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Unlocking the secrets of the Early Jurassic of North Africa: first record of pseudoplanktonic crinoid *Seirocrinus* (Crinoidea, Pentacrinidae) from Morocco and Algeria

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ABSTRACT
The Pliensbachian (Lower Jurassic) age-based Lower Marly Limestone Formation of the Moulay Idriss Zerhoun area (Morocco) and the Ain Ouarka Formation of the Ksour Mountains (Algeria) have yielded rare crinoids. Although crinoids have previously been described from the Jurassic of Algeria, their Pliensbachian occurrence is being reported here for the first time. On the other hand, one isocrinid taxa [*Terocrinus subsulcatus* (Münster in Goldfuss)] was also recorded from the Pliensbachian strata of Morocco. Additionally, now, from both Morocco and Algeria, *Seirocrinus subangularis* (Miller), belonging to the family Pentacrinitidae, is documented. This is a cosmopolitan and pseudoplaktonic crinoid species that is well-known from Asia, Europe, and North America. The taxonomic evaluation of the genus *Seirocrinus* is provided. The present records from Algeria and Morocco are the first finds of *Seirocrinus* from the African continent. *Ticinocrinus moroccoensis* sp. nov. represented by a cup of a rare cyrtocrinid (Cyrtocrinida) is associated with *S. subangularis* from Morocco. Globally, this is the second record of the genus; the first *Ticinocrinus* being described from the Pliensbachian of Switzerland. Thus, the present records from Morocco and Algeria are also the oldest cyrtocrinids from the southern margin of the Tethys.

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KEYWORDS
Africa; Morocco; Algeria; Jurassic; echinoderms; crinoids

Previous research on Jurassic crinoids from Morocco and Algeria

Morocco

Five isocrinid (Isocrinida) taxa have been mentioned previously from the Jurassic of Morocco. First, Abrard (1920) recorded *Chladocrinus jurensis* (Quenstedt 1852) (= *Isocrinus* (*Chladocrinus*) *jurensis)*; see, e.g., Hess and Messing (2011) from the Toarcian of the South Riffian Ridges in northern Morocco. Later, Termier and Termier (1949), from the same area, suggested the presence of *Chariocrinus cristagalli* (Quenstedt 1852) and *Chladocrinus bajociensis* (d'Orbigny 1850–1852) (= *Isocrinus* (*Chldocrinus*) *bayocensis*) in the Bajocian–Bathonian, *Balanocrinus pacomei* de Loriol (1879) in the Bathonian and *Terocrinus subsulcatus* (Goldfuss, 1826–1833) in the Pliensbachian strata.

Benzaggagh et al. (2015) were the only authors to describe and illustrate Jurassic (late Oxfordian – late Tithonian) roveacrinids from the External Rif Chain in northern Morocco. These authors carefully examined ossicles in thin sections and classified them into 47 types of skeletal sections and assigned them into 6 different groups, based on their geometric shapes. They concluded that the stratigraphic distribution of the investigated skeletal sections allowed to identify 7associations corresponding to relative frequency biozones for the late Oxfordian – late Tithonian interval. According to the authors, these biozones can be correlated with the ammonite zones.

Algeria

Several taxa of stalked crinoids have been recorded from the Jurassic deposits of Algeria; however, many of them need to be revised, especially the millericrinids (Millericrinida), as their finds consist only of isolated columnals.

D'Orbigny (1850–1852), Coquand (1852, 1854, 1862), Peron (1883) and Sieverts-Doreck (1939) mentioned *Chladocrinus tuberculatus* (Miller 1821) (= *Isocrinus* (*Chladocrinus*) *tuberculatus*), from several Sinemurian (Lower Jurassic) localities in the central and northern parts of Algeria. De Loriol (1882–1889) added another isocrinid, *Balanocrinus peroni* (de Loriol, 1882–1889), which is commonly reported from the Upper Jurassic of Algeria. Termier and Termier (1949) mentioned the occurrence of *Margocrinus pentagonalis* (Goldfuss, 1830) (= *Balanocrinus pentagonalis*) in the Callovian–Oxfordian deposits of Algeria.

Coquand (1880), de Loriol (1882–1889), and Stefanini (1932) described and illustrated millericrinid pluricolumnals from the Lower – Upper Jurassic of various regions of Algeria and classified them into 16 different species, *Apiocrinus* sp., *Apiocrinus crassus* (d'Orbigny, 1850–1852), *A. hodnaensis* Coquand (1880), *A. infinitesimalis* Coquand (1880) *A. münsterianus* d'Orbigny, 1850–1852, *A. murchisonianus* d'Orbigny, 1850–1852, *A. roissyanus* Orbigny, 1850–1852, *Millericrinus* sp., *M. boissieri* Pictet, 1863-1868, Coquand (1880), *M. hirsatus* Coquand (1880), *M. thotellierei* Coquand (1880), *M. peroni* de Loriol, 1882–1884,*M. polydactylus* d'Orbigny, 1850–1852, *M. reboudi* Coquand (1880), *M. sparsinodus*

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Coquand (1880), *M. status* (Quenstedt 1852). Rasmussen mentioned (1961) in Upper Jurassic? strata of Algeria a millericrinid taxon, *Apiocrinites*? *boissieri* (Quenstedt 1867), but the author did not illustrate the specimen of this species nor its specific locality.

Unexpectedly, 'percevalicrinids' have been reported from the Pliensbachian of Algeria (Salamon et al. 2023), suggesting that this crinoid group appeared in the fossil record about 40 million years earlier than previously assumed.

Geological background

The Maghrebian Cenozoic orogenic domain extends parallel to the northern part of Africa, between the Mediterranean Sea and the Saharan platform. It is classically separated into two distinct systems: the Tell-Rif (Tell in Algeria and Tunisia; Rif in Morocco) and the Atlas (Figure 1A); both, during the Mesozoic, were parts of the southern margin of the western Tethys. Their geodynamic evolution since Triassic times (Roca et al. 2004) comprises of: (a) a rifting episode during the Late Triassic and Early Jurassic; (b) a post-rift episode of thermal subsidence and Tethyan oceanic accretion from the Middle Jurassic up to the Late Cretaceous; and (c) episodes of convergence and compression? during the Cenozoic.

At the end of Triassic and probably the beginning of Hettangian (Lower Jurassic), the northen Maghreb (north of the South Atlas Fault) was formed by continental lands and large sabkhas extending far south up to the lower Sahara (Choubert and Faure-Muret 1960–1962). Volcano-sedimentary events occurred, related to the first rift activities and are well-recorded all around the future central Atlantic Ocean. During the Early Jurassic (Hettangian–Toarcian), extended carbonate shelf, post-dating the Triassic rifting, was established all over the northen Maghreb. From the Pliensbachian (Carixian–Domerian) to the early Bathonian, open shelf conditions were developed in the Atlas domain (Kazi Tani 1986; El Kochri and Chorowicz 1996) in response to the persistent of thermal subsidence (Piqué et al. 2002). The Middle Jurassic – Late Cretaceous sedimentary record has been attributed to successive cycles of sea-level fluctuations during a post-rift stage which was unaffected by significant tectonic deformations (not necessary) (Frizon de Lamotte et al. 2008).

