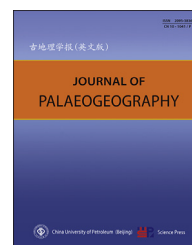




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Palaeobiogeography

Copernicrinus zamorae gen. et sp. nov., the oldest thiolliericrinid crinoid (Crinoidea, Echinodermata) from the Bajocian strata of Algeria, Africa



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Abstract The thiolliericrinids (Thiolliericrinidae) are comatulids (Comatulida), which retained their stalks as adults. Here, we report a centrodorsal from the Bajocian strata (Middle Jurassic) of the Djebel Kérdacha area, northwestern Algeria (Africa). It is the first thiolliericrinid report from outside of Europe and also the oldest representative of the Thiolliericrinidae whose first occurrence is from the Oxfordian. The crinoid is assigned to *Copernicrinus zamorae* gen. et sp. nov. The reported new taxon shows strong similarities with the stemless ‘true’ comatulids, *Solanocrinites*; the only difference is the presence of a facet to the stem in *Copernicrinus*. The closest comparable thiolliericrinid to *Copernicrinus* is the Oxfordian *Thiolliericrinus*, interpreted as a descendant of the latter. The origin and overview of all thiolliericrinid representatives are also discussed herein.

Keywords Thiolliericrinidae, Crinoids, Coral facies, Bajocian, Jurassic, Algeria, Southern Tethys margin

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1. Introduction

The thiolliericrinids (Thiolliericrinidae A.H. Clark, 1908) are a group of Jurassic–Cretaceous stalked crinoids that were included in the comatulids (Comatulida A.H. Clark, 1908) by Hess and Messing (2011). Previously, Rasmussen (1961) classified them as an uncertain order but later included them within the family Thiolliericrinidae, order Comatulida (Rasmussen, 1978). These crinoids, on the one hand, have features typical of comatulids (such as the presence of a centrodorsal very commonly covered with cirri), but also possess elements noted in bourgueticrinids (Bourgueticrinina Sieverts-Doreck, in Ubaghs, 1953), *i.e.*, the presence of a stem with synarthrial articulations. The columnals of thiolliericrinids closely resemble bourgueticrinid columnals, which can be small or large. They can be low, discoidal to tall, barrel-shaped, sub-cylindrical, or hourglass-shaped, with synarthries of opposite ends oriented differently. The stem was attached to the substrate by an expanded terminal disk with synarthrial articulation tilted obliquely relative to the substrate. The thiolliericrinid cup was comprised of five basals that were typically hidden. The radials (5 in number) were massive, and the first primibrachials were axillary. All brachial plates were united only by muscular articulations. According to Klikushin (1987), these crinoids had crowns that could be firmly closed. Hess and Messing (2011) believed that the crown might be able to close due to the presence of secundibrachials and tertibrachials that were asymmetrical.

Until now, it was believed that the first occurrence of thiolliericrinids was from the Oxfordian (Late Jurassic) and the last ones from the Hauterivian (Early Cretaceous). Here, we document the remains of thiolliericrinids from the Bajocian (Middle Jurassic) deposits of Algeria. Globally, this is the oldest thiolliericrinid record and the one outside Europe. Herein, this article establishes the monotypic genus and species *Copernicrinus zamorae*, based on one centrodorsal accompanied by columnals.

2. Geological background

The study area lies in northwestern Algeria, where, in response to the convergence of the

African and Eurasian plates, two main SW-to-NE-trending orogenic systems developed by the Late Cretaceous (Durand-Delga and Fontboté, 1980). The resulting orogenic belts are the Rif–Tell domain to the north and the Atlas Mountains to the south (Fig. 1A).

The Rif–Tell domain (Rif in Morocco and Tell in Algeria and Tunisia) was formed in response to the closure of the Maghrebian Tethys and the inversion of the associated paleomargins (Leprêtre *et al.*, 2018). It includes three main parallel tectonic zones, from north to south (Wildi, 1983): 1) the Alpine Internal Zone, originated from the former northern European margin of the Maghrebian Tethys; 2) the Maghrebian Flysch nappes, regarded as the former sedimentary cover of the Maghrebian Tethys; and 3) the Alpine External Zone, interpreted as the North-African paleomargin inversion during the Cenozoic collision.

The Atlas Mountains are oriented approximately SW–NE. They comprise a set of inverted intraplate belts (the Saharan Atlas and Aures in Algeria, the High Atlas and Middle Atlas in Morocco, and the Tunisian Atlas) derived from the inversion of several rim basins associated with the development of the Atlantic and Tethys oceans during the Mesozoic (e.g., Frizon de Lamotte *et al.*, 2000).

The Saharan Atlas (also called the Pre-Saharan Atlas) corresponds to a poorly deformed intra-continental belt extending between the Aures Range and the Moroccan High Atlas, about 1000 km along in the SW–NE direction. To the north, this belt is juxtaposed to tabular and stable blocks (poorly deformed or undeformed by the Tertiary compressive events) of the High Plateaus (or the Oran Meseta). The Saharan Atlas is a flat area bounded to the south by the Sahara Basin and composed of Phanerozoic sedimentary rocks that were affected by low-magnitude deformations (Frizon de Lamotte *et al.*, 2013). The southern border of the Saharan Atlas is marked by the South Atlas Fault (SAF) system (Fig. 1A), a discontinuous sequence of faults with directions varying between 45° and 90° (Jacobshagen, 1992). This major tectonic break extends from the Agadir in Morocco to the Gabes in Tunisia.

The Saharan Atlas is subdivided into three parts (Ritter, 1902): the Ksour Mountains in the west (the focus of the present study), the Djebel Amour in the

