Journal of Palaeogeography, 2023, 12(3): 434—447 (00307)

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Palaeobiology and palaeoecology

The unexpected occurrence of enigmatic ‘percevalicrinids’ (Echinodermata, Crinoidea) in the Lower Jurassic strata of North Africa — Implications for their stratigraphic and palaeogeographic distribution and discussion on their belonging to the subfamily Balanocrininae

Mariusz A. Salamon [a,*], ***Madani Benyoucef*** [b], ***Karolina Paszcza*** [a], ***Fayçal Mekki*** [b], ***Imad Bouchemla*** [b], ***Bartosz J. Płachno*** [c]

[a] *University of Silesia in Katowice, Faculty of Natural Sciences, Będzińska 60, PL-41-200 Sosnowiec, Poland*
[b] *Laboratoire de Géomatique, Ecologie et Environnement, Mustapha Stambouli University, 29000 Mascara, Algeria*
[c] *Jagiellonian University in Kraków, Faculty of Biology, Institute of Botany, Gronostajowa Street 9, PL-30-387 Cracow, Poland*

Abstract The marl and limestone alternations of the Lower Jurassic Ain Ouarka and Ain Rhezala formations (Pliensbachian—Toarcian) in the western Saharan Atlas, Northwest Algeria, yield a diverse micro- and macrofauna, including moderately numerous crinoids, which are represented by remains of isocrinids, i.e., *Balanocrinus ticinensis* Hess and columnals of the genus *Percevalicrinus*. So far, the latter genus has been observed from the Upper Jurassic—Lower Cretaceous strata of Eurasia, North America, and the African continent. Thus, the present find is the oldest record of this crinoid genus, and the second one from the southern Tethyan margin. In this paper, it is shown that *Percevalicrinus*, which is traditionally regarded as a representative of the subfamily Balanocrininae, displays several features of the subfamily Isocrininae. The crinoid assemblage and associated facies and invertebrate fauna are typical of a low-energy deep outer shelf/ramp (below the storm wave-base) setting.

Keywords Echinoderms, Crinoids, Isocrinids, Percevalicrinids, *Percevalicrinus*, Lower Jurassic, Algeria, Maghrebian Tethys

* Corresponding author.
E-mail address: paleo.crinoids@poczta.fm (M.A. Salamon).
Peer review under responsibility of China University of Petroleum (Beijing).
https://doi.org/10.1016/j.jop.2023.05.002

Received 13 March 2023; revised 1 April 2023; accepted 19 May 2023; available online 23 May 2023

1. Introduction

‘Percevalicrinids’ belong to the order Isocrinida Sieverts-Doreck — one of the nine post-Paleozoic crinoid orders. They are known from Jurassic and Cretaceous strata, mostly from the Boreal Province. These crinoids are characterized by the presence of large basals that form a contiguous circle. Moreover, the lower edge of the basals possesses an inconspicuous median prolongation that partially covers the edge of the topmost columnal. Their arms are at first divided at primibrachial 2, and are divided further once or twice with variable intervals (e.g., Klikushin, 1979, 1981, 1992; Hess and Messing, 2011). Columnals are quite characteristic: circular to pentagonal and covered by short, uniform crenular pattern. With one exception, *Percevalicrinus inderensis*, adult specimens have a very similar, basically indistinguishable pattern of the columnal articular surface, which makes them classified as true ‘isocrinids’ rather than balanocrinids (Balanocrininae). In contrast, juvenile columnals are extremely tall and all representatives of ‘percevelicrinids’ are identical. They are usually covered with short and thick crenulae, which to some extent resemble millericrinids (Millericrinida). The internodes consist of 5–17 columnals. Hess and Messing (2011) distinguished four genera within the subfamily Balanocrininae Roux of the family Isocrinidae. These are: *Balanocrinus* Agassiz in Desor, *Laevigatocrinus* Klikushin, *Singularocrinus* Klikushin, and *Percevalicrinus* Klikushin. However, the affiliation of *Percevalicrinus* with Balanocrininae is not obvious. Rasmussen (1961) and Jäger (1981a, 1981b, 1981c) included *Percevalicrinus tenellus* (Eichwald) known from Spitzbergen as *Neocrinus* Thomson or *Chladocrinus* Agassiz. The last two genera are included, along with *Isocrinus* von Meyer, *Chariocrinus* Hess, *Hispidocrinus* Hess, *Hypalocrinus* A.H. Clark, *Raymondicrinus* Klikushin, and *Tyrolecrinus* Klikushin, to the subfamily Isocrininae Gislén. In contrast, Klikushin (1982, 1992) pointed out that the genus *Percevalicrinus* strongly differs from representatives of the genera *Neocrinus* and *Chladocrinus*. The same author (Kliksuhin, 1992) also stated that *Percevalicrinus* is remarkably similar (or even identical) to the genus *Singularocrinus* Klikushin, which is also included in the Balanocrininae; however, we do not agree with this statement. Columnals of *Singularocrinus* represent typical balanocrinid-type remains (comp. e.g., Hess and Messing, 2011, fig. 30/2a–c). According to Klikushin (1992), the only difference is in the fact that the latter genus is known only from the Upper Triassic (Carnian–Norian) of the Caucasus. Jäger (2010) included columnals with lateral surfaces distinctly ornamented with spines, bumps, and thickenings also in *Percevalicrinus*. Similarly, Benyoucef *et al.* (2022) classified specimens from Berriasian and Valanginian strata of the Ouarsenis Massive in western Algeria (Fig. 1A) as belonging to this genus. Jäger (2010) suggested that this type of columnals may belong to another isocrinid. He also mentioned smaller individuals as “listed under *Isocrinus*? *bleytonensis* and might belong to *Percevalicrinus* sp. in fact”. Jäger (2010) summarized that some cirrals, radials, brachials, or pinnulars classified by him as *Isocrinus*? *bleytonensis* may belong to *Percevalicrinus*. All of the above suggest that this group of crinoids should be referred to as ‘percevalicrinids’ in working terms, as it is difficult to unambiguously place this taxon either in Balanocrininae or Isocrininae (see also the discussion in section 8.2). There is also a problem with the ornamentation of unnaturally tall juvenile columnals, which are more like millericrinids than isocrinids. Finally, it becomes even more confusing when we look at the stratigraphic ranges of these crinoids. Hess and Messing (2011) noted *Percevalicrinus* from the Upper Jurassic (Tithonian)–Lower Cretaceous (Valanginian) interval, ignoring the fact that Jäger (2010) had recorded them from the Barremian of France. Current data show that the stratigraphic range of ‘percevalicrinids’ must be drastically shifted down to the Lower Jurassic (Pliensbachian), that is, by more than 40 million years.