(1) Fringing the west Mediterranean Sea, the Alpine Tell-Rif chain (Durand-Delga and Fonboté 1980), resulted from the closure of the western end of the Tethys Ocean. It includes three main structural and palaeogeographic domains, from north to south: (a) the internal zones belonging to the AlKaPeCa (AlKaPeCa for Alboran, Kabylie, Peloritan, and Calabria) microcontinent, that originated from the former northern European margin of the Maghrebian Tethys; (b) the Maghrebian flysch nappes, regarded as the former sedimentary cover of the Maghrebian Tethys; and (c) the external

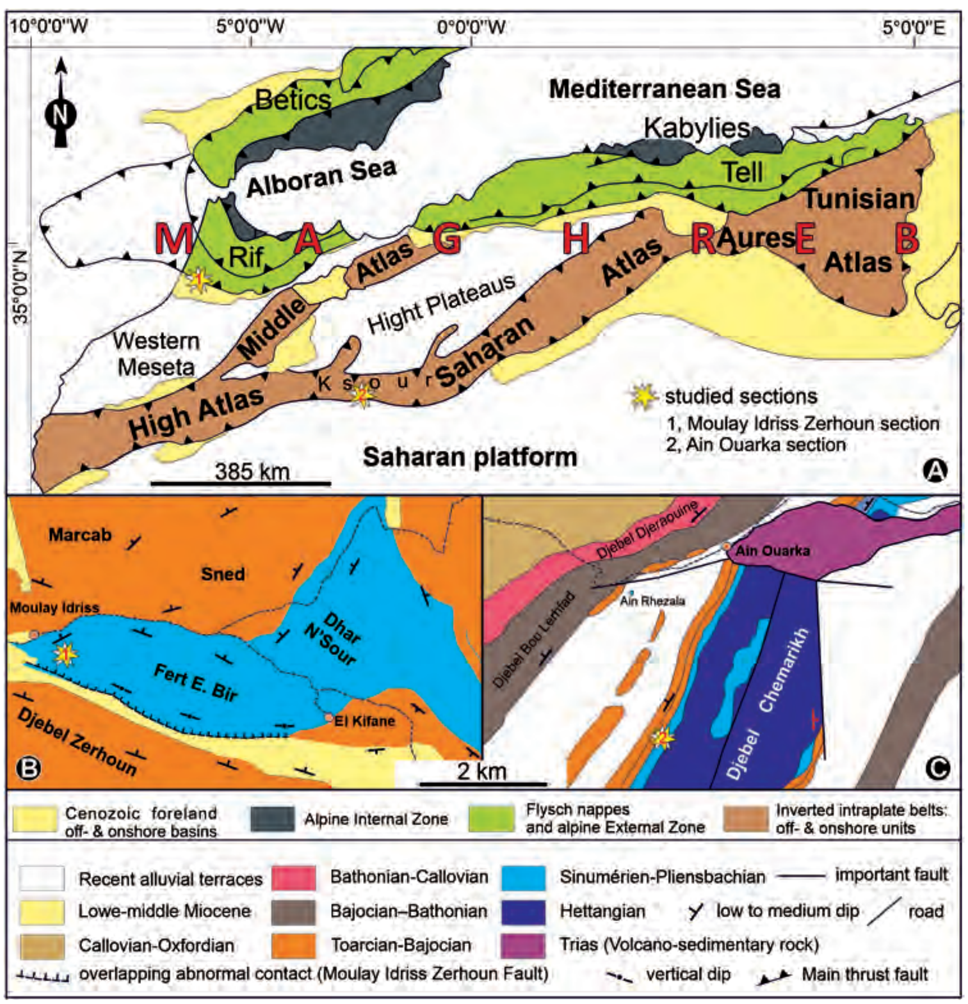

Figure 1. Geographic and geological framework of the study area. A. Structural scheme of the Western Mediterranean region (modified after Etheve et al. 2016). The structural features are shown, differentiating the Alpine and intracontinental belts, respectively. B, C. Simplified geological maps of Moulay Idriss Zerhoun (South Riffian Rides domain, B) and Ain Ouarka (Ksour Mountains, C) areas showing the position of the Jurassic formations bearing crinoid species described in the text.

zones, located between the Flysch trough and the Atlas domains, interpreted as the North-African palaeomargin inverted during the Cenozoic collision. The studied Moroccan section is located in the southwestern foreland of the Rif Belt.

(2) The Atlas domain is a mountain range that extends more than 2,500 km from the Atlantic Ocean (the western end of the Moroccan High Atlas) to Algeria (the Saharan Atlas) and the Pelagian Sea (the eastern end of the Tunisian Atlas). It is an 'intracontinental' chain (i.e. intraplate) developed in the foreland of the Tell-Rif belt at the site of a pre-existing continental extensional basin (Mattauer et al. 1977). Within the Atlas belt, several segments are distinguished: the N70°E trending High Atlas and the N45°E trending Middle Atlas in Morocc; the N60°E trending Saharan Atlas s. str. (*sensu stricto*) and the Aures-Mellegue in Algeria. These latter two chains are separated by the nearly E-W Zibane Zone. In Tunisia, the Atlas system is composed of the Tunisian trough, or 'Diapir zone' which forms the northernmost part of the Atlas chain, and the Tunisian Atlas s. str. comprising the Central and the Southern Tunisian Atlas. The Saharan Atlas s. str. extends SW-NE approximately about 700 km, between the Moroccan High Atlas and the Aures Range. And is subdivided into a series of subranges (Ritter 1902): the Ksour Mountains to the west, the Djebel Amour in the centre, and the Ouled Nail Mountains to the east. The studied Algerian section is situated in the western segment of the Saharan Atlas (Ksour Mountains).

Position of the study Jurassic formations

The studied crinoids (Pliensbachian in age) come from two formations: the Lower Marly Limestone Formation in the Moulay Idriss Zerhoun area (NW Morocco; UTM coordinates: N34°3'362"; W5° 30'728", southwestern foreland of the Rif Belt, Figures. 1A and 2A) and the Ain Ouarka Formation in the west of Djebel Chemarikh (UTM coordinates: N32°42'51.10"; W0°9'49.30", western of the Saharan Atlas Range, Figures. 1C, 3A and B).

Description and age of the studied formations

The Lower Marly Limestone Formation (Morocco)

In the Moulay Idriss Zerhoun area (NW Morocco, Figure 1A,B), the Lower Jurassic deposits crop out immediately to the north of the Moulay Idriss Zerhoun Fault (Figure 1B), forming two large outcrops: the Fert El Bir anticline, extending E-W between the Moulay Idriss village and the El Kifane locality, and the Dehar N'Sour anticline to the east.

The Pliensbachian sequence consists of four informal formations (Faugères 1978), from bottom to top: the Cherty Limestone Formation (20 to 25 m-thick, middle Carixian – lowermost upper Carixian); the Lower Marly Limestone Formation (30 to 100 m-thick, upper Carixian – lower Domerian); the Intermediate Bedded Limestone Formation (50 m-thick, uppermost lower to middle Domerian); and the Upper Marly Limestone Formation (0 to 80 m-thick, uppermost middle to upper Domerian).

The studied crinoids come from the Lower Marly Limestone Formation (Figure 2), which was sampled at a site located near the thermal spring of Moulay Idriss Zerhoun. This formation consists of irregular alternations of marl (up to 5 m-thick) and decimetric-thick limestone beds (Figure 2A,B), with a rich fauna of brachiopods (spiriferids, rhynchonellids, and terebratulids) and bivalves (mainly pectinids and *Pholadomya*), belemnite rostra, rare nautiloids, ammonites, and iron oxide concretions. The trace fossil, *Thalassinoides* occurs as horizontal traces on the lower bedding surface of limestone beds (Figure 2C). Faugères (1978) recorded the following Pliensbachian ammonites: *Liparoceras* (*Becheiceras*) gr. *bechei-gallicum* Spath (Ibex Zone, middle Carixian – Gibbosus subzone, middle Domerian), *Protogrammoceras celebraum* (Fucini) (Stokesi subzone; lower Domerian, and *Prodactylioceras italicum* (Fucini) (Davoei Zone, Maculatum subzone–Margaritus Zone, Stokesi subzone; upper Carixian – lower Domerian; see Meister et al. 2011) thus, spanning an age from the Maculatum subzone (upper Carixian; lower Pliensbachian) to the Stokesi subzone (lower Domerian; middle Pliensbachian).

The Ain Ouarka Formation (Algeria)

The Lower Jurassic succession in the Ksour Mountains is exposed near the village of Ain Ouarka (Figures. 1B and 3A). Mekahli (1998) proposed for the succession three formal subdivisions (from bottom to top): the Chemarikh (Hettangian – Sinemurian); the Ain Ouarka (Sinemurian – Pliensbachian); and the Ain Rhezala (Toarcian). The studied crinoids are from the upper part of the Ain Ouarka Formation.