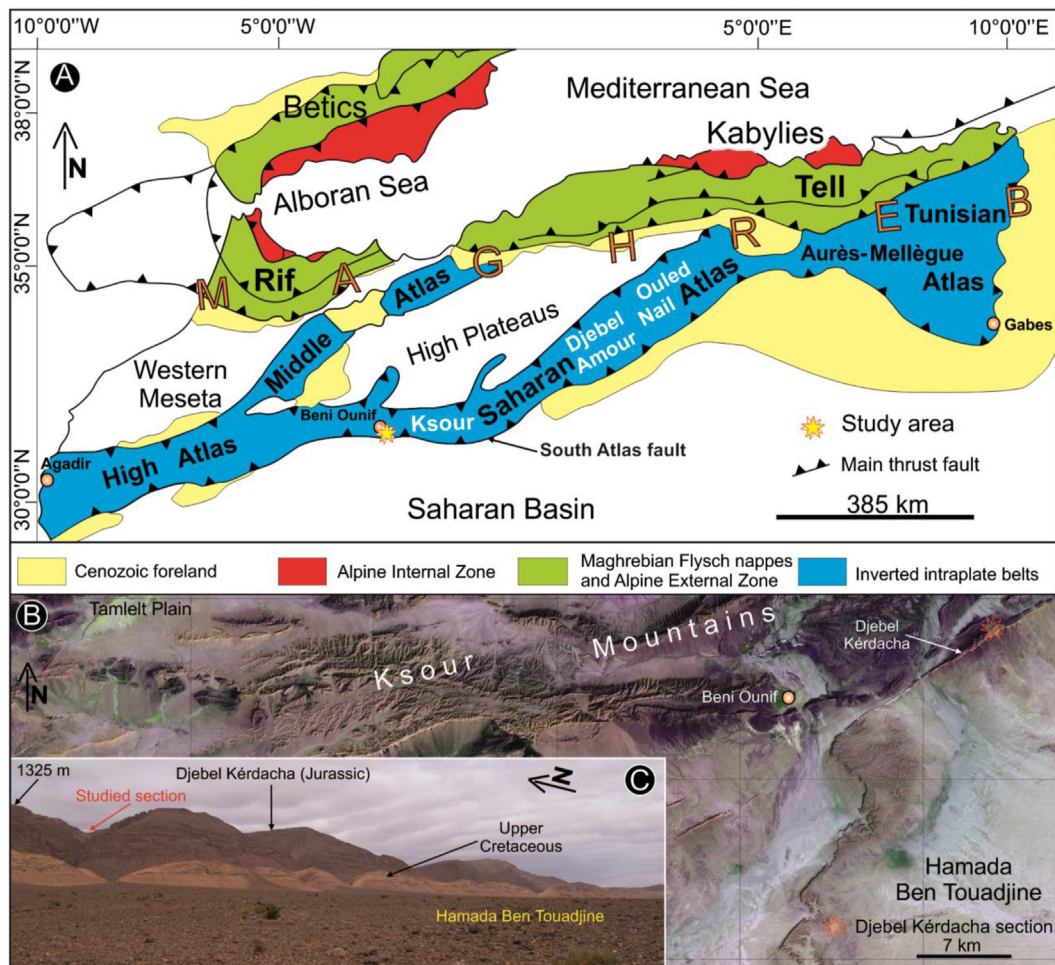


Fig. 1 Geological background of the study area. **A)** Structural map of the Western Mediterranean region depicting the main orogenic systems (modified from Michard *et al.*, 2008). The geological “Maghreb” essentially corresponds to the Rif–Tell and Atlas tectonic domains; **B)** Satellite images showing the position of the studied Djebel Kérdacha section; **C)** Panoramic view of the southern foot of the Djebel Kérdacha, showing the position of the studied Djebel Kérdacha section and the contact between the Jurassic (dark outcrop) and Cretaceous (clear outcrop) outcrops.

center, and the Ouled Nail Mountains in the east (Fig. 1A and B; Ritter, 1902).

The investigated area is on the southern edge of the Ksour Mountains, on the Algerian–Moroccan border, a few tens of kilometers from Beni Ounif town (Fig. 1). The study area forms a clear topographical barrier rising above a Saharan Plateau (Hamada Ben Touadjine) with altitudes reaching 1325 m at the highest point of Djebel Kérdacha. The latter extends over some 20 km, rising gradually from SW to NE (Fig. 1B and C). The Djebel Kérdacha corresponds to Jurassic deposits and develops a knee-shaped anticline structure. The Upper Cretaceous outcrops are inversely dipping and form an upside-down syncline structure (Fig. 1C).

3. Material and methods

Sampling at close intervals was carried out. Loose samples (marls) were soaked in water for several days and then washed on a series of sieves with decreasing mesh (300 μm , 250 μm , 180 μm , 125 μm) under a strong jet of water. The retrieved residues from each sieve were dried, steamed, and then sorted under a Euromex Dzet Optika ST-40-2L binocular loupe, housed at the Faculty of the Nature and Life Sciences of the Mustapha Stambouli University (Mascara, Algeria), to identify their microfossil content. Six microcells with fossils, mainly crinoids, from different intervals of the Djebel Kérdacha section were sent to Poland. Sorted crinoid

specimens were fixed on stubs using double-sided carbon adhesive tape and covered with a thin layer of gold for scanning electron microscope (SEM) image taken from the Hitachi S-4700, housed at the Institute of Geological Sciences, Jagiellonian University in Kraków, Poland.

The crinoids from the Djebel Kérdacha section in western Saharan Atlas, Algeria are housed at the Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia in Katowice, Poland, under the catalogue number GIUS 8–3689/Baj.

4. Collected fauna

The richly fossiliferous Kérdacha section is characterized by abundant echinoid and ophiuroid remains, annelid tubes, bryozoans, and crinoids. More than 100 columnals, brachials, cirrals, and one centrodorsal were collected. All these remains were found in the following samples: K3, K4, K6, K28 (two cells), and K46 (Fig. 2).

Sample K3 (Pliensbachian): *Balanocrinus ticinensis* (Hess, 2006), *Chladocrinus basaltiformis* (Miller, 1821).

Sample K4 (Pliensbachian): *Chladocrinus basaltiformis* (Miller, 1821).

Sample K6 (Pliensbachian): *Balanocrinus ticinensis* (Hess, 2006), *Chladocrinus basaltiformis* (Miller, 1821).

Sample K28 (Toarcian): *Isocrinus* cf. *jurensis* (Quenstedt, 1852).

Sample K46 (Bajocian): *Copernicrinus zamorae* gen. et sp. nov.

5. Description and age of the lithostratigraphic units

The lithostratigraphy of the Jurassic deposits outcropping on the southwestern border of the Ksour Mountains matches the subdivisions proposed by Bassoullet (1973), Mekahli (1998), and Salhi (2002). The studied Djebel Kérdacha section includes three formations, namely, the Lithographic Limestone Formation, the Marly Limestone Formation and the Kérdacha Formation (Fig. 2).

5.1. Lithographic Limestone Formation (Formation des Calcaires Lithographiques; Mekahli, 1998)

The Lithographic Limestone Formation is a 40 m-thick lithostratigraphic unit which consists mainly of dark grey to black, hard, well-stratified lithographic

limestones (0.10–0.25 m-thick) interbedded with thin grey marls (0.03–0.07 m-thick). The beds become thicker (0.20–0.40 m) towards the top, forming large cliffs. The limestone beds are laterally continuous over hundreds of meters and contain ammonites, belemnites, pectinid bivalves, brachiopods, and rare trace fossils, such as *Zoophycos* and *Chondrites*. The microfacies consist predominantly of bioturbated fine-bioclastic wackestone with sponge spicules, fragments of echinoderms, thin-shelled bivalves and calcispheres. The interbedded marls yielded crinoid and ophiuroid remains (samples K3, K4, and K6) with rare planktonic foraminifera and ostracods (Fig. 2).