2. Geological background

The Maghrebian orogenic domain comprises two different systems: the Tell-Rif to the north and the Atlas (High and Middle Atlas in Morocco, Saharan Atlas and Aurès Mountains in Algeria, and Tunisian Atlas in Tunisia), and also poorly deformed, broadly tabular domains (the so-called Western, or Moroccan, and Eastern or Oran Mesetas) only present in its western part (Fig. 1A).

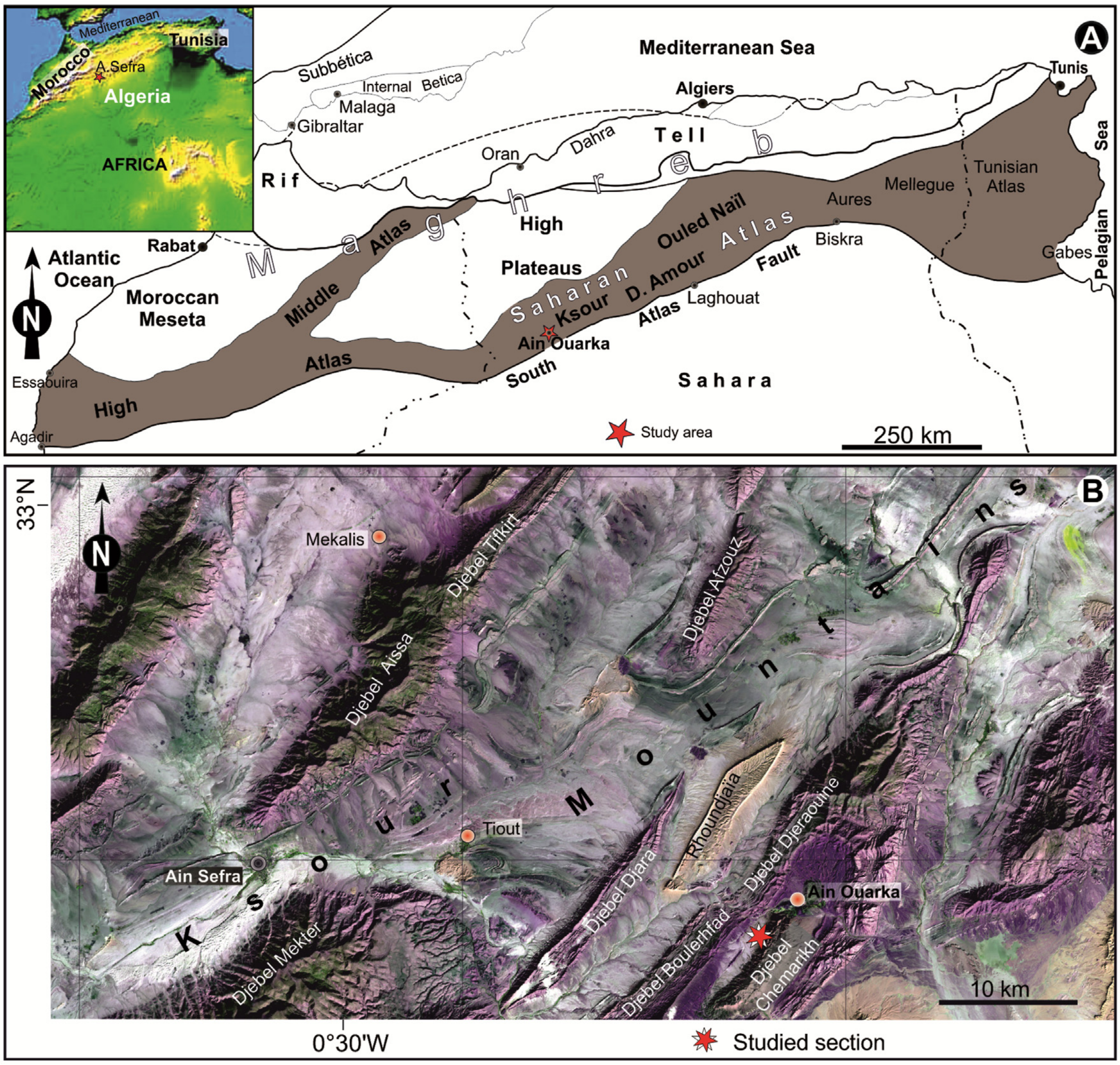

Fig. 1 Geographic location of the study area in northern Africa. **A)** Main palaeogeographic units of the Maghreb; the red asterisk denotes the bearing crinoid species described in the text; **B)** Satellite image showing the position of the studied section (see also Fig. 2).

The Saharan Atlas extends between the Moroccan High Atlas and the Aures Range. It can be subdivided into a series of subranges (Ritter, 1902): the Ksour Mountains in the west, which is the focus of the present study, the Djebel Amour in the center, and the Ouled Nail Mountains in the east (Fig. 1A).

At the end of Triassic times and probably at the beginning of the Hettangian, Maghreb (north of the South Atlas Fault; Fig. 1A) was occupied by land and large sabkhas extending far south to the Lower Sahara (Choubert and Faure-Muret, 1960—1962). Magmatic events occurred, related to the first rift activities that are known all around the future central Atlantic Ocean. At the Hettangian—early Sinemurian an extended carbonate shelf (dolostone of Chemarikh Formation in the Ksour Mountains), post-dating the Triassic rifting, was established all over the Maghreb. From the Pliensbachian to the early Bathonian, more open shelf conditions developed in the future Atlas (Kazi Tani, 1986; Aït Ouali, 1991; El Kochri and Chorowicz, 1996) in response to the persistence of the thermal subsidence (Piqué *et al*, 2002). Deposits of this interval times, are represented in the Ksour Mountains, by the Ain Ouarka, the Ain Rhezala, the Breccia of Raknet El Kahla, the Tniet El Klakh, and the Tifkirt formations (Bassoullet, 1973; Mekahli, 1998). From the Bathonian to the Early Cretaceous, the decrease in subsidence rate led to the progressive filling of the Atlasic trough with the deposition of initially fine, then coarse siliciclastic sediments ('Grès des Ksour' of Delfaud and Zellouf, 1993) representing the northward progression of the palaeo-Niger river and delta system by which the detrital material from the Saharan shield was transported to the Tethys. The Middle Jurassic—Late