This last formation overlies the Chemarikh Formation and is overlain by the Ain Rhezala Formation (Figure 3A). Based on its respective facies and stratonomic patterns, the Ain Ouarka Formation was divided into two informal members: the chert-bearing limestone-marl and the spaced limestone-marl alternation. The first member consists of regular and monotonous alternations of thin, hard, cherty sublithographic limestone beds (5–4 cm-thick) and dark green interbedded marl (5–2 cm-thick). The limestone beds contain ammonites and belemnites. The deposits are mainly mudstones and wackestones containing sponges, radiolarians, microfilaments (i.e. fragments of thin-shelled bivalves), benthic and planktonic foraminifers, and echinoderms.

The second member (Figure 3B) consists mainly of green laminated marl (10–50 cm-thick) with grey limestone (5–10 cm-thick) alternations, containing ammonites (Figure 3C) and belemnites. The limestone beds, laterally continuous over hundreds of metres, have undulating basal and/or upper surfaces. The microfacies is mudstone to wackestone containing microfilaments, spherical radiolarians, planktonic foraminifers, and rare calcispheres. Interbedded marls yielded foraminifers and stalked crinoids.

The lower part of the chert-bearing limestone-marl member was dated by Bassoullet (1973) and Mekahli (1998) as lower-upper SinemurianSemicostatum and Turneri ammonite zones, based on the occurrence of *Asteroceras* sp., *Arnioceras miserabile*, *A.* aff. *semicostatum* and *A.* cf. *speciosum* and the Obtusum Zone characterised by the presence of *Asteroceras* sp., *A. meridionale, A.* aff. *margarita*, *Phylloceras* sp., *Lytoceras* sp. and *Gleviceras* gr. *doris*. The spaced limestone-marl alternation member yielded ammonites of (a) the Sinemurian – lower Pliensbachian transition *Oxynoticeras* sp., (b) the Ibex Zone (lower Pliensbachian) by *Tropidoceras mediterraneum*, *T. calliplocum*, *Protogrammoceras* sp., and *Lytoceras* sp., (c) the Davoei Zone *Protogrammoceras* cf. *volubile, Juraphyllites* sp., *Phylloceras* sp., *Lytoceras* sp., (d) the Algovianum Zone by

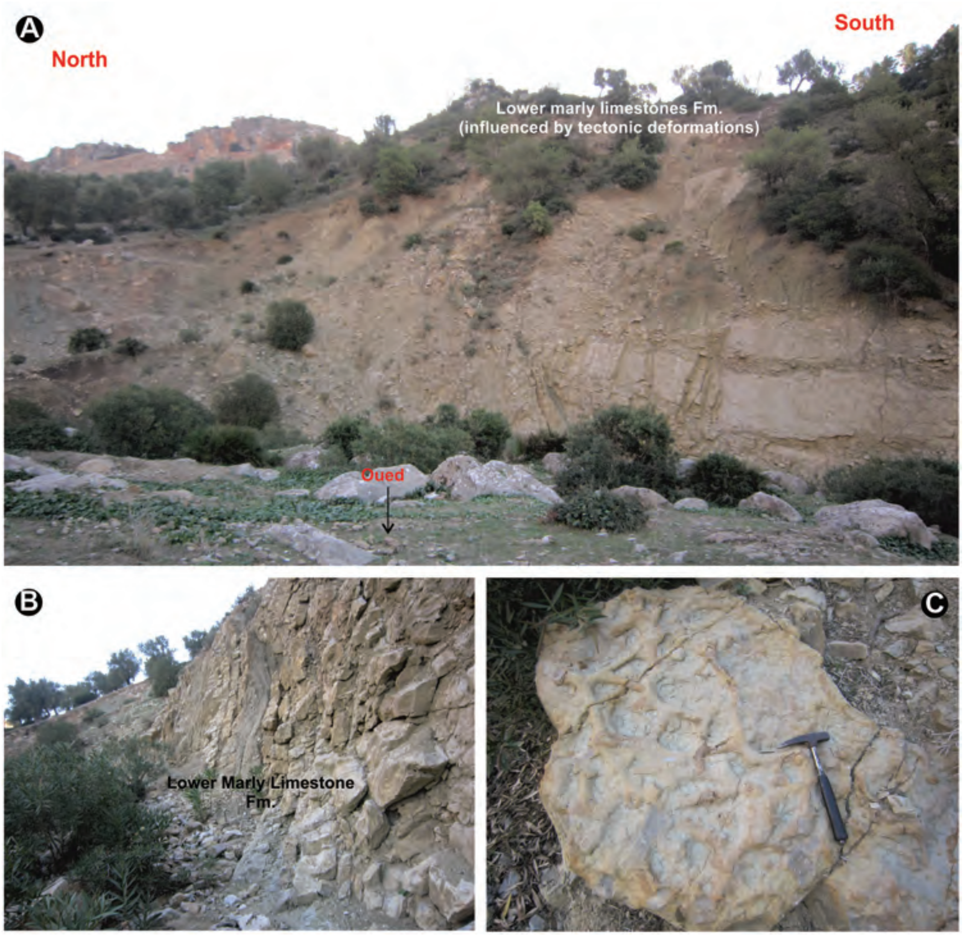

Figure 2. Outcrop pictures of the Lower Marly Limestone Formation near Moulay Idriss Zerhoun town. A. Panoramic view showing deformed, centimetric to decimetric, limestones interbedded with green marl; B. Detail view of rhythmic limestone-marl alternations. C. Horizontally Y-shaped branching burrows (*Thalassinoides* network) at the base of a limestone bed.

Reynesoceras sp., *Protogrammoceras* sp., *Arieticeras algovianum*, *Lioceratoides* aff. *inclytum*, *Arieticeras* gr. *bertrandi*, *Protogrammoceras* gr. *bonarelli* and brachiopods (*Pygope aspasia* and *Securithyris erbaensis*), and (e) the Emaciatum Zone by the presence of *Tauromeniceras elisa* (see also Bassoullet 1973; Mekahli 1998 for details).

Remarks on the Pliensbachian palaeoenvironment of the two study sections

The fine-grained crinoid-bearing sediments of the studied Moroccan and Algerian sections are interpreted as suspension deposits in a low-energy and a deep outer shelf/ramp (below the storm wave base) setting. This inference is based on the abundance of open marine environment macrofauna (ammonites) and microfauna (thin-shelled bivalves, calcispheres, pelagic crinoids (roveacrinids), and radiolarians) (e.g. Lukeneder et al. 2012). This setting is also supported by the lack of neritic benthic macrofauna and the absence of sedimentary structures (such as hummocky cross-stratification). An outer shelf (outer ramp) environment was also proposed by Mekahli (1998) and Salamon et al. (2023) for the Lower Jurassic rocks of the Ain Ouarka area (Algeria) and by Faugères (1978) and Benzaggagh (2020) for the Pliensbachian deposits of the Moulay Idriss Zerhoun area (Morocco).

Materials and methods

The first step consisted of the examination of slab surfaces in the field in Morocco in 2022. Unfortunately, during this stage, the crinoids or their remains were not documented. In parallel with this phase of work, MAS and MB collected indurated samples in the field in 2022. Their total weight was 6.5 kg. Samples were transported to the Laboratory of the Faculty of Natural Sciences, Institute of Earth Sciences, Poland, at the University of Silesia in Katowice, Poland. Samples were soaked with Glauber's salt; they were boiled and frozen five times. The residues were then washed under running tap water and sieved on a sieve column (Ø1.0, 0.315, and 0.1 mm mesh sizes). The final step consisted of drying the respective washed residues at 180°C. Residue was hand-picked for the microscopic study.