The dating of the Lithographic Limestone Formation is imprecise. It has been assigned to the Middle Lias (~late Pliensbachian) based on the presence of the brachiopod, *Aulacothyris resupinata* (Sowerby) (Mekahli, 1998). Vörös (2014) noted that *A. resupinata* indicates a Sinemurian or an early Pliensbachian age, although it is very common in the late Pliensbachian or even in the Toarcian. Alméras *et al.* (2015) suggested an early Toarcian age.

5.2. Marly Limestone Formation (Formation des Marno-Calcaires; Mekahli, 1998)

The Marly Limestone Formation is about 80 m-thick (Fig. 2). It is mainly comprised of thick green to yellowish-green marls intercalated with grey and brown, centimeter- to decametric-thick bivalve- and brachiopod-rich bioclastic limestone, coral limestone, and oolitic limestone beds. The coral and oolitic limestone facies are characterized by coarse- to medium-grained, friable to compact fossiliferous, discontinuous beds with straight to irregular bounding surfaces. The lowermost and upper parts of the formation consist of an alternation of laminated green marls (0.20–0.80 m-thick) and lithographic limestone beds (0.05–0.50 m-thick) with bioclastic wackestone texture. Several microfacies types were identified in this formation. In the lower part of the formation, ooid-bioclastic grainstones with radial and micritic ooids were observed. Upwards, there are thin beds with coral-bioclastic floatstones. On the surface of corals, there are thin microbial crusts, numerous borings, and serpulid encrustations. Microbial crusts are commonly developed on skeletons. In addition, scattered ooids, bivalves, and gastropods are common in the micritic matrix. In the middle part of the formation (interval of ~80–90 m, Fig. 2) in the limestone beds, bioclastic wackestone microfacies is also observed, where the bioclasts are thin-shelled brachiopods, bivalves, echinoderms and sponge spicules.

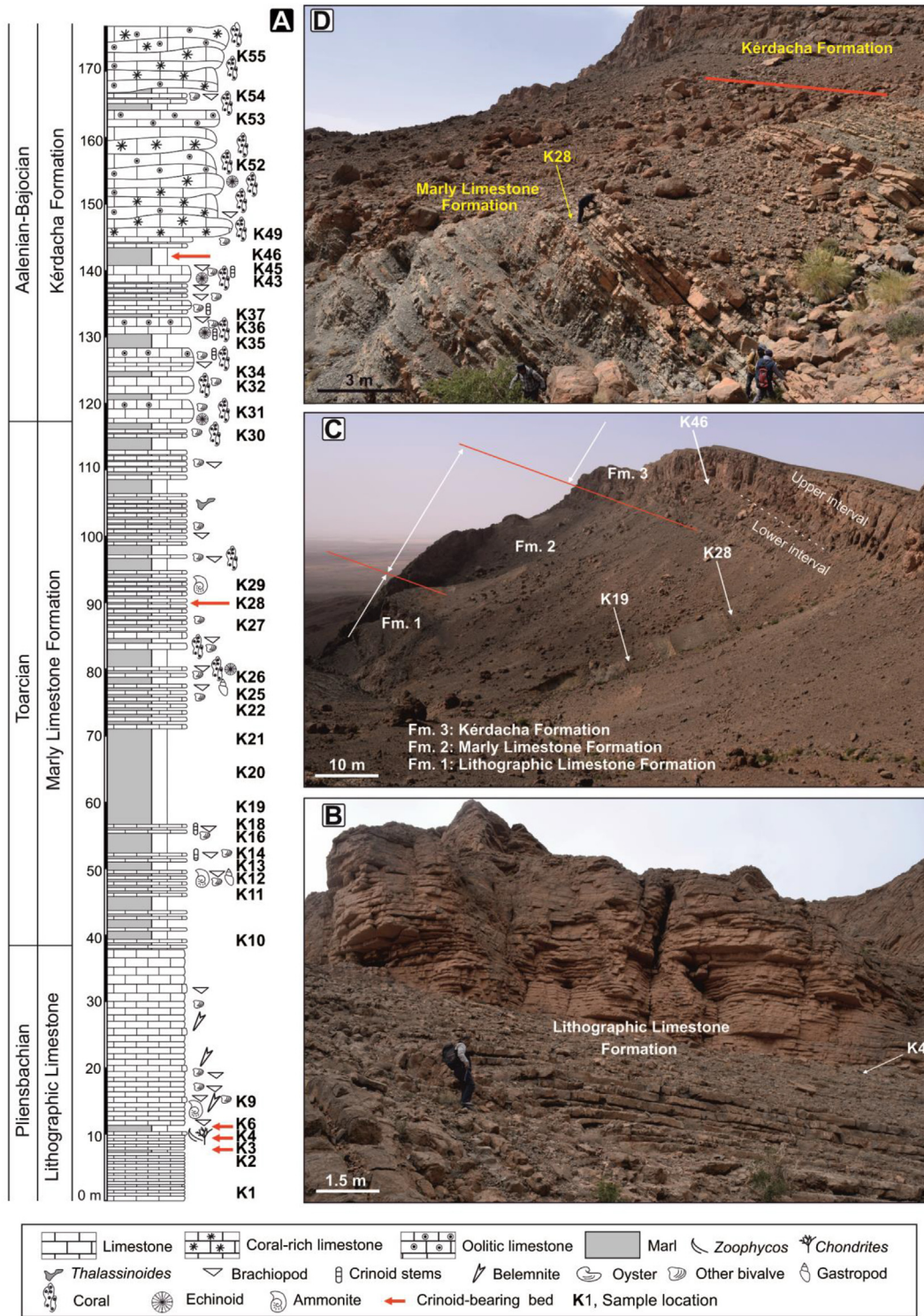


Fig. 2 The Lower–Middle Jurassic Djebel Kerdacha section. **A)** Measured lithostratigraphic section showing the position of the crinoid-bearing beds; **B–D)** Panoramic views showing the Lithographic Limestone, Marly Limestone, and Kerdacha formations and the sampling locations.

The marly intervals yielded ostracods and foraminifera (e.g., *Lenticulina dorbignyi* (Roemer)) of late Toarcian age (Mekahli, 1998; Salhi, 2002). The uppermost marls yielded the foraminifera, *Lenticulina quenstedti* (Gümbel) (Mekahli, 1998). Genus *Lenticulina* first appeared during the Aalenian. In the present study, crinoid remains (sample K28) from the middle part of the Marly Limestone Formation were recorded (Fig. 2).