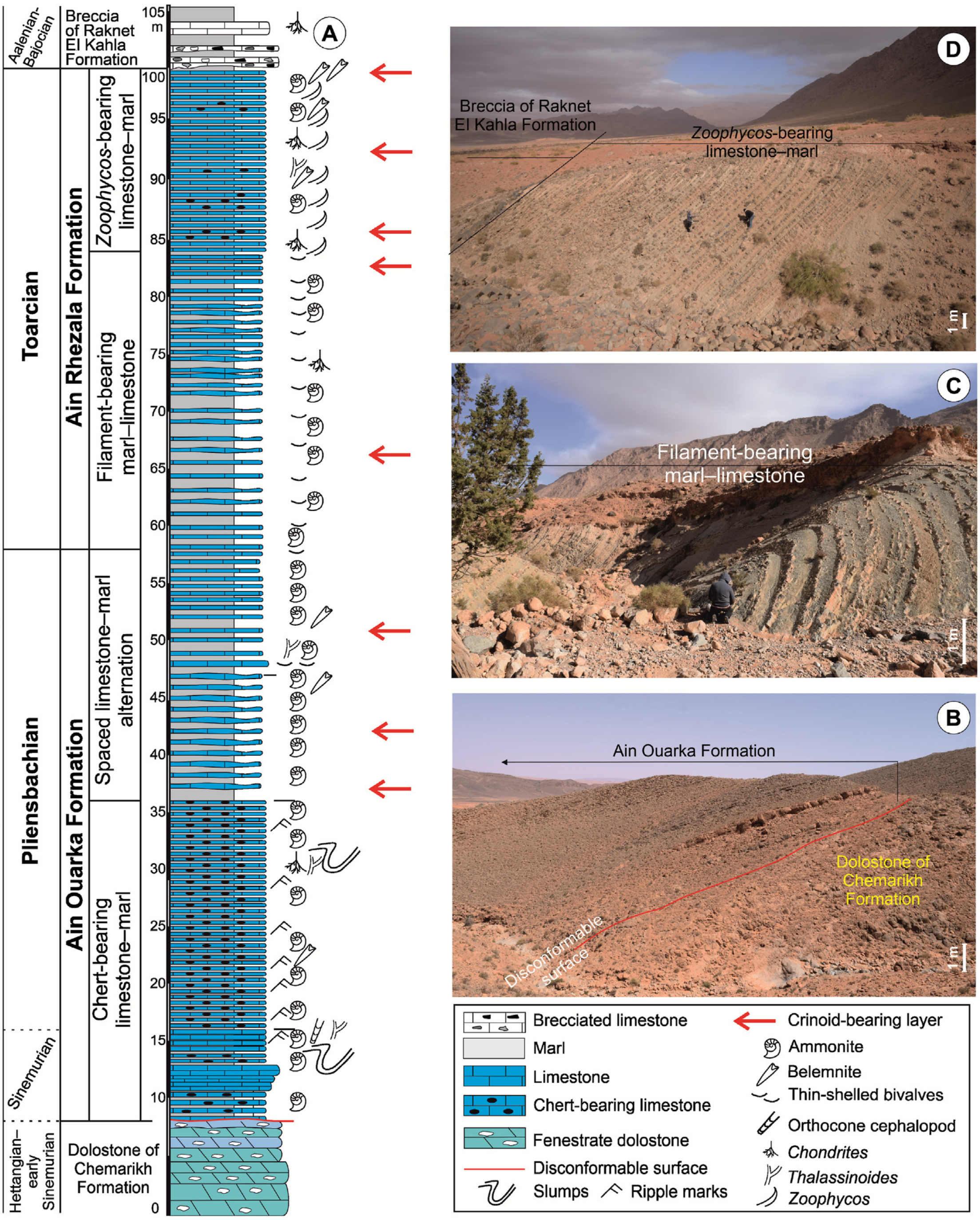

Fig. 2 Ain Ouarka section of the Lower Jurassic at the western foot of Djebel Chemarikh. **A**) Measured stratigraphic section; **B**) Panoramic view showing the contact between the dolostone of the Chemarikh Formation (infra-Liassic dolostone) and the Ain Ouarka Formation (Sinemurian—Pliensbachian); **C**) Panoramic view showing the lower part (the filament-bearing marl—limestone member) of the Toarcian Ain Rhezala Formation; **D**) Panoramic view showing the upper part (the *Zoophycos*-bearing limestone—marl member) of the Ain Rhezala Formation.

Cretaceous sedimentary record has been ascribed to successive cycles of sea-level fluctuations during a post-rift stage unaffected by significant tectonic deformation (Frizon de Lamotte *et al*, 2008).

3. Stratigraphic section and age assignments

The general lithostratigraphy of the Mesozoic succession in the Ksour Mountains matches the subdivisions proposed by Bassoullet (1973) and Mekahli (1998) that have subsequently been accepted by most investigators (see Sebane *et al*, 2007; Benyoucef *et al*, 2017; Mekki *et al*, 2019; Bouchemla, 2021; Ferrari and Benyoucef, 2021; Mahboubi *et al*, 2021). The studied section (32°42′51.10″N; 0°9′49.30″W), called the Ain Ouarka, is located 2.5 km south of the hydrothermal source of Ain Ouarka (Fig. 1B), and is divided into two formations.

3.1. Ain Ouarka Formation

Disconformably overlying the dolostone of Chemarikh Formation (Hettangian—lower Sinemurian) and underlying the Ain Rhezala Formation (Toarcian) (Fig. 2), the Ain Ouarka Formation (Mekahli, 1998) is divided into two informal members.

(i) The chert-bearing limestone—marl member, consists mainly of dark gray regular alternations of thin, hard, chert-bearing limestone beds (4—5 cm-thick) and dark green marl bands (2—5 cm-thick). The limestone beds contain ammonites and belemnites. The microfacies consist predominantly of mudstone to wackestone containing sponge spicules, radiolarians, microfilaments, benthic and planktic foraminifers, and echinoderm bioclasts.

The lower part of the chert-bearing limestone—marl member was placed by Bassoullet (1973) and Mekahli (1998) in the Sinemurian Semicostatum and Turneri zones based on ammonites (*Asteroceras* sp., *Arnioceras miserabile*, *Arnioceras* aff. *miserabile*, *Arnioceras* aff. *semicostatum*, and *Arnioceras* cf. *speciosum*) and in the Obtusum Zone (*Asteroceras* sp., *Asteroceras meridionale*, *Asteroceras* aff. *margarita*, *Phylloceras* sp., *Gleviceras* gr. *doris*, and *Lytoceras* sp.).