The Algerian marls and limestones were sampled at more or less close intervals; loose samples (marls) were soaked in water for several days and then washed in a series of sieves with decreasing mesh sizes (300 µm, 250 µm, 180 µm, 125 µm) under a strong jet of water. The

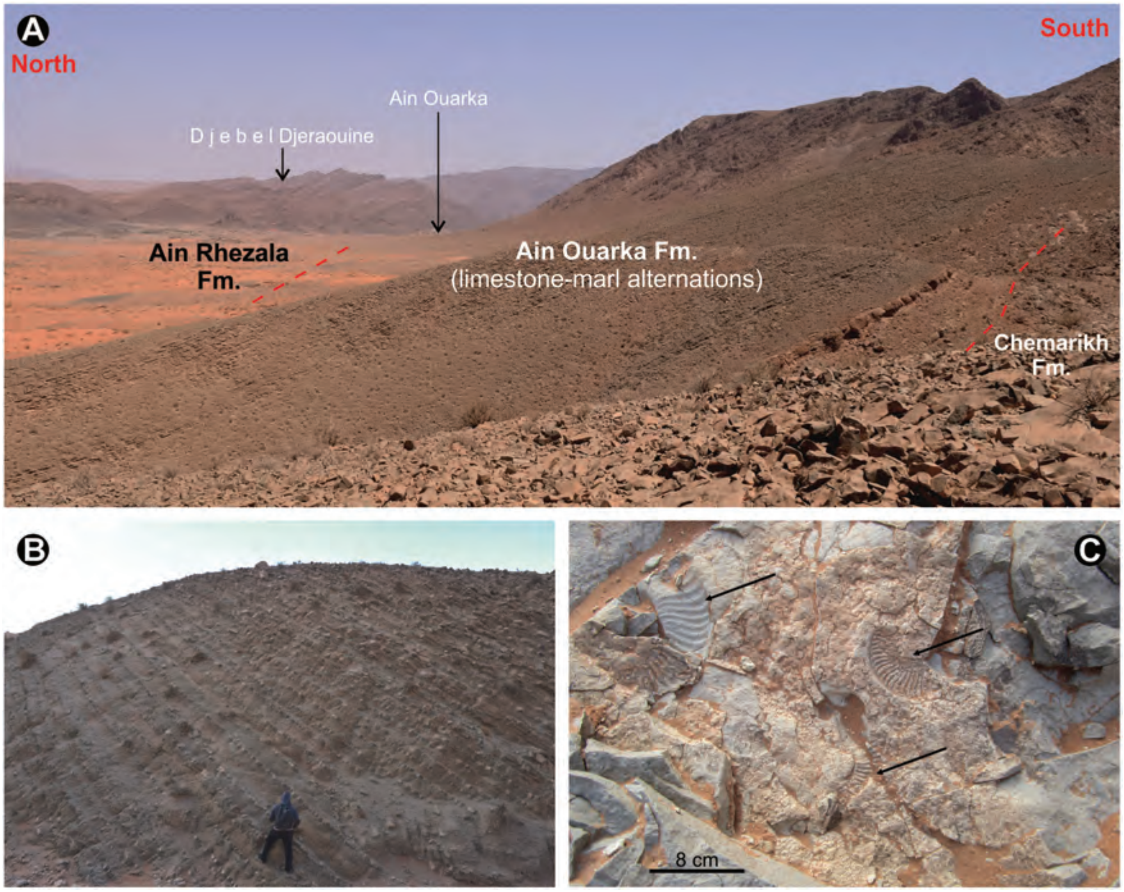

Figure 3. A. Panoramic view showing the study succession close to the Ain Ouarka village. B. Detail view showing spaced limestone-marl alternation member of the upper part of the Ain Ouarka Formation. C. Ammonite-rich limestone interbedded within the spaced limestone-marl member.

residues recovered from each sieve were dried and steamed and then sorted with a Euromex Dz and Optika ST-40-2 L binocular magnifier to pick out the micropalaeontological content. For hard samples, thin sections were made for both microfacies and microfaunal purposes.

The collected crinoids were photographed with a scanning electron microscope (SEM) of the Hitachi S-4700, housed at the Institute of Geological Sciences, Jagiellonian University in Kraków, Poland, and a Canon D530 camera at the Institute of Geological Sciences, University of Silesia in Katowice, Poland.

All studied crinoids are housed at the University of Silesia in Katowice, Faculty of Natural Sciences, Institute of Earth Sciences, Poland, under catalogue number: GIUS 8–3689/1–9.

Results

The remains of bivalves, brachiopods, belemnite rostra, one crinoid cup classified as a new species, *Ticinocrinus moroccoensis*, and one columnal and three pluricolumnals of *Seirocrinus subangularis* (Miller) were recorded in the analysed residue from Moroccan samples. In the case of the Algerian washed sediment residue, five seirocrinid columnals were collected associated with foraminifers, echinoids, asteroid and ophiuroid remains.

The present article characterises in detail the pentacrinitid crinoid *Seirocrinus* columnals and pluricolumnals from the African continent (Morocco and Algeria). A cyrtocrinid (Cyrtocrinida Sieverts-Doreck) cup classified as *Ticinocrinus moroccoensis* n. sp., is also described from the Pliensbachian strata of Morocco.

Systematic palaeontology

Isocrinids

Order Isocrinida Sieverts-Doreck, 1952
Suborder Pentacrinitina Gray, 1842
Family Pentacrinitidae Gray, 1842
Genus *Seirocrinus* Gislén, 1924

Type species

Pentacrinites subangularis Miller (1821), p. 59 [= *Pentacrinites fasciculosus* von Schlotheim (1813), p. 56, nom. nud.; = *P. bollensis* von Schlotheim (1813), p. 56, nom. nud.; = *Pentacrinus hiemeri* König (1825), p. 2; = *Extracrinus lepidotus* Austin and Austin, 1847, in 1843–1849, p. 106; = *Pentacrinites briaroides* Quenstedt (1852), p. 607; = *Pentacrinites colligatus* Quenstedt (1852), p. 608].

Seirocrinus subangularis (Miller, 1821)
Figure 4

1755. *Pentacrinites fusciculosus* Knorr, pl. 11b
1755. *Pentacrinites bollensis* Knorr, pl. 11c
1821. *Pentacrinites subangularis* Miller, p. 59, pl. 1, pl. 11, Figs. 1–5

Material

Six columnals (or their fragments) and two pluricolumnals from Morocco and Algeria.