5.3. Kérdacha Formation (Formation de Kérdacha; Bassoullet, 1973)

The Kérdacha Formation is about 60-m thick and consists of grey to brownish, decimetric- to meter-thick, coral-bearing, bioclastic, oolitic, and peloidal limestone beds intercalated by greenish marls (Figs. 2 and 3). Two intervals can be distinguished (Fig. 2A–C). The lower interval (interval of ~118–145 m; Fig. 3A) has a platy coral-bioclastic floatstone/wackestone microfacies (Fig. 3A and G). In addition to platy corals, there are numerous fine bioclasts of echinoids, serpulids, and bivalves. The uppermost marl bed yielded crinoid remains (*Copernicrinus zamorae* gen. et sp. nov.; sample K46; Fig. 2A and 3A). A distinct microfacies type was identified in the upper interval above the marl bed. In the limestone beds, numerous redeposited gray-coated grain-bioclastic rudstone/floatstone with crushed bioclasts of corals, gray intraclasts, bivalves and ooids were observed in the yellow micritic matrix. Upwards in the succession, ooid-bioclastic grainstones are present (Fig. 3A and H). The upper part of the formation is dominated by massive beds of coral-bioclastic floatstone/bafflestone formed by numerous massive scleractinian coral colonies that are not always in growth position. The scleractinian corals have platy, massive, branching and encrusting forms (Fig. 3B–F). The recorded genera include *Isastrea*, *Cladophyllia*, *Dimorpharaea*, *Montlivaltia*, *Dendraraea*, *Thecosmilia*, and *Stylosmilia*. Corals are commonly bored (*Gastrochaenolites* and *Trypanites*) and encrusted with serpulids; thin microbial crusts are also noted on several surfaces. Together with corals, the associated faunas include bivalves (*Chlamys*, *Nanogyra*, *Plagiotoma*, and *Lopha*), brachiopods (*Rhynchonella* and *Aulacothyris*), short-length crinoid stems, echinoids, small gastropods, ammonites, foraminifera, and sponges (Fig. 3I).

Based on the occurrence of the benthic foraminifera *Dentalina oolithica* and the ostracod *Procytheridea*, the upper part of the Kérdacha Formation was assigned a Bajocian age (Mekahli, 1998; Salhi, 2002).

6. Paleoenvironment of the Lower–Middle Jurassic deposits in the Djebel Kérdacha section

6.1. Lithographic Limestone Formation (Pliensbachian)

The fine-grained sediment of the Lithographic Limestone Formation is interpreted as a deposition from suspension. The presence of fine bioclastic wackestone texture, open marine fauna (ammonites, belemnites, and sponge spicules), trace fossils *Chondrites* and *Zoophycos*, are all suggestive of sedimentation under weak hydrodynamic conditions, below storm-wave base. This interpretation is supported by the presence of pelagic crinoids at some marly intervals along with the lack of sedimentary structures, and is suggestive of shallow waters and strong bottom currents (e.g., hummocky cross-stratification). *Chondrites* is a burrow of deposit-feeding infaunal organisms, such as annelids and/or sipunculoids (Osgood, 1970) and is commonly noted in deep water sediments (Bromley and Ekdale, 1984; Mekki *et al.*, 2019). Besides being a good anoxic indicator, it commonly co-occurs with *Zoophycos* (Bromley and Ekdale, 1984). *Zoophycos*, like *Chondrites*, also occurs in low-oxygen conditions (Ekdale and Lewis, 1991). Thus, the *Zoophycos*–*Chondrites* association suggests a low-oxygen environment below storm-wave base (see also Bouchemla *et al.*, 2023). A low-energy deep outer shelf/ramp environment was also proposed by Mekahli (1998).

6.2. Marly Limestone Formation (Toarcian)

This fine-grained deposit of marl and lithographic limestones matches low-energy settings. The concentration of brachiopods, corals, and ooids that were partially dispersed and pushed seaward by currents indicates medium- to high-energy conditions. Mekahli (1998) and Salhi (2002) proposed a shallow lagoonal environment of deposition. Upwards, the gradual disappearance of shallow subtidal ooid and coral deposits suggests the decrease in wave energy and a rise in sea level.

6.3. Kérdacha Formation (Aalenian–Bajocian)

The coral-bearing limestones of the Kérdacha Formation were deposited in shallow subtidal inner carbonate platform and represent shallow-water photic environments within a shallowing-upward succession. The sedimentary succession represents