(ii) The spaced limestone—marl alternation member is represented by an alternation of soft green laminated marl (10—50 cm-thick) and limestone beds (5—10 cm-thick) with an undulating surface at the base and/or at the top. It contains ammonites and belemnites. The limestone beds are laterally continuous over hundreds of meters. The microfacies consist mainly of biomicrites (mudstone to wackestone) with filaments, spherical radiolarians, planktonic foraminifers, and rare calcispheres.

This member yielded Pliensbachian ammonites. They represent the passage from the Sinemurian—lower Pliensbachian (*Oxynoticeras* sp.), the Ibex Zone (*Tropidoceras mediterraneum*, *Tropidoceras calliplocum*, *Protogrammoceras* sp., and *Lytoceras* sp.), the Davoei Zone (*Protogrammoceras* cf. *volubile*, *Juraphyllites* sp., *Phylloceras* sp., *Lytoceras* sp.), the Algovianum Zone (*Reynesoceras* sp., *Protogrammoceras* sp., *Arieticeras algovianum*, *Lioceratoides* aff. *inclytum*, *Arieticeras* gr. *bertrandi*, *Protogrammoceras* gr. *bonarelli*, *Pygope aspasia*, and *Securithyris erbaensis*), and the Emaciatum Zone (*Taurometeniceras elisa*) (see Bassoullet (1973) and Mekahli (1998) for details).

3.2. Ain Rhezala Formation

The Ain Rhezala Formation (Mekahli, 1998) overlies the Ain Ouarka Formation and underlies the Breccia of the Raknet El Kahla Formation (Aalenian—Bajocian) (Fig. 2). It is subdivided into two informal members, based on their respective faunal, ichnological, and lithological features.

(i) The filament-bearing marl—limestone member is made mainly of green to whitish laminated marl (10—50 cm-thick) and gray limestone (5—10 cm-thick) alternations bearing thin-shelled posidoniid bivalves ('filaments') and ammonites. The limestone beds show rare, highly branched burrows assigned to Chondrites isp. The microfacies consists of mudstone—wackestone containing microfilaments and ostracods.

The member contains Toarcian ammonites of the Polymorphum Zone (*Eodactylites* sp., *Eodactylites* gr. *mirabile*), the Bifrons Zone (*Hildocerasbifrons angustisiphonatum*, *Hildocerasbifrons* gr. *sublevisoni crassum*, *Hildocerasbifrons sublevisoni*, *Hildocerasbifrons* semipolitum, *Hildocerasbifrons lusitanicum*, and *Phymatoceras* gr. *elegans*), the Gradata Zone (*Crassiceras gradatum*, *Calliphylloceras nilssoni*, *Pseudogrammoceras subregale*, *Polyplectus discoides*, *Polyplectus pinnai*, *Alocolytoceras* sp., *Collinites*, and *Phylloceras* sp.), the Bonarelli Zone (*Pseudogrammoceras* sp.), and the Speciosum Zone.

(ii) The Zoophycos-bearing limestone—marl member consists of a regular and monotonous alternation of thin-to medium-bedded limestones (7—15 cm-thick) and green to light gray marl (15—40 cm-thick). The limestone beds contain numerous ammonites and belemnites and are commonly rich in trace fossils, represented by well-preserved Zoophycos, associated with Chondrites and Thalasinoides. In mudstone—wackestone, quartz grains, calcispheres, sponge spicules, very thin bivalve shells (‘filaments’), pelagic crinoids (Saccocoma) and other fine bioclasts are observed. The ammonites (Grammoceras aff. striatulum, Pseudogrammoceras gr. fallaciusum, Pseudogrammoceras cf. muelleri, Harpoceras cf. serpentinum, Harpoceras sp., Hammatoceras gr. bonarellii, Esericeras sp., Lytoceras sp., and Phylloceras sp.) collected by Mekahli (1998) and Bouchemla (2021) indicate the upper Toarcian Bonarellii Zone.

4. Material and methods

The Early Jurassic crinoid collection from the Ain Rhezala and Ain Ouarka formations of the western Saharan Atlas (Algeria) is housed in the Faculty of Natural Sciences, Institute of Earth Sciences of the University of Silesia in Katowice, Poland, and acronymed under the catalogue number of GIUS 8—3689/Per.

The marl and limestone were sampled at a 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 size (300 μm, 250 μm, 180 μm, 125 μm) under a strong jet of water. The residuals recovered from each sieve were dried and steamed and then sorted with a Euromex Dz and Optika ST-40-2L binocular magnifier to pick the micropaleontological content. For hard samples, the thin sections were made for both microfacial and microfaunal purposes. The sorted crinoid specimens were fixed on stubs using double-sided carbon adhesive tape and then covered with a thin layer of gold. They were then photographed with a Hitachi S-4700 scanning electron microscope (SEM), housed at the Institute of Geological Sciences, Jagiellonian University in Kraków, Poland.

5. Results

Thirty-six columnals/pluricolumnals belonging to ‘percevalicrinids’ were collected. They were found in two Pliensbachian samples (Ao15 and Ao18) and two Toarcian samples (Ao23 and Ao34). Additionally, from the Pliensbachian samples Ao15 and Ao18, 7 columnals, 11 cirrals, 2 primibrachials, and 3 secundibrachials were picked. The ornamentation of the articular facets of the columnals was mostly poorly visible; however, these specimens resemble the remains of *Balanocrinus ticinensis* Hess known from the Pliensbachian strata of Switzerland.

The smallest columnals of *Balanocrinus* cf. *ticinensis* are nearly as high as wide. Their diameter is about 0.7 mm. The diameters of the larger columnals vary between 1.8 mm and 2.6 mm. The columnals are pentagonal to subpentalobate. The adradial face is covered by a maximum of 35 marginal crenulae and probably 50 adradial crenulae. The petal floors are rhombic and relatively large, which is typical for *Balanocrinus*. The lumen is rather small and circular. The latera are covered by tubercles, and in one specimen they are arranged in rows or smooth. Cirrals have smooth surfaces and are elliptical in cross-section. Their length varies from short in the proximal case to long in distal cirrals. The proximal facets of the primibrachials are muscular. They have large muscle faces. Their lateral surfaces are smooth. Secundibrachials also have smooth surfaces and large muscular facets with distinct muscle fields.