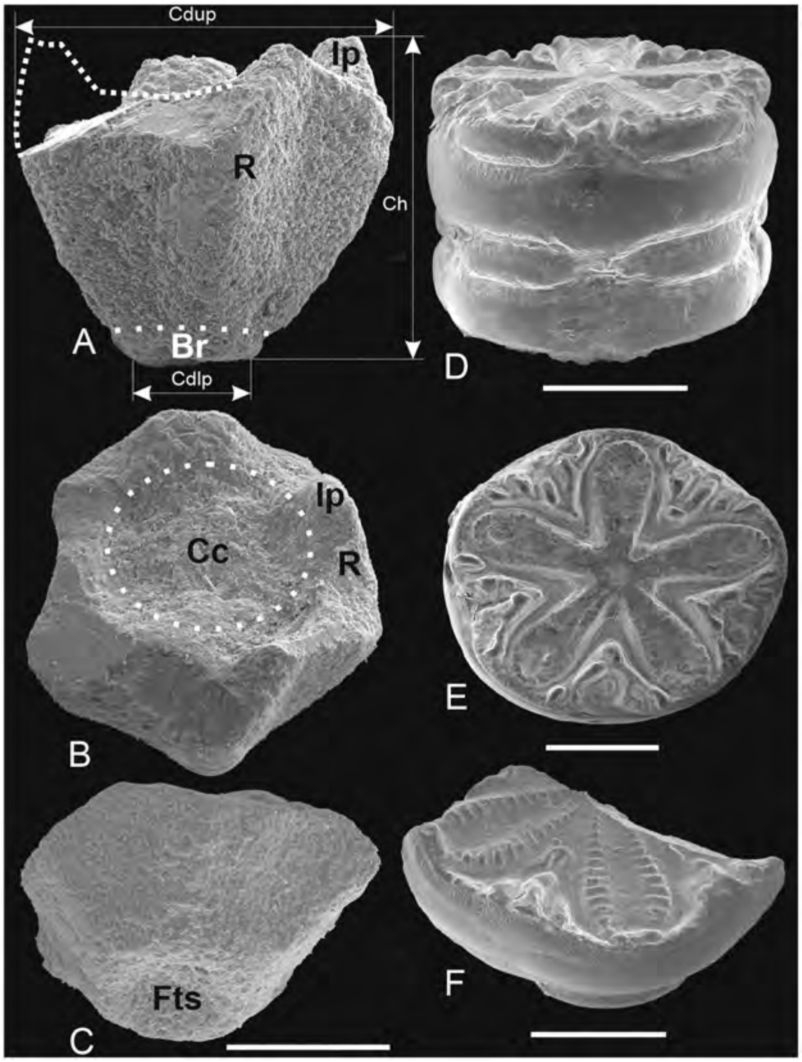

Figure 4. Crinoids from the Pliensbachian of northern Africa. Acronym number: GIUS– 3689/9, 1–3 respectively. Scale bar equals 1 mm. A-C. Cup of *Ticinocrinus moroccoensis* new species. Morocco. A. Lateral view. B. Upperside view. C. Lowerside view. Ip – interradial process, R – radial, Br – brachial ring, Cc – central cavity, Fts – facet to stem, Cdlp – cup diameter in the lowermost part, Cdup – cup diameter in the uppermost part, Ch – cup height. D-E. pluricolumnal and columnals of *Seirocrinus subangularis* (Miller 1821), Morocco and Algeria. D – oblique view of pluricolumnals. E – columnal, facet. E – oblique view of partly preserved columnal.

Repository

Laboratory of Palaeontology and Stratigraphy of the University of Silesia in Katowice, Poland. Catalogue number: GIUS 8–3689/1–8.

Description

Columnal diameter ranges from 1.7 mm to 3.9 mm. Pluricolumnal height varies from 2 mm to 4 mm. Distal columnals are pentagonal to rounded pentagonal; larger distal columnals are circular but in some cases, they are even subcircular. All proximal columnals are subpentalobate. The most proximal columnals are low, and there is a characteristic alternation; it is not distinct from those farther distally. Distinct intercalation is visible in the internodal. It is clearly visible throughout the entire pluricolumnals. First-order internodal and nodal columnals are the largest among all the columnals. They are progressive in diameter for subsequent orders of internodals. Articulation between all columnals is symplectial. Petal floors are narrow and pyriform. Their maximum width is at their outer end. Petal floors are surrounded by a maximum of 36 thin and small crenulae. They decrease in size towards the inner end of the petal floors. All petals are separated by rugose areas; rugose areas are large and triangular and interlock on adjacent columnals. Cirri scars are small. Their width is 12–24% of the nodal diameter. A sharp and narrow cupule occurs above the cirri scars. The lateral surface is smooth or inflated. Lumen is small and circular.

Distribution

According to Simms (1989), there are two Triassic and Lower Jurassic *Seirocrinus* species [*S. subangularis* (Miller 1821) and *S. klikushini* Simms (1989)]; however, Klikushin (1992) argued that there are three other species [*S. acutipelvis* (Quenstedt 1876), *S. alaska* (Springer 1925), and *S. laevisutus* (Pompeckij 1897)], and their stratigraphic range is Late Triassic (Norian) – Middle Jurassic (Bathonian) of Asia (Indonesia, Turkey), Europe (Austria, Bulgaria, England, France, Germany, Hungary, Luxembourg, Portugal, Romania, Switzerland), and North America (Canada, USA). Klikushin (1992) noted that the remains assigned to '*Pentacrinus* ex gr. *subangularis*' are from the Bajocian-Bathonian of eastern Siberia. These forms do not yet have names, but the existence of *Seirocrinus* in the Middle Jurassic is certain.

Figure 5. *Seirocrinus subangularis* from the collection of Centre for Nature Education, Jagiellonian University in Kraków, Poland, acronyme number: CEP-DG -775. Place of origin: Ohmeden, Germany. A. Stem portions. B. Stems portions with cirri (c).

Cyrtocrinids

Order Cyrtocrinida Sieverts-Doreck, 1952
Suborder Cyrtocrinina Sieverts-Doreck, 1952
Superfamily Eugeniacrinitoidea Roemer, 1855 in Bronn and Roemer, 1851–1856
Family Phyllocrinidae Jaekel, 1907
Genus *Ticinocrinus* Hess, 2006
Type species. *Ticinocrinus coronatus* Hess, 2006, p. 35–36.

Ticinocrinus moroccoensis new species
Figure 4

Type material

The holotype is housed in the Earth Sciences Museum, University of Silesia, Katowice, Poland, and is catalogued under registration number GIUS 8–3689/9. The specimen is from marlstones and limestones of late Carixian (Pliensbachian) age from the South Riffian Ridges, Morocco.

Etymology

moroccoensis, after the name of country of provenance, Morocco.

Locus typicus

The Roman Hot Springs in the Foothills of Mount Zerhoune, 500 m SE of the city centre of Moulay Idriss Zernoun; UTM coordinates: N34°3‘'362“”; W5°30‘'728‘'” (same as that of the section).

Stratum typicum

Lower Marly Limestone Formation, upper Pliensbachian, see Figure 2B.

Measurements

Cup diameter in lower part: 0.60 mm; cup diameter in its upper part: 2.10 mm; cup height: 2.18 mm (see Figure 4A).

Diagnosis

Cup small and pentalobate and comprised of five bulging, tall radials. Radial faces small and sunken. Radial cavity wide and deep. Interradial processes sharp. Basals are short, indistinct, and continuously pass into radials. Facet-to-stem circular.

Description

Cup is small. It is pentalobate and comprised of indistinct and low basal circles. Radials number five and are tall and bulging. Radial facets are small and sunken. They have smooth aboral surfaces. Radial cavity is wide and deep. Interradial processes are tall and sharply pointed. Facet to stem is circular and symplectial. It has a pronounced concave and circular central area.

Discussion

Previously, only one representative of the genus *Ticinocrinus* was known (e.g. Hess and Messing 2011). Hess (2006) erected this new genus with a single species, *Ticinocrinus coronatus* from the Pliensbachian of Switzerland. This form has pentalobate or star-shaped cups, consisting of five bulging, high and rather massive radials with small articular facets. They are deeply set within the blunt interradial processes. The basals of this taxon are very low but distinct and form a characteristic circlet. This is one of the features that distinguishes *T. coronatus* from *T. moroccoensis*. In the case of the latter, the basals are short, indistinct, and continuously pass into radials. The second difference is related to the shape of the radials in the aboral view; in *T. coronatus* they are more rounded, whereas in *T. moroccoensis* they are slightly sharper.

Distribution

Lower Jurassic (late Carixian, Pliensbachian) of Africa (Morocco).

Discussion

What are pentacrinitids?

Some authors (e.g. Bourseau and Roux 1989; Bourseau et al. 1991) treated all isocrinids as a homogeneous group and classified them in the family Pentacrinitidae d'Orbigny, spanning from the Middle Triassic (Anisian) to the Upper Jurassic (Oxfordian) (Klikushin 1992). The cited authors rejected the concept of two families for isocrinids (Isocrinida Sieverts-Doreck); the extinct Pentacrinitidae Gray, and the extant Isocrinidae Gislén as proposed by Rasmussen (1978).

Hess and Messing (2011) classified Pentacrinitina as a suborder, and the second suborder of Isocrinida was Isocrinina Sieverts-Doreck. The classification of Hess and

Messing (2011) is followed in this contribution. Hess and Messing (2011) noted that Pentacrinitina differs from Isocrinina in possessing endotomic branching of the arms, strongly cirriferous columns with laterally compressed cirri, and columnal articular facets with a distinctive pattern. In fact, their characteristic columnals and/or cirrals, safely and conclusively puts? classify them in the subfamily Pentacrinitina.