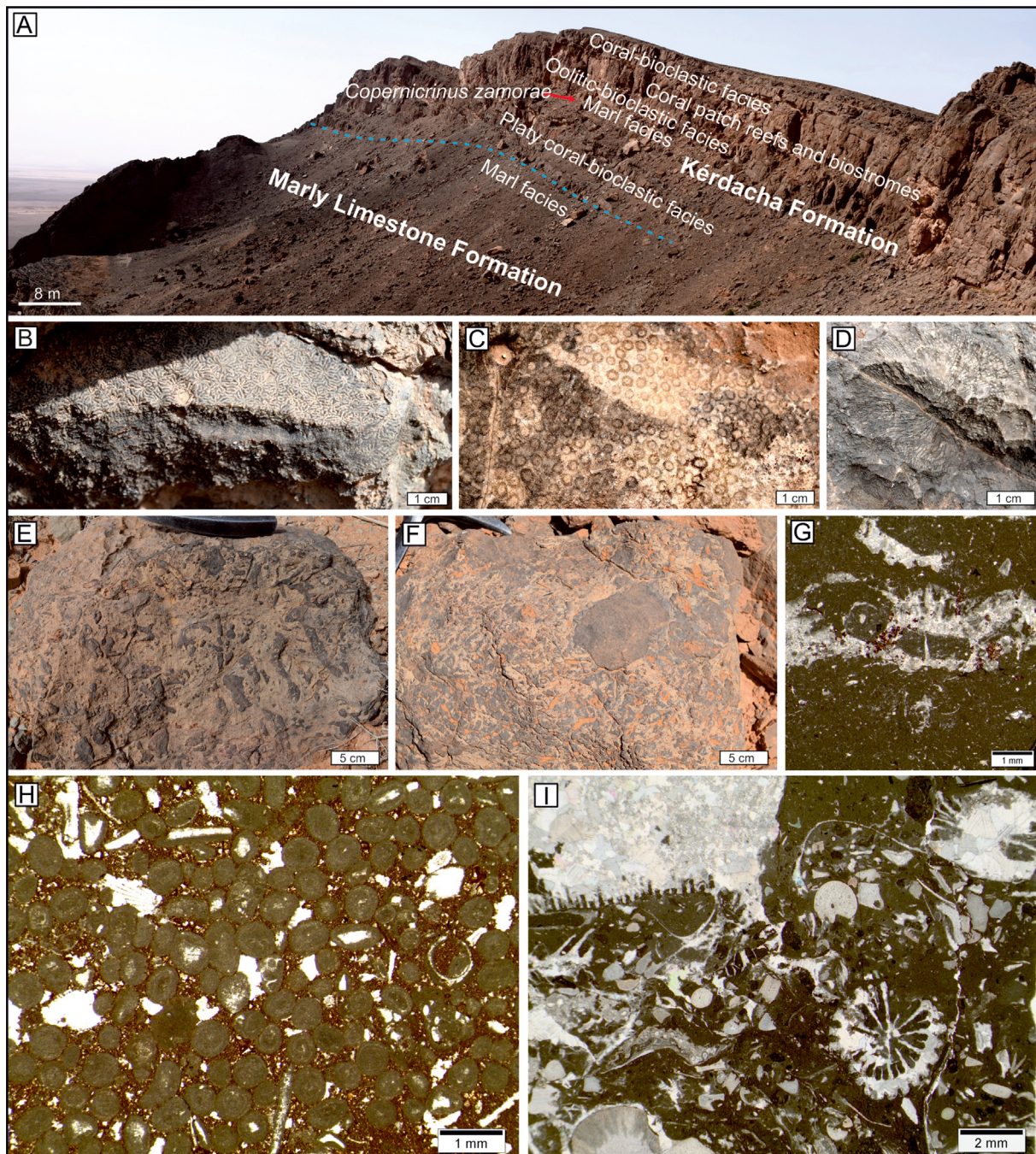


Fig. 3 Simplified sedimentary succession with main facies and microfacies examples. **A)** Position of *Copernicrinus zamorae* gen. et sp. nov., in the sedimentary succession of the Aalenian–Bajocian Kérdacha Formation; **B–F)** Coral-bioclasic facies (floatstone/bafflestone) in massive limestone beds of the upper interval of Kérdacha Formation; **G)** Platy coral-bioclasic floatstone microfacies in the lower interval of Kérdacha Formation; **H)** Oolitic-bioclasic grainstone; **I)** Coral-bioclasic floatstone microfacies in the upper interval of Kérdacha Formation with patch-reefs and biostromal facies.

coral colonization of an oolitic-bioclasic back-shoal environment. Corals commonly form meter-scale patch reefs and coral-bioclasic autobiotromes or parabiotromes (*sensu* Kershaw, 1994). The Kérdacha Formation sediments were deposited in low- to

moderate-energy conditions within a protected, sheltered environment, thus, allowing the deposition of micritic and peloidal sediments. The mentioned coral bioconstructions well refer to the Bajocian coral patch reefs known, e.g., from the Moroccan Central

High Atlas (Addi and Chafiki, 2013; Addi, 2015), that grew in the so-called optimum of the Bajocian reefal window and may refer to one of the most important episodes of reef building span in the Aalenian–early Bajocian of the Moroccan Atlas (e.g., Sadki and Sha, 2018).

6.4. *Paleoenvironment and position of the thiolliericrinids in the Djebel Kérdacha section*

All occurrences of thiolliericrinids (for details, see Klikushin, 1987; Salamon *et al.*, 2019) were always associated with corals. This was already pointed out by Klikushin (1987), who distinguished three types of coral-algal or coral-sponge bioconstructions within which thiolliericrinids were common. One type of such structure within the Berriasian and Valanginian deposits of Crimea was called the barrier reefs. They were characterized by their large sizes, up to 15 m thick and even several hundred meters long. They were comprised of nodules of calcareous algae and colonial corals, and within them there were lenses of the coarse-grained sandstones and pockets saturated by the quartz pebbles. Reef-dwellers (oysters), *Prohinnites*, *Trichites*, *Heterodicerias*, and nerineid gastropods were common within them. Another type was so-called ‘tower-like’ bioherms with discoid shapes and moderate sizes (Klikushin, 1987). Their thickness did not exceed 8 m, and their length was a maximum of 20 m. Colonial hexacorals, stromatoporoids and calcareous algae were common within them. The interfaces between the bodies of the reef-forming organisms were filled with loose calcareous-argillaceous masses. Therefore, the characteristic tube-like forms appeared in the weathering process of these bioherms. Small oysters, brachiopods, calcareous sponges, bryozoans, small solitary corals, serpulids, and other organisms were also among the reef dwellers. Traces of boring organisms were also frequent within them. The last type of bioconstruction recorded also from Crimea was the ‘yet-formed’ bioherms (Klikushin, 1987). They were small lenses (not more than one meter thick and up to 10 m long) enclosed within the strata of the microphytolithic or bioclastic stratified limestones. These structures were built by colonial and solitary corals accompanied by calcareous algae, sponges, stromatoporoids, oysters, brachiopods, echinoid spines and the so-called microencrusters (cf., Krajewski and Schlagintweit, 2018). Thiolliericrinids, although present within the ‘yet-formed’, were rare. The deposits of the Kérdacha Formation are assigned to this last type of bioconstruction.

7. Paleontology

Remarks. Taxonomy and terminology after Hess and Messing (2011). All isocrinid taxa counted above will be described elsewhere.

Order Comatulida A. H. Clark, 1908.

Suborder Comatulidina A. H. Clark, 1908.

Superfamily Solanocrinitoidea Jaekel, 1918.

Family Thiolliericrinidae A. H. Clark, 1908.

Copernicrinus new genus

Type species. *Copernicrinus zamorae* gen. et sp. nov., by monotypy.

Etymology. In honour of Mikotaj Kopernik (in Latin: Nicolaus Copernicus), Polish polyhistorian and astronomer, and creator of the heliocentric model of the Solar System, which was published in his book *De revolutionibus orbium coelestium*. The Senate of the Republic of Poland adopted 2023 as the year of Copernicus.

Diagnosis. Centrodorsal small, relatively low, truncated conical, and distinctly 5-sided. Upper side of a centrodorsal is flat. Cavity is circular and narrow. Centrodorsal is covered by large, rather circular cirri sockets; and some sockets are ovoid or compressed oval in shape. Every socket has an extensive neural canal, most commonly rounded, sometimes ellipsoidal or even irregular. Cirrus sockets are arranged in 10 columns of 1 socket or 2 sockets per column. Sockets are separated by distinct ridges. Facet to stem is circular, unusually wide and concave.

Copernicrinus zamorae new genus and species (Fig. 4)

Type material. The holotype is centrodorsal stored at the Museum of Department of Natural Sciences, University of Silesia in Katowice, Poland, with the specimen numbered GIUS 8–3689/Baj/Cz.

Type locality. Djebel Kérdacha (Western Saharan Atlas, northwestern Algeria); coordinates: 32.189578, –0.893760.

Type level. Greenish marl interval at the middle part of the Kérdacha Formation.

Accompanying material. Five columnals. Columnals are tentatively assigned to *Copernicrinus*, because they have much larger diameters than the facet to stem located on the centrodorsal. Moreover, facet to stem is covered by three indistinct bulges separated from each other by 120°. This type of ornamentation was not observed on columnals.