6. Palaeoenvironment of the Lower Jurassic deposits in the Ain Ouarka area

The fine-grained sediment is interpreted as suspension deposits. The abundance of open marine macrofauna (ammonites and belemnites) and microfauna (thin-shelled bivalves and calcispheres, regarded as possibly calcified radiolarians), and *Zoophycos* trace fossils, all indicate a low-energy deep outer shelf/ramp setting below the storm wave base (e.g., Bruhwiler *et al*, 2009; Lukeneder *et al*, 2012), which is supported by the lack of benthic marine fauna and absence of sedimentary textures indicative of strong bottom currents. This interpretation is also supported by the presence of pelagic crinoids (*Saccocoma*) and radiolarians at some intervals. The trace fossils *Zoophycos* and *Chondrites* were produced by the members of endobenthic fauna adapted to nutrient exploitation within sediments. Both these traces reflect *Zoophycos* ichnofacies. An outer shelf (outer ramp) environment was also proposed by Bouchemla (2021) and Mahboubi *et al.* (2021) for the Lower Jurassic rocks of the Ain Ouarka area.

7. Systematic paleontology

In the absence of a complete revision of the genus *Percevalicrinus*, we use the systematics proposed by Hess and Messing (2011).

Order: Isocrinida Sieverts-Doreck, 1951.

Suborder: Isocrinida Sieverts-Doreck, 1951.

Family: Isocrinidae Gislén, 1924.

Subfamily: Balanocrininae Roux, 1981.

Genus: *Percevalicrinus* Klikushin, 1977.

Type species: *Picteticrinus beaugrandi* de Loriol, in de Loriol and Pellat (1875, p. 298).

***Percevalicrinus* sp.** (Fig. 3).

Material: 36 columnals and pluricolumnals.

Repository: Laboratory of Palaeontology and Stratigraphy of the University of Silesia in Katowice, Poland, with the catalogue number: GIUS 8—3689/Per.

Description: Only juvenile columnals were found. The distal-most columnals are circular or pentagonal and extremely high; even five times higher than wide. The medial and proximal-most columnals are pentagonal to substellate. They are moderately high. The articular face is covered with thick and short crenulae. They occur in numbers from 8 up to 24. Cirrus scars are placed at the lower part of the nodals. They are medium to large and directed obliquely upward. These scars are distinct depressed, circular to slightly oval. The distal lip is prominent and may protrude beyond the lower margin. A shallow cupule may develop above the cirral scar of the nodals and the distal part of the adjacent supranodals. In some cases, the central pore of the cirral scar interrupts a thickened transverse ridge at each end. Lateral surfaces are smooth and synarthrial.

Distribution: Representatives of 'percevalicrinids' occur from the Lower Jurassic (Pliensbachian) to the Lower Cretaceous (Barremian) of Africa (Algeria), Eurasia (England, France, Germany, Spitsbergen, Russia) and North America (Greenland, United States).

8. Discussion

8.1. *Palaeogeographic and stratigraphic distribution of 'percevalicrinids'*

According to Klikushin (1979, 1981, 1982, 1992; see also Benyoucef *et al*, 2022) five species of the genus *Percevalicrinus* are known. Meek and Hayden (1859) described *Pentacrinus asteriscus* from the Oxfordian of Nebraska, United States. The same taxon was later classified as *Isocrinus knighti* Springer by Springer (1909), and both were included in *Percevalicrinus asteriscus* (Meek and Hayden) by Klikushin (1992). *Pentacrinus asteriscus* and/or *I. knighti* were also mentioned from the Oxfordian of the central United States (Dakota, Idaho, Missouri, Nebraska, Wyoming) by Meek and Hayden (1859, 1861, 1864), Meek and Engelmann (1861), Meek (1864), Peale (1879), Boyle (1893), Clark (1893a, 1893b), Stanton (1899), Knight (1900), Logan (1900), Schuchert (1905), Fisher (1906), Whitfield and Hovey (1906), Grabau and Shimer (1911), Clark and Twitchell (1915), Shimer (1921), Mansfield (1927), Neely (1937), Imlay (1947), Moore and Laudon (1948), Moore *et al.* (1952), and Pipiringos (1957) (Fig. 4). Darton (1899; 1905) identified extremely long columnals from the Oxfordian of South Dakota as *Pentacrinoides aristicus* and *Pentacrinoides asteristicus* [sic!], but Klikushin (1992) classified this material as belonging to *Percevalicrinus*.

Somewhat later, Eichwald (1868) distinguished another 'percevalicrinid', *Pentacrinus tenellus* Eichwald, which was synonymized with *Percevalicrinus tenellus* by Klikushin (1982). This form was originally described from the Berriasian near Moscow. Sokolov and Bodylevsky (1931) indicated the presence of *Pentacrinus*? sp. in the Berriasian of Spitsbergen, Norway. This taxon was also recognized by Klikushin (1992) as a 'percevalicrinid' (*Percevalicrinus tenellus*). The same author, referring to the unpublished research of Simonov and Alekseev, indicated the presence of this taxon in Berriasian strata of the Volga Basin and the west Siberian Plain (Klikushin, 1979, 1981). In addition, Klikushin (1992 and the literature cited therein) claimed that this taxon also occurs in the Berriasian of eastern Greenland (Fig. 4).

Another representative of the genus *Percevalicrinus* is *Percevalicrinus beaugrandi* (Loriol), first described from the Tithonian of France by de Loriol (1877—1879, 1882—1889) as *Picteticrinus beaugrandi*. *Picteticrinus* Étallon was treated by de Loriol and Pellat (1875, in p. 298), as a junior homonym and classified by Hess and Messing (2011) as nomina dubia; however, Klikushin (1981, 1982, 1992) included it in genus *Percevalicrinus*. This taxon was mentioned in France also by Pellat (1880), Biese (1930), and Dacqué (1933). Moreover, Klikushin (1981) recorded this species in the Tithonian (Volgian) of Russia (environs of Moscow, Volga Basin, Arctic Ural (Jatrina River)) and Taimyr (Fig. 4).