The family Pentacrinitidae consists of two genera: *Pentacrinites* Blumenbach and *Seirocrinus* Gislén. The column of the Middle Triassic (Anisian) – Upper Jurassic (Oxfordian) *Pentacrinites* is short (much less than 0.5 m), but sometimes it may reach up to 1 m [e.g. *P. fossilis* (Blumenbach).

The *Pentacrinites* columnals are pentalobate to stellate, sometimes subpentagonal in outline. Their articular facets have smooth radial areas, and their symplectial areolae are narrow. Internodes are short, and the proximal part of the stem has only nodal columnals exposed. The distal part of the *Pentacrinites* stem has a few internodals, commonly three or four larger and intercalated smaller internodals (e.g. Głuchowski 1987, pl. 23/1–8, 24/1–6, text-fig. 17/1; Simms 1989, pl. 2, figs. 1–12, 16, pl. 3, figs. 1–5, 7, 8, pl. 4, figs. 1, 2 and; Simms 1999, figs. 189, 191; Hess 1999, fig. 213; Seilacher and Hauff 2004, figs. 8a, 9c; Salamon and Zatoń 2007, Fig. 2e; Hess and Messing 2011, figs. 20, 21; Salamon and Feldman-Olszewska 2018, fig. 3H; Figure 5A, B here). The cirri are numerous and very long, narrow, and elliptical or rhombic in outline; they have aboral and adoral ridges. The *Pentacrinites* cirri covers the stem and cup completely; all pinnules are free (e.g., Głuchowski 1987, pl. 25, fig. 25/1–3; Simms 1989, pl. 2, fig. 15, pl. 4, fig. 3–6, 14; Seilacher and Hauff 2004, fig. 8B, 9A-E; Seilacher 2011, fig. 6b; Salamon and Feldman-Olszewska 2018, fig. 3I, J; Fig. 5B here).

The second representative of Pentacrinitidae, *Seirocrinus*, is known only from the Upper Triassic (Norian) – Middle Jurassic (Bathonian) deposits (e.g. Klikushin 1992). The stem is rounded, pentagonal, or circular in outline. The height of its internodes, in the distal part of long columns, gradually increases to more than 100 internodals. The nodals of *Seirocrinus* have five very small cirrus sockets and they are circular or subelliptical in outline. The columnal facets have symplectial areolae which are narrow elliptical to pyriform. The facets are bordered by numerous small crenulae. The radial areas are rugose (e.g., Simms 1989, fig. 5, figs. 1–12, 14, 15; Hall 1991, figs. 3-5; Klikushin 1992, pl. 1, figs. 9–12, pl. 2, fig. 3, pl. 3, figs. 3, 4, pl. 4, figs. 2, 3; Hess 1999, figs. 194–197, 199; Seilacher and Hauff 2004, figs. 2A, C, fig. 7; Hess and Messing 2011, fig. 23/1c; Matzke and Maisch 2019, figs. 2, 6; Hunter et al. 2020, figs. 1, 4). The cirri of *Seirocrinus* are short, slender, compressed, rounded, and rhomboidal in outline. Typically, they are adpressed in oblique furrows in the surface of the stem (e.g. Klikushin 1992, pl. 2, figs. 1, 2, pl. 3, fig. 5, pl. 4, figs. 1, 2; Seilacher and Hauff 2004, figs. 2B, 3B-H).

Hess and Messing (2011) also included the family Eocomatulidae Simms in the suborder Pentacrinitina that contained only one genus, *Eocomatula* Simms (Upper Triassic, Norian to Lower Jurassic, Pliensbachian). These authors also noted that *Eocomatula* shares a lot of apomorphic characters with Pentacrinitidae (e.g. endotomous arm branching and rhomboidal cirrals). Simms (1989), on the other hand, they considered *Eocomatula* to be a transitional form between Pentacrinitidae and Paracomatulidae; the latter group was included by Hess and Messing (2011) under order Comatulida. Hagdorn and Cambell (1993) noted that *Eocomatula* differs from *Paracomatula* considerably: *Eocomatula* has a thick column consisting of six to seven pentastellate nodals, cirrals with rhomboidal articula, and arms branching endotomously beyond the tertibrachials.

Seirocrinus representatives: overview and their distribution

Seirocrinus acutipelvis (Quenstedt, 1876)

Quenstedt (1876) described *Seirocrinus acutipelvis* (sub-*Pentacrinus*) from the Pliensbachian of Germany (Figure 6). Columnals of this taxon possessed petal floors that are surrounded by small and numerous crenulae. The crenulae decrease in size towards their inner ends. The petals are separated by rugose areas, and decrease in size towards the inner end of petal floors. The cirri of *S. acutipelvis* are small.

The presence of this taxon in the Lower Jurassic rocks of Germany was confirmed by de Loriol (1882–1889. Simms (1989) synonymised this form with *S. subangularis*, whereas Klikushin (1992) treated it as a separate species, although the latter author did not indicate the characters that would distinguish *S. acutipelvis* from *S. subangularis.*

Seirocrinus alaska (Springer, 1925) and *Seirocrinus klikushini* Simms, 1989

Springer (1925) identified *Pentacrinus* cf. *P. subangularis* Miller in a Black Island black shale outcrop in the Canning River (Alaska, USA) and, subsequently, described it as a new subspecies, *P. subangularis alaska* (= *Seirocrinus alaska*). Later, this subspecies was transferred to the genus *Seirocrinus*, as a separate species (Klikushin 1979, 1982, 1987).

As no other representative has ever been found in the Canning River, Springer (1925) suggested an Early Jurassic age for the crinoid remains on the premise that they were also known from the Early Jurassic of western Europe. Later, however, the same remains were found in northern Alaska in sediments that 'were so closely associated with the Triassic that was impossible to separate them' (Leffingwell 1919, p. 120). Stanton, in Martin (1926, p. 265) noticed that 'if crinoids confirm the Early Jurassic age, other invertebrates point to the Late Triassic'. These statements and finds from the northeast and far east of Russia led Klikushin (1979) to conclude that this taxon is present only in the Norian (Upper Triassic) (Figure 6).

According to Simms (1989), the available evidence suggests that Springer's original material is of Early Jurassic age and hence probably conspecific with *S. subangularis*. The Late Triassic material figured by Klikushin (1979, 1982) is a form quite distinct from the type species and was renamed by Simms (1989) as *Seirocrinus klikushini* Simms. Simms (1989) added that this species can be distinguished from *S. subangularis* by the consistently different number of brachials per brachitaxis and the lack of branching of the first endotomous side branch. He suggested that it may well be directly ancestral to the latter species, although the two species are separated by a large stratigraphic interval.