Measurements. Centrodorsal diameter in basal part: 1.19 mm; centrodorsal diameter in proximal part: 2.09 mm; centrodorsal height: 1.27 mm; cirrus scar sockets diameter: 0.43–0.71 mm.

Etymology. In honour of Dr. Samuel Zamora Irazo, foremost authority on fossil echinoderms.

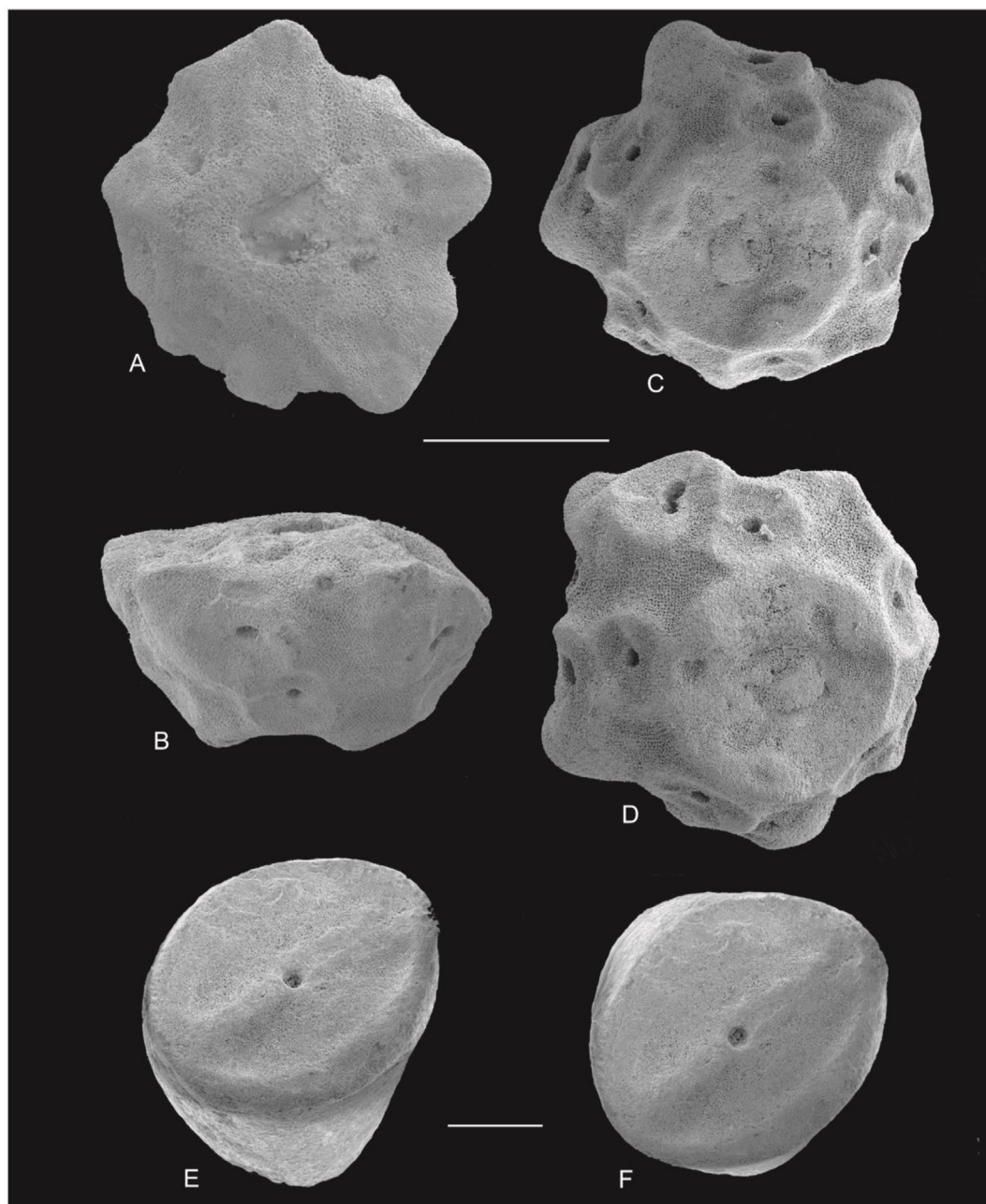


Fig. 4 *Copernicrinus zamorae* gen. et sp. nov., Bajocian, Algeria, Djebel Kérdacha. GIUS 8–3689/Baj/Cz; A–D) Centrodorsal: distal (A), aboral (B), lateral (C), and oblique (D); E–F) Columnal: slightly oblique (E), and articular face (F). Scale bar equals 1 mm.

Diagnosis. Type species by monotypy.

Description. Centrodorsal is small, relatively low, truncated conical, and distinctly 5-sided. Upper side of a centrodorsal is flat and central cavity is circular and narrow. Its lateral surface is covered with large cirral sockets that are grouped in 10 rows. There is one or a maximum of two sockets in each row. Each socket is elevated and separated from the next by a distinct ridge. Cirral sockets are most commonly rounded, less

common ovoid or compressed oval. There is a distinct neural canal that is rounded, ellipsoidal or even irregular, inside each socket. Total number of sockets is 15. Facet to stem is circular, wide and concave. It is covered by three indistinct bulges separated from each other by 120° . Radials and basals are unknown. Columnals are small, low, discoidal, or larger, high, with concave latera. Articular facet is circular or ellipsoidal. Fulcral ridge is serrated in some columnals.

Marginal ridge is twinned, with twins almost perpendicular to each other on both sides of the columnal. Lumen is small and circular.

Stratigraphic distribution. Bajocian (Middle Jurassic) of Algeria.

8. Discussion

8.1. Origin of thiolliericrinids

Among the post-Paleozoic crinoids, only isocrinids (Isocrinida) and comatulids (Comatulida) had cirrals. [Klikushin \(1987\)](#) argued that the origin of thiolliericrinids must be considered in close connection with the origin of comatulids and pentacrinids (Pentacrinidae [Gray, 1842](#)). This author concluded that the

initial form for comatulids was *Pentacrinites* (see [Klikushin, 1987](#), fig. 18). He also considered that *Paracomatula helvetica* [Hess \(1951\)](#), in having a centrodorsal consisting of several nodal columnals and a crown already typical for comatulids, is a great example of a transitional form between pentacrinids and comatulids (see [Fig. 5](#)). [Rasmussen \(1978\)](#) argued that thiolliericrinids developed from *Solanocrinites*-like forms through pedomorphosis during the Jurassic. [Hess and Messing \(2011; see also Hess, 2014\)](#) added that significant changes were observed in the development of thiolliericrinids, which consisted of the reduction of basal and the loss of cirri, resulting in their permanent fixation to hardgrounds. According to [Klikushin \(1987\)](#), these crinoids reached their highest diversity shortly before their demise (during the Early Cretaceous).