The next two 'percevalicrinids' were distinguished by Klikushin (1979, 1981). First, the most completely preserved *Percevalicrinus aldingeri* Klikushin, was known from the lower Valanginian of the west Siberian plain, Taimyr (Boyarka, Maymecha, Sabyda, and Suolema rivers), and the Anabar River. Spath (1947) mentioned remains of isocrinids from the Berriasian of Greenland, which were assigned to *P. aldingeri* by Klikushin (1992). The latter was included in the synonymy of *P. aldingeri*. The remains of *Neocrinus tenellus* (Eichwald) mentioned by Rasmussen (1961) are from the Hauterivian rocks of England, France, and the Valanginian and Hauterivian strata of Germany. Benyoucef *et al.* (2022) described the stem and cup remains of this taxon from the Berriasian and Valanginian of Algeria, and so far, this was the only African find of 'percevalicrinid'. The last representative of the

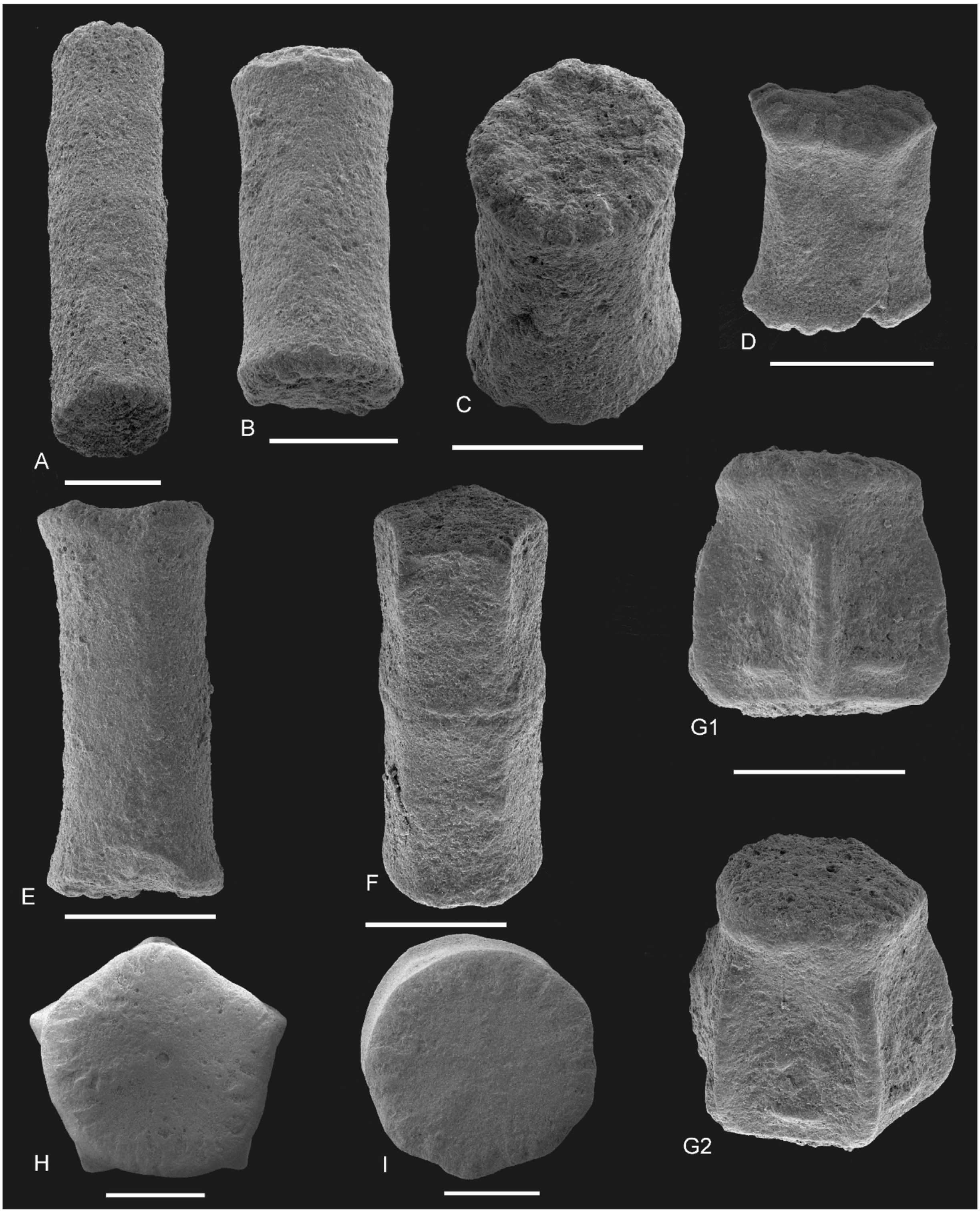

Fig. 3 Juvenile 'percevalicrinids' and true 'balanocrinids' (*Balanocrinus* cf. *ticinensis* Hess) from the Pliensbachian Ain Ouarka Formation of Algeria. Acronym number: GIUS 8—3689/Per. Scale bar equals 1 mm. **A—B)** Extremely tall distal columnals, oblique view (latera plus articular surface); **C)** Distal columnal, oblique view (latera plus articular surface covered with thick and short crenulae resembling those of millericrinids); **D)** Medial? columnal, oblique view (latera plus articular surface covered with thick and short crenulae resembling to millericrinid); **E)** Extremely tall distal columnal, lateral view; **F)** Pluricolumnal consisting of two medial columnals, oblique view (latera plus articular surfaces with invisible crenulation); **G)** Medial/proximal nodal columnal, lateral view (G1) and oblique view (G2) (latera plus articular surface). **H—I)** *Balanocrinus* cf. *ticinensis* Hess, medial/proximal (H) and proximal (I) columnals, articular surface.