Seirocrinus laevisutus (Pompeckij, 1897)

The other *Seirocrinus* species is *Seirocrinus laevisutus* (Pompeckij 1897, sub *Pentacrinus*) = (*Extracrinus*) (= *Pentacrinus goniogenos* Pompeckij 1897; = *Pentacrinusrotiensis*; Springer 1918; = *Pentacrinus* Pompeckij; Biese 1937); (non *Pentacrinus levisutus* de Loriol, 1886 in 1882–1889 = *Chladocrinus*). Pompeckij (1897) described two co-occurring species, *Pentacrinus laevisutus* and *P. gonionenos*. The latter species has a pentagonal stem shape, but this one is in *P. laevisutus* circular and represents only the proximal parts of the stem of *S. laevisitus* (see Klikushin 1987). *Pentacrinus rotiensis* described by Springer (1918) from the Lower Jurassic deposits in the Roti Island, Indonesia has a stem and calyx structures similar to those of *S. laevisitus*. *S. laevisitus* and differs from the widespread *S. subangularis* in the structure of the base of the calyx and the smooth radial triangles on the facets. Forms of this

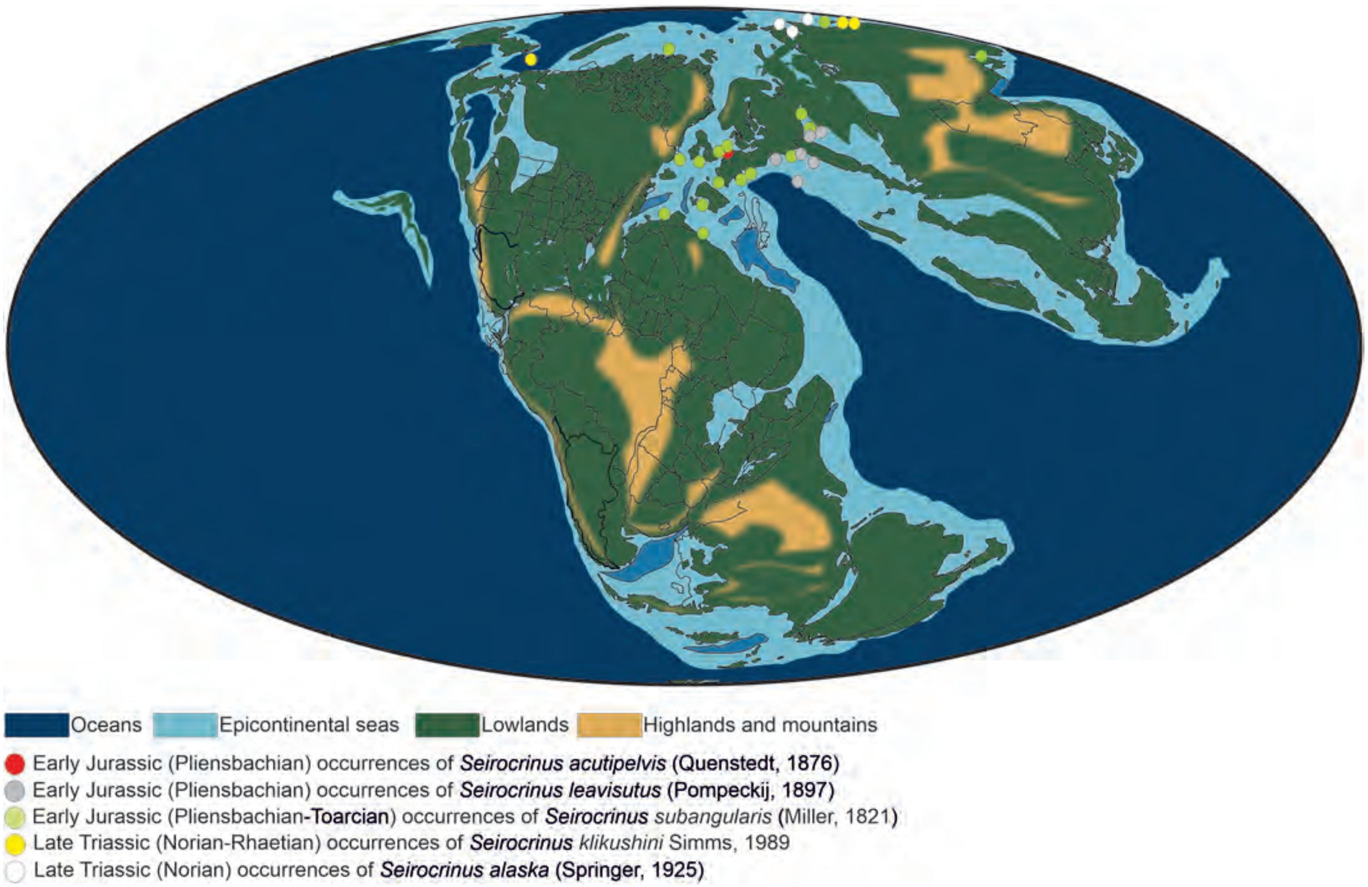

Figure 6. Palaeogeographic map showing the distribution of *Seirocrinus* during the Late Triassic – Early Jurassic. Maps modified after Scotese (2014) and Salamon et al. (2019, 2023). Data after references cited in subchapter 6.1.

type with characteristic articular facets of columnals of the form type are present in *S. subangularis* as described by many authors-from the Pliensbachian of Bulgaria, Hungary, Italy, Portugal and Spain (for details see Klikushin 1992). It can be assumed that these southern European finds assigned to *S. laevisutus* are widely distributed in the Tethys areas.

Nutsubidze et al. (1972, p. 179) mentioned the presence of '*Pentacrinus* cf. *laevisutus* Pompeckij and *P. margaritatus* Pompeckij' from the Lower Jurassic deposits of Mount Kakheti. Because in characterising the Early Jurassic strata of Georgia, the two names, *P. laevisutus* and *P. goniogenos,* are usually noted together. The latter author concluded that *S. laevisutus* is found in the Pliensbachian of Bulgaria, Georgia, Hungary, Indonesia, Romania, and Turkey (Figure 6).

Seirocrinus subangularis (Miller, 1821)

The latest representative of *Seirocrinus* is *S. subangularis* (Miller 1821, sub *Pentacrinites*). It is known from the Pliensbachian – Toarcian of Asia (Russia), Europe (Belgium, Bulgaria, England, France, Germany, Luxembourg, Portugal, and Switzerland), and North America (Canada): Miller (1821), Parkinson (1822), Schlotheim (1820–1823, 1825, 1832), Goldfuss (1826–1833, Klöden (1834), Roemer (1836), Bronn (1837–1838, Buch (1839), Leonhard (1840), Desor (1847), Quenstedt (1851, 1852, 1856, 1858, 1861, 1867, 1868, 1876, 1885), Bronn and Roemer (1851–1856 in Bronn and Roemer 1851–1856), Daubrée (1852), Morris (1854), Oppel (1854), Geinitz (1856), Moesch (1857), Chapuis (1858), Ooster (1865), Dumortier (1869), Choffat (1880), Loriol (1891), Hoernes (1884), Fox-Strangways (1892), Woodward (1893), Toula (1900), Schuchert (1904), Stolley (1910), Hauff (1921, 1936, 1960), Beringer (1926), Wanner (1934), Joly (1936), Putzer (1938), Stchépinsky (1946), Liniger (1958), Müller (1963, 1978, 1983), Krümbiegel and Krümbiegel (1979), Urlichs et al. (1979), Ebner and Graf (1986), Jäger et al. (1986), Simms (1988, 1989), Hall (1991), Klikushin (1992) and Hess and Messing (2011) (Figure 6).

Klikushin (1992), referring to reports from Toula (1886), noted that *S. subangularis* may also be present in the Lower Jurassic strata of Austria, and he pointed to the coexistence of two Lower Jurassic crinoids: *S.* cf. *subangularis* and *Hispidocrinus* cf. *scalaris* (Goldfuss, 1831 in Goldfuss 1826–1833). Since, Toula (1886) neither provided the description nor any illustration of *S. subanularis*, the presence of this species in Austria should be treated with caution. It should be noted that as the distal and median columnals of both species have a different structure of articular facets, the faces of the proximal columnals are very similar (compare pl. 1, fig. 6 to pl. 10, fig. 14 in Klikushin 1992). Klikushin (1992) also noted that reports of *S. subangularis* occurrences in the Liassic of China are mistaken. Sun et al. (1960), from the Guangdong Province in southeastern China, mentioned accumulations of *S. subangularis*. However, Klikushin (1992) stated that the reported columnals neither belong to the species *S. subangularis* nor to the genus *Seirocrinus*. Although, Chinese authors have certainly documented some representatives of the genus *Hispidocrinus*. Klikushin (1992), based on the different dimensions of the specimens, and the varying number of plates in the arms (often incompletely preserved), erroneously placed several species under *S. subangularis*. The latter author added that *S. subangularis* was supposed to be synonymous with the following taxa: *Pentacrinites bollensis* Schlotheim (1813) nom.