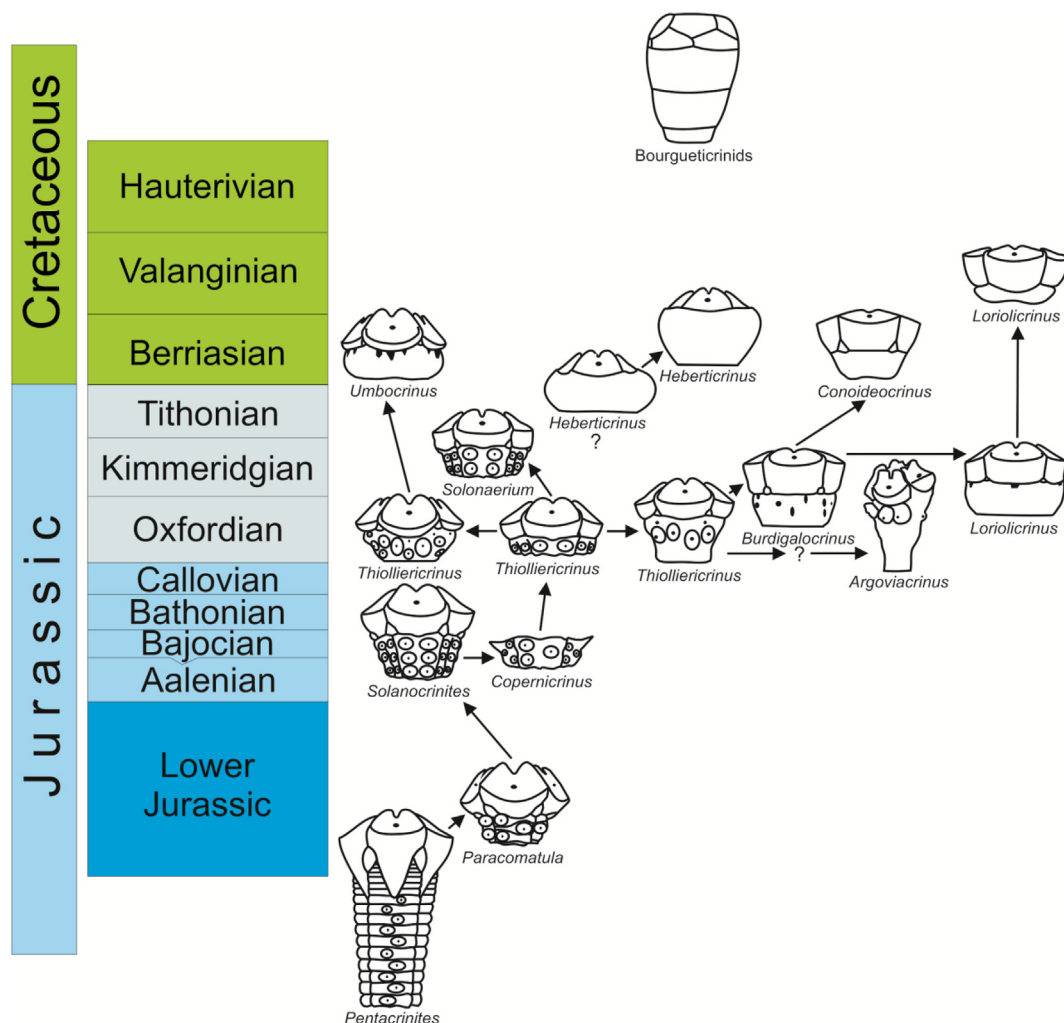


Fig. 5 A scheme presenting presumed origin and development of thiolliericrinids (idea taken from [Klikushin, 1987](#); crinoid diagrams redrawn from [Klikushin, 1987](#); [Hess and Messing, 2011](#); data compiled after [Étallon, 1859](#); [Thurmann and Étallon, 1861](#); [Jaekel, 1891, 1918](#); [Rasmussen, 1961, 1978](#); [Klikushin, 1987](#); [Hess and Spichiger, 2001](#)).

8.2. Overview of thiolliericrinids — Relationships, stratigraphic and paleogeographic distribution

8.2.1. *Solonaerium* and *Copernicrinus*

Klikushin (1987) refigured Goldfuss (1831, in Goldfuss, 1826–1833, pl. 51/2) and Quenstedt (1876, p. 176) specimens under *Solonaerium sigillatum* (Quenstedt, 1876) and considered them to be the initial forms to all thiolliericrinids. This form had high radials, relatively large basals, and a regular disposition of the cirrus sockets arranged in 10 columns of 2 or 3 sockets (see Fig. 5). However, *Solonaerium* Étallon, in Thurmman and Étallon (1861), cannot be considered as the oldest thiolliericrinid as its first occurrence is from the Kimmeridgian, Upper Jurassic (Nattheim in Württemberg, Germany; Rasmussen, 1978, Fig. 6). On the other hand, in the Kimmeridgian, the presence of a 5-sided form with cirrus sockets distinctly arranged in 10 columns was somewhat surprising. Our new data suggested that the oldest record of thiolliericrinids should be considered as *Copernicrinus zamorae* gen. et sp. nov., now documented from Bajocian sediments. It is a distinctly 5-sided form, small but with relatively large cirrus sockets, an extremely large facet to stem, and large cirrus sockets arranged in 10 columns of 1 or 2 sockets separated by distinct ridges. These features make it possible to consider the African specimen as one of the representatives related to the stemless *Solanocrinites* Goldfuss, 1829 (Goldfuss, 1826–1833), a genus characterized by strong intraspecific variations (e.g., Rasmussen, 1961). According to Hess and Messing (2011), the Jurassic (Bajocian–Tithonian) *Solanocrinites* had “Centrodorsal moderately high discoidal or truncated conical, more or less 5-sided form, with 10 columns of 1–3 large cirrus sockets separated by distinct ridges ...”, as also in *Copernicrinus*. In addition, the presence of a facet to the stem suggests our material should be linked with thiolliericrinids, which are not free-moving but comatulids derived through paedomorphosis, reverting to attachment by a column (Hess, 2014).