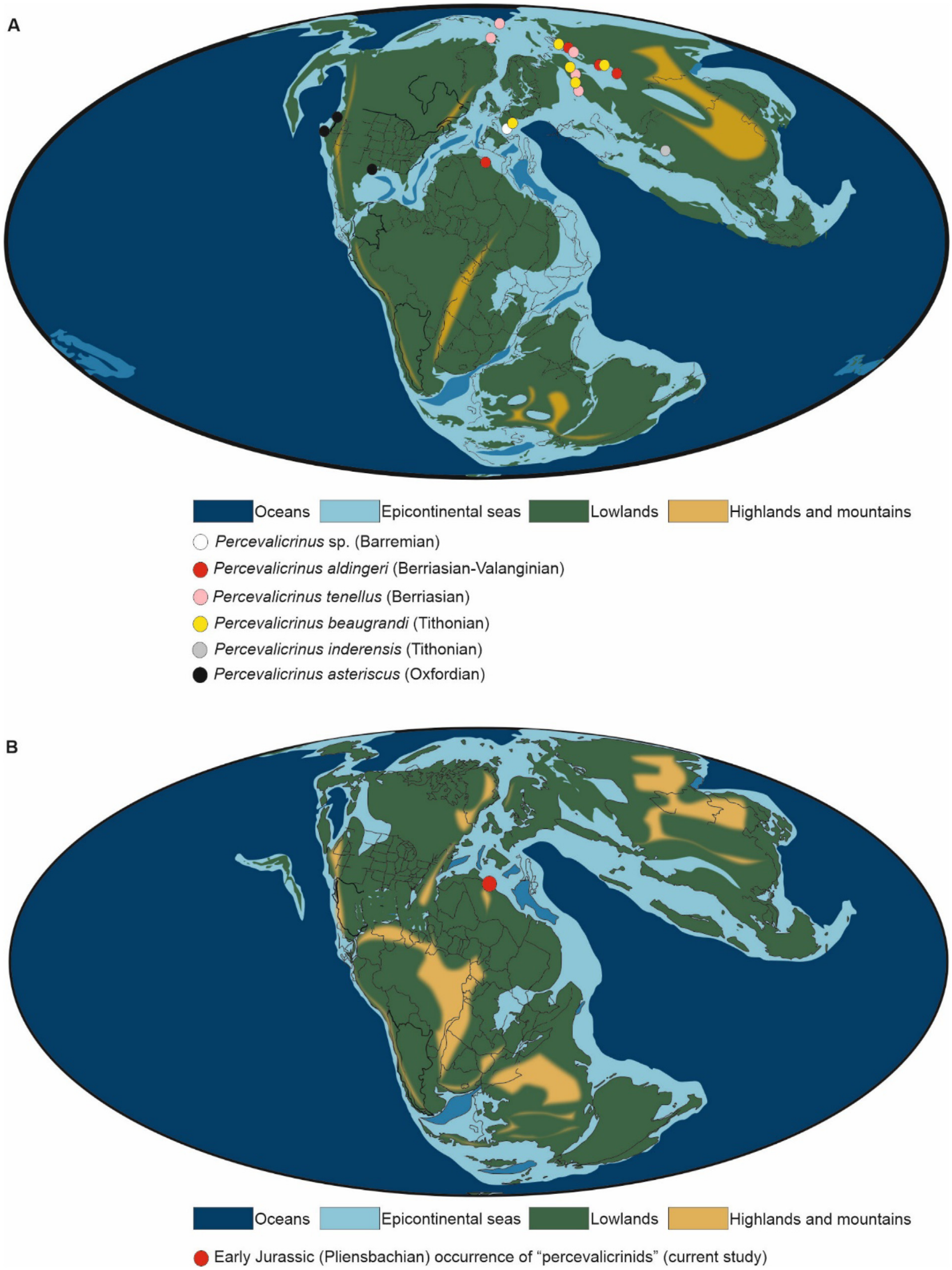

Fig. 4 Palaeogeographic map showing the distribution of ‘percevalicrinids’ during the Late Jurassic—Early Cretaceous. Maps slightly modified after Scotese (2014) and Salamon *et al.* (2019). Data from Rasmussen (1961), Klikushin (1979, 1981, 1992), Jäger (1981a, 1981b, 1981c, 2010), Hess and Messing (2011), and Benyoucef *et al.* (2022).

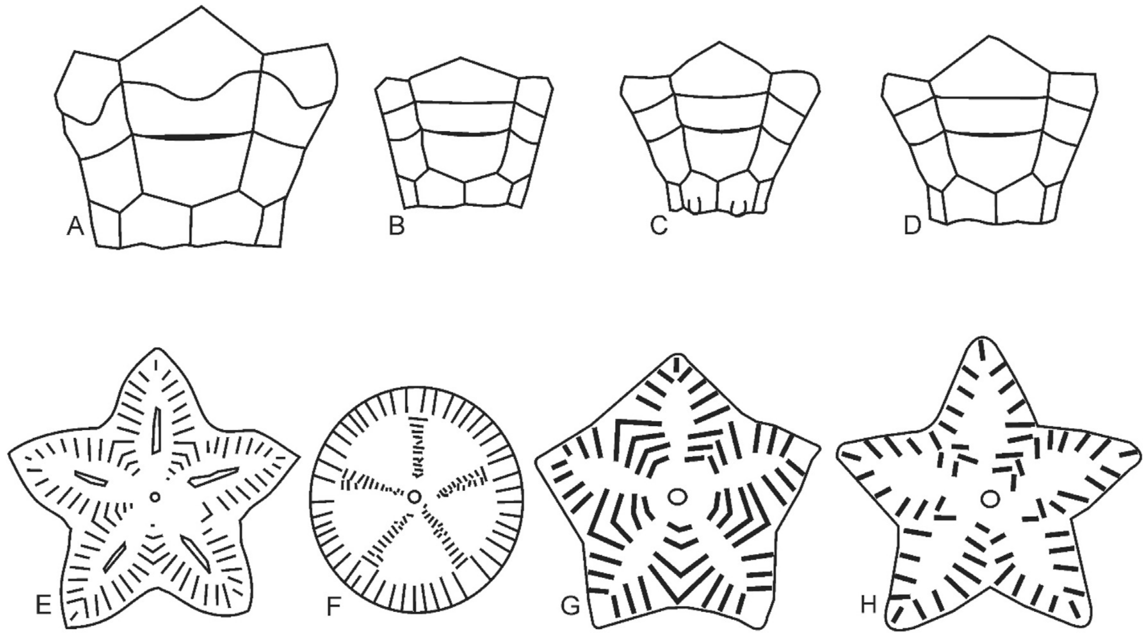

Fig. 5 'Percevalicrinid' cups and different isocrinid columnals showing the differences between them. **A)** Cup of *Percevalicrinus aldingeri*; **B)** Cup of *Percevalicrinus asteriscus*; **C)** Cup of *Percevalicrinus beaugrandi*; **D)** Cup of *Percevalicrinus tenellus*; **E)** Medial columnal of *Percevalicrinus inderensis*; **F)** Typical balanocrinid (*Balanocrinus subteres*) distal/medial columnal; **G)** Typical isocrinid (*Isocrinus*) medial columnal; **H)** Medial columnal of *Percevalicrinus beaugrandi*. Not to scale. All data compiled and redrawn after Rasmussen (1961), Klikushin (1979, 1981, 1992), Jäger (1981a–1981c, 2010), Hess and Messing (2011), and Benyoucef *et al.* (2022).

genus *Percevalicrinus* is *P. inderensis* Klikushin, erected by Klikushin (1981) based on columnals and pluricolumnals. This form was known only from the latest Tithonian of western Kazakhstan (Klikushin, 1992) (Fig. 4).

Jäger (2010) illustrated interesting material from Serre de Bleyton (France) of Barremian age and described it as *Percevalicrinus* sp., shifting the known stratigraphic range of 'percevalicrinids' from lower Hauterivian to Barremian. The current finds push further back the first appearance of these crinoids into the Pliensbachian. Additionally, this is the second finding of 'percevalicrinids' from a low latitude (Fig. 4).

