MCT). The range and mean of the six stereom types of *Ammoniacrinus* are indicated. 1-4 stereom types identified in median and proximal columnals. 5-6 stereom types identified in distal columnals.

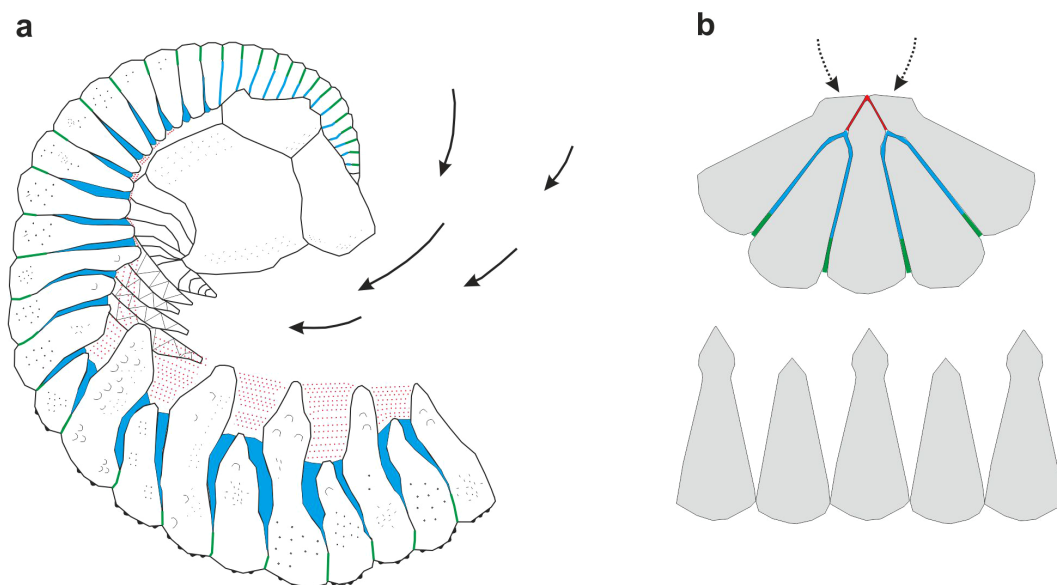


Figure 8 | Reconstruction of life time position of *Ammonicrinus*. (a) Enclosure of the ammoniacrinid crown in response to the external stimuli. (b) Schematic sketches of LCEE (lateral columnal enclosure extensions) of the mesistele in coiled (above) and uncoiled (below) positions. Modified from ref. 28. Inner ligaments (blue), outer ligaments (green), muscles (red).

it was controlled by muscles, not by MCT as previously hypothesized²⁸. On the other hand, bellow-like partial opening might have been enabled by the outer MCTs which could have been stayed taut when the muscles contracted and following the relaxation of muscles, the stem could have been snapped back by its tensionally loaded ligaments. However, although this hypothesis cannot be excluded, because of the relatively small surface area of muscles compared to the area of MCTs on the remainder of the columnal facet, this remains speculative. It seems obvious that the opening of the stem would have been much more passive than closing. The opening could have only been facilitated by water currents or slow MCTs motion. Similar situation can be observed in the arms of living crinoids, where there are only two small orally-located fields for the attachment of the adoral muscles and larger aboral ligaments holding the arms flexed aborally. Given the above, the feeding of ammoniacrinids by stem-pumping mechanism²⁸ should be viewed with caution. It seems reasonable that the ability to rapidly enclose the ammoniacrinid crown was not connected with feeding but rather with protection against external stimuli such as predators⁴⁸.

A key conclusions from the presented data is that muscles might have not been necessarily confined to the crinoid arms. Importantly, it seems that muscular articulations must have been acquired independently in the Devonian flexible crinoid *Ammonicrinus*. So far, it has been widely accepted that muscles have evolved only once, during the Early Devonian². Among various crinoid clades, only advanced cladids and their post-Paleozoic descendants are believed to have developed muscles. Our study shows that representatives of another crinoid clade (*Flexibilia*) might have also evolved muscles as connecting tissue between adjacent plates. The question concerning why two independent crinoid clades (which diverged in the early Paleozoic) utilized muscles at around the same time (during the Devonian) is difficult to answer. The presence of muscles certainly served a significant advantage for feeding, locomotion and predator avoidance. As highlighted above, at least in the case of ammoniacrinids, the necessity to cover the tiny crown by coiling the stem and the development of spines, could be particularly linked to the increased predation pressure during the so-called Middle Paleozoic Marine Revolution (MPMR)^{49–53}. During this time, diversification of various groups of predators (placoderms, sarcopterygian fishes, platyceratid gastropods) took place, resulting in anti-predatory adaptations among benthic invertebrates^{49–51}.

Methods

52 variously oriented thin sections of several distal and median columnals (Fig. 2) polished down to about 25 μm were coated with carbon and examined with a cathodoluminescence (CL) microscope equipped with a hot cathode at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw. The CL images were recorded with Kappa video camera. CL-emission spectra of selected specimens were analysed using a UV-VIS spectrograph. The following parameters were used for both CL microscopy and spectroscopy: an electron energy = 14 keV, a beam current = 0.1–0.2 mA, and integration times for CL-emission spectra of luminescent samples = 100 s.

A few additional thin sections were analysed with the aid of the Energy Dispersive Spectroscopy performed on a Scanning Electron Microscope Philips XL–20 coupled with the EDS detector ECON 6, system EDX-DX4i at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw using the following parameters: accelerating voltage = 25 kV, working distance = 34 mm, a beam diameter $\sim 5 \mu\text{m}$. The microstructure of the articular surface of a few well preserved median columnals was also SEM investigated.

The specimens are housed at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (ZPAL.V.42D/1–52).

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Author contributions

P.G., E.G. and M.A.S. designed research. E.G. carried out field excavation. P.G. conducted microstructural analyses. All authors contributed to the discussion and writing of the paper.

Additional information

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