nudum; = *Pentacrinites fasciculosus* Schlotheim (1813) nom. nudum; = *Pentacrinus hiemeri* König (1825); = *Pentacrinites lepidotus* Austin and Austin, 1842 in 1843–1849; = *Pentacrinites briaroides* Quenstedt (1852). According to Klikushin (1992), the names '*subangulatus*' or '*angularis*' (e.g. Roux 1987) are simply clerical or typographical errors. Simms (1989), on the other hand, included several subspecies in the synonymies of *S. subangularis* [e.g. *Seirocrinus subangularis goldfussi* (Quenstedt 1876), *S. s. amalthei* (Quenstedt 1876), or *S. s. parvus* (Beringer 1926)]; but according to Klikushin (1992), there are characters that justify distinguishing them. *S. s. amalthei* (non *Pentacrinus basaltiformis amalthei* Fraas 1858 = *Chladocrinus*) and *S. s. goldfussi* (sub *Pentacrinus briaroides goldfussi*, non *Pentacrinites goldfussi* Roemer 1839 = *Millericrinus*) were listed in the Pliensbachian of Germany (Quenstedt 1876). The youngest *S. s. parvus* (Beringer 1926 sub *Pentacrinus*) (non *Isocrinus parvus* Howchin 1921 = *Pentacrinus australis*) occurs in the Toarcian of Germany (Beringer 1926).

Functional morphology and palaeoecology of Seirocrinus

Seirocrinus is an example of a pseudoplanktonic crinoid form with the longest stem ever noted in a crinoid taxa. Seilacher et al. (1968) pointed that the length of the internodes gradually increases and may reach more than a thousand columnals near the end of a 20-m-long stem. Simms (1989) noted that the largest seirocrinid stem could reach up to 26 m in length. Later, Simms (1986, 1999) tried to answer the question: why did these crinoids have such long stems? These crinoids probably produced huge amounts of larvae, which had to populate relatively rare drifting logs on the surface of the ocean. Then after, the larvae, colonise the driftwood, they must have grown very quickly, because, as stated by Simms (1999), seirocrinids could live up to 15 years. Recent experimental research by Hunter et al. (2020) showed that a colony of *Seirocrinus* living on a drifting log could live up to 20 years. Simms (1999) stated that a very fast growth rate is indicated by the growth lines on the arms. Crinoids achieved this through a highly efficient (endotomous) arm branching pattern. Wignall and Simms (1990) referred to the pentacrinitids (*Pentacrinites fossilis* and *Seirocrinus*) as 'all or nothing rule' in relation to their way of life, which means that they occurred on a piece of drifting tree trunk in great numbers and reached various sizes. On the other hand, other pieces of wood were to be completely devoid of crinoids. These authors explained that the larvae preferred to colonise those logs where their parents were already present rather than new inhabit , unoccupied ones. This constant supply of new crinoids added to the weight of the log and accelerated the collapse of the entire colony. As a result, each crinoid family committed a slow, inadvertent suicide. Recently, Matzke and Maisch (2019), studying the colonies of seirocrinids from the collection of the Staatliches Museum für Naturkunde, Stuttgart, Germany, proved the existence of two generations of these crinoids and, in the case of one log, considered highly probable the existence of a colony of four generations.

Seirocrinus did not have a holdfast, but a closely spaced rhomboidal in juveniles and rounded, short and slender cirri with a dense tuft of them acting as a holdfast attached to the driftwood. It is estimated that arm height might have reached as much as 50 cm, and the endotomous arm branching provided a very dense filtration fan (Hess 1999). Hess (1999) noted that on the large tree trunks floating near the sea surface, the large *Seirocrinus* must have been hanging down. Seilacher and Hauff (2004) and Seilacher (2011) claimed that pentacrinitids actively filtered their food using their densely packed cirri, which produced currents that carried food towards the arms. Hess (2010) refuted this view, suggesting that short and long stems are equally common in pentacrinids (see, e.g. Hess 1999, fig. 196). The latter author added that seirocrinids preferentially inhabited places of the least resistance and were bark-free, which were the most efficient places for attachment for tow-net filtrators. He suggested that the pseudoplanktonic crinoids fed by several mechanisms including tow-net filtration, capture of phytoplankton concentrated around logs, and zooplankton moving vertically in water during diurnal migration.

Remarks on similarities of Ticinocrinus *to other cyrtocrinids*

Hess (2006) distinguished a new genus, *Ticinocrinus,* which along with *Phyllocrinus* d'Orbigny, *Apsidocrinus* Jaekel and *Nerocrinus* Manni and Nicosia are included in the family Phylocrinidae Jaekel (Hess and Messing 2011). This new genus included one new species, *T. coronatus* represented by one pentalobate and a small calyx comprised of five bulging and high radials and five low basals (Hess 2006). Hess (2006) noted that morphologically similar forms to *Ticinocrinus* include *Nerocrinus* Manni and Nicosia; but, unlike *Nerocrinus*, the stem of *Ticinocrinus* is well-developed. However, the stem has never been documented. The only noted feature is the distinctly rounded, concave and broad facet of the stem of *Ticinocrinus* (e.g. Hess and Messing 2011, fig. 89/5b). According to Hess (2006), the peculiar shape of the calyx and apparently vestigial arms indicate that this genus may be more specialised than *Nerocrinus*. Hess (2006) also disagreed with Manni and Nicosia's (1999) opinion, who included *Nerocrinus* in the family Nerocrinidae within the order Dadocrinida (suborder Cyrtocrinina, superfamily Eugeniacrinitoidea), based on the presence of distinct basals. Further, Hess (2006) argued that the reduction, fusion or absorption of basals, is a relatively simple process that does not justify the creation of a new higher taxon.

The shape of the calyx of *Ticinocrinus* is also very similar to that of *Hoyacrinus* Delogu and Nicosia (1986); the family Hoyacrinidae, known from the Kimmeridgian (Upper Jurassic) in Italy, and *Fischericrinus* Castellana et al. (family uncertain), from the Bajocian (Middle Jurassic) of Italy. However, the two genera have no clear basals (for more details, see Hess 2006; Hess and Messing 2011).

The new species *Ticinocrinus morrocensis* n. sp. described here is the oldest cyrtocrinid recorded from Africa. The other African cyrtocrinids are *Apsidocrinus* Jaekel collected from a lower Albian (Lower Cretaceous) ammonite specimen (*Cleoniceras besairiei* Collignon) from Madagascar (Salamon et al. 2023); *Phyllocrinus* sp. from Barremian, and *Hemibrachiocrinus* sp. from Berriasian-Barremian (Lower Cretaceous) of Algeria (Benyoucef et al. 2022).

Conclusions

In the Pliensbachian strata of Algeria and Morocco (Africa), crinoid remains consisting of columnals and pluricolumnals of *Seirocrinus subangularis* (Miller) have been collected. *Seirocrinus* is a cosmopolitan planktonic crinoid previously known from Asia, Europe, and North America. The present find is the first record of *Seirocrinus* in Africa. In Moroccan strata, this crinoid genus was accompanied by the cyrtocrinid cup *Ticinocrinus moroccoensis*, a new species classified under the family Phyllocrinidae. This new species is the second representative of the genus *Ticinocrinus*; the first one is known from the Pliensbachian of Switzerland. This species is the oldest cyrtocrinid recorded from Africa, since the others African cyrtocrinids were recorded only from the Lower and the Middle Cretaceous strata of Algeria and Madagascar.

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Authors' contributions

M.A. Salamon: Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, writing original draft, writing, review and editing; M. Benyoucef: Data curation, field works, resources, software, writing original draft; M. Benzaggagh: Field works, writing original draft, writing, review and editing; İ. Hoşgör: Methodology, writing original draft; S. Jain: Investigation, methodology, writing original draft, writing, review and editing; B.J. Płachno: Investigation, writing original draft, writing, review and editing and; O. Rahmonov: Methodology, writing original draft. All authors read and approved the final proof.

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