8.2. Are there five 'percevalicrinid' species?

Juvenile columnals of all known representatives of 'percevalicrinids' are indistinguishable. They are all very tall, oval, or pentagonal in outline and their articular surfaces are covered by thick and short crenulae (Fig. 3; e.g., Jäger, 2010; Benyoucef *et al*, 2022), which makes them similar to millericrinids. On the contrary, the columnals of adults more closely resemble the columnals of isocrinids (Isocrininae Gislén) than those of balanocrinids (Balanocrininae Roux). Typical columnals of balanocrinids are pentagonal, occasionally with sharp edges. Their facet is covered with sharply terminated and rhombic petal floors. The petal floors are separated by thin adradial crenulae; each petal floor is surrounded by 5–8 marginal crenulae. The adradial crenulae are narrow (Fig. 5F; e.g., Salamon, 2008a, 2008b, 2008c, 2009; Hess, 2014a; 2014b). Columnals of this type are found in *Balanocrinus*, *Laevigatocrinus*, and *Singularocrinus*, which beyond any doubt should be associated with Balanocrininae. In the case of *Percevalicrinus*, such columnals have never been documented (Fig. 5E, H; Klikushin, 1977, 1992; Jäger, 2010; Hess and Messing, 2011; Benyoucef *et al*, 2022). This calls into the question: what prompted Klikushin (1977) to include the genus *Percevalicrinus* in the Balanocrininae? The question is all the more pertinent because Roux (1981) established this subfamily solely based on the columnal facets, with characters of the crown identical to Isocrininae. The columnal facets of all the above-mentioned representatives of *Percevalicrinus*, except *P. inderensis* (Fig. 5E), are similar or almost identical to each other (Eichwald, 1868, fig. 1, pl. 16; Hucke, 1904, fig. 5, pl. 23; Aldinger, 1935, fig. 10; Spath, 1947, figs. 10 and 11, pl. 5; Rasmussen, 1961, figs. 1a, 2, 3, pl. 10; Klikushin, 1979, figs. 4–6, pl. 7; Klikushin, 1992, fig. 7/1–2, 9/1–6; Jäger, 2010, figs. 3a and 6a, pl. 3; Hess and Messing, 2011, fig. 27/3b, 3c; Benyoucef *et al*, 2022, fig. 5i, l). All these columnals are pentagonal, stellate to substellate with slightly embayed sides and fairly sharp angles (Fig. 5H). The articular surfaces are covered by a circular or slightly elongated lumen in the case of distal and medial columnals; it is elongated or even drop-shaped in the case of proximal columnals. Crenulae may be thicker and less numerous in the distal columnals; they become thinner and more numerous in the proximal columnals. The latera may be smooth or covered with fine outgrowths or nodules forming a characteristic keel. The only exception is the columnals of *Percevalicrinus inderensis* Klikushin, which is known from stem fragments. Klikushin (1992, figs. 1—10, pl. 8) illustrated stellate and substellate columnals that were covered by thin and very numerous crenulae in a maximum numbering up to 96, which were grouped around very long, remarkably thin, and deep petal floors (Fig. 5E). Therefore, the affiliation of this taxon to *Percevalicrinus* seems even more doubtful. Hess and Messing (2011) recalled that typical Isocrininae (Fig. 5G), such as *Isocrinus pendulus* (von Meyer) or *Isocrinus nicoleti* (Thurmann in Thurmann and Étallon), have diameter/height ratios of 6 or even more in columnals from the mesistele, whereas those of typical Balanocrininae such as *Balanocrinus subteres* (Münster in Goldfuss) or *Balanocrinus pentagonalis* (Goldfuss) are below 3. In *Percevalicrinus inderensis* the diameter/height ratio ranges from 5 to even more than 7.

In the case of the four remaining 'percevalicrinids' (*Percevalicrinus aldingeri*, *Percevalicrinus asteriscus*, *Percevalicrinus beaugrandi*, *Percevalicrinus tenellus*; Fig. 5A—D), the structure of their cups is known. Here it can be also seriously doubted whether they do indeed belong to four different species. The cup of *Percevalicrinus aldingeri* is the largest of all *Percevalicrinus*, but more importantly, it has a first primibrachial (IBr1) with a unique trapezoidal shape (inverted trapezoid), whose upper (distal) base is strongly concave in aboral view. At the same time, the base of its primaxillary (IAx) in the aboral view is strongly convex. The size of the cups of the other forms is comparable, but only the cup of *Percevalicrinus beaugrandi* clearly differs from the others mentioned above. While the shapes of its radials, IBr1 and IAx are identical to those of *Percevalicrinus astericus* and *Percevalicrinus tenellus*, its radials are the only ones with a small teardrop-shaped protuberance in the lower part (Fig. 5C). The only slight difference that distinguishes the cup of *Percevalicrinus asteriscus* from *Percevalicrinus tenellus* is the shape of IAx. All other elements of the cup are identical in shape and size. In both cases, the IAx is flattened pentagonal, but in *Percevalicrinus tenellus* it is only slightly higher (Fig. 5D).

9. Conclusions

In the Pliensbachian and Toarcian strata of Algeria (North Africa), abundant high columnals and pluricolumnals have been documented and classified as *Percevalicrinus* within the subfamily Balanocrininae. As the systematic affiliation of *Percevalicrinus* to Balanocrininae was questioned, these crinoids were given the provisional name of 'percevalicrinids'. The basis of distinguishing five species of *Percevalicrinus* has been questioned and it has been suggested that they probably only belong to two, at most three, taxa. So far, the oldest representatives of 'percevalicrinids' were known only from the Tithonian sediments (Upper Jurassic); they have now been found in the Pliensbachian and Toarcian (Lower Jurassic), as well. Thus, globally, this is the oldest Early Jurassic record of 'percevalicrinids', and only the second documented occurrence from the African continent.

Availability of data and materials

Data supporting the findings of this research are available upon request from the corresponding author.

Funding

This research project has been supported by the National Science Centre, Poland (www.ncn.gov.pl) — Grant No. 2020/39/B/ST10/00006.

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; K. Paszcza: Writing original draft, writing, review and editing; F. Mekki: Methodology, writing original draft; I. Bouchemla: Data curation, formal analysis, methodology, software, visualization; B.J. Płachno: Investigation, methodology, writing original draft, writing, review and editing. All authors read and approved the final proof.

Conflict of interest

All authors declare no conflict of interest.

In addition, all authors disclose any financial relationships in the submitted manuscript (Funding and Acknowledgements sections).

Acknowledgements

We thank Prof. Franz Fürsich, an anonymous reviewer and journal editors for their useful comments that improved this manuscript.

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