8.2.2. *Thiolliericrinus*

To date, it has been argued that the representatives of thiolliericrinids appeared during the Oxfordian (Late Jurassic). The first record of them is *Thiolliericrinus* Étallon, 1859, with *Thiolliericrinus flexuosus* Goldfuss, 1831 (Goldfuss, 1826–1833) as a type species. Étallon (1859) considered this species identical with *Apiocrinites flexuosus* Goldfuss (1831, in Goldfuss, 1826–1833) based on isolated columnals and

established *Thiolliericrinus flexuosus* as a new species. Étallon (1859) and de Loriol (1877–1879) described and figured genus and the type species in details. To avoid secondary homonymy with *Apiocrinites flexuosus* Goldfuss, which although is indeterminable and probably belongs to a genus of this family, Klikushin (1987) and Hess and Messing (2011) emphasized that the genus *Thiolliericrinus* is characterized by strong intraspecific variations. The shape and size of centrodorsal are the most variable features among all thiolliericrinids. The centrodorsal was covered with cirrus sockets, which covered it randomly or clustered in 10 rows with a maximum of 3 sockets in one row. In some cases, the centrodorsal could be strongly elongated and covered by randomly arranged small and large cirrus sockets (compared with Fig. 5). Gislén (1924) restricted the genus to species with large cirrus sockets, at variance with the type species. The radials of *Thiolliericrinus* were large; its basals were small, and they may have been concealed (e.g., in type species) or exposed (Fig. 5). The last occurrence of this genus is from the Hauterivian (Lower Cretaceous) and recorded from France, Germany, Portugal, and Switzerland (Fig. 6). Hess and Messing (2011) mentioned that its presence was also from the Czech Republic, probably referring to the reports of Remeš (1905), who mentioned *Thiolliericrinus heberti* de Loriol, in Pictet (1868) and *T. flexuosus* from the Tithonian of Štramberk (Czech Republic). However, the calyces presented by the latter author should be associated with *Heberticrinus* that had swollen centrodorsals within which radials were hidden; additionally, they were devoid of cirrus sockets (see pl. 2a–c, 3a–c, 4a, b, 5, 6a–d in Remeš, 1905).

8.2.3. *Burdigalocrinus* and *Loriolicrinus*

Klikushin (1987) thought that the Oxfordian representative of thiolliericrinids, *Burdigalocrinus* Jaekel, 1918, was derived from *Thiolliericrinus*; the present authors concur with this view. *Burdigalocrinus* had a moderately high centrodorsal area that was covered by several small and rounded cirrus sockets that lacked a visible articular ridge. All cirrus sockets were widely separated, irregularly arranged, and vestigial. This type of cirrus socket occurs in one of the morphotypes of *Thiolliericrinus*, in which the centrodorsals are elongated and covered in their upper part by irregularly arranged and vestigial cirrus sockets (comp. Fig. 5). The last occurrence of *Burdigalocrinus* was from the Berriasian (Lower Cretaceous) of Crimea (Fig. 6). This taxon was also noted from the Oxfordian of Portugal (e.g., Hess and Messing, 2011, Fig. 6). *Loriolicrinus* Jaekel, 1918, known from the Oxfordian,

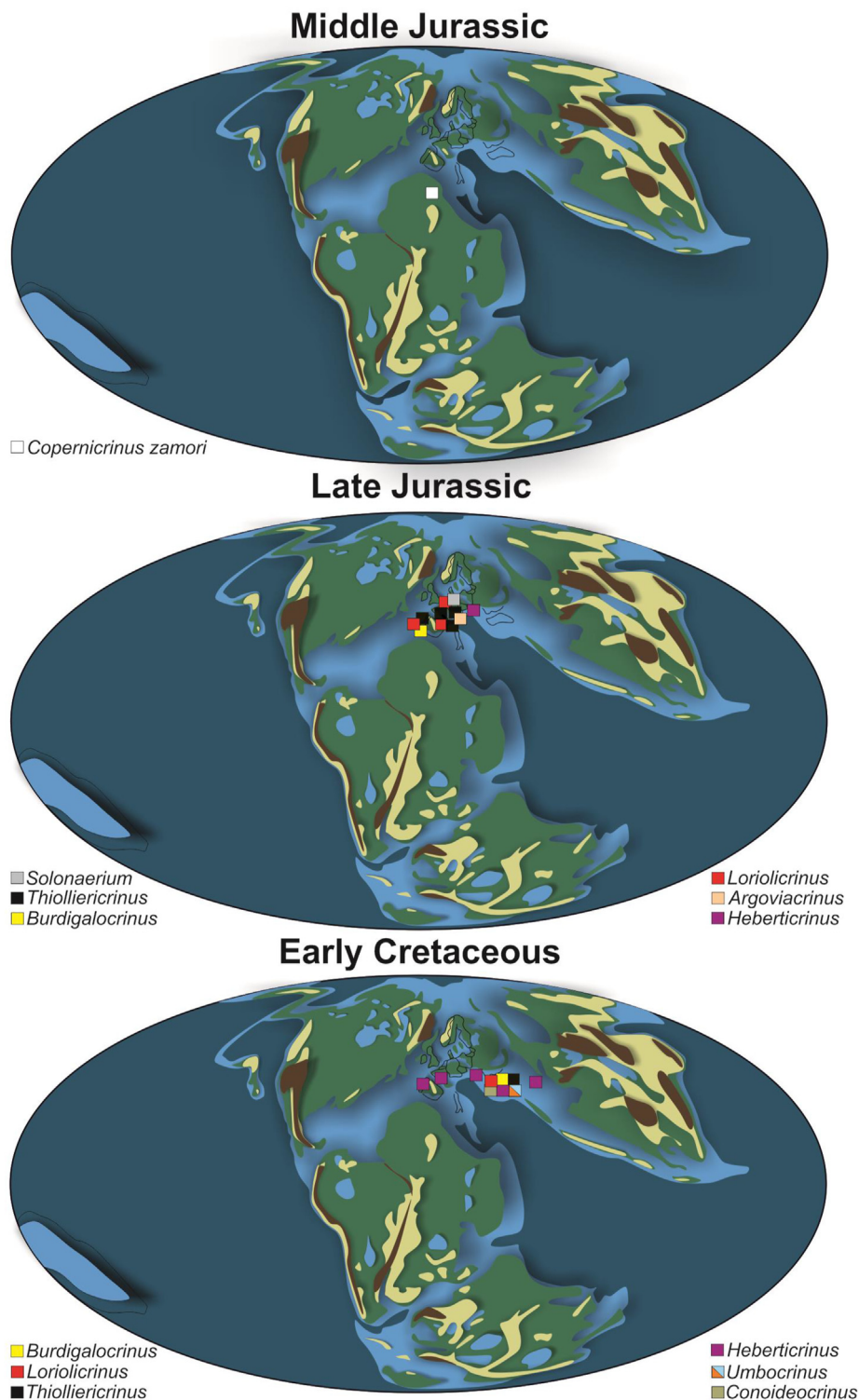


Fig. 6 Thiolliericrinid distribution during the Middle Jurassic–Early Cretaceous (modified after Scotese, 2014).

was considered a descendant of *Burdigalocrinus*. Its centrodorsal was low and lacked cirrus sockets, but it had a small fossa near the radial-centrodorsal suture (see Fig. 5). The last occurrence of *Loriolicrinus* was

from the Valanginian (Lower Cretaceous). In the case of Cretaceous forms, the fossae near the radial-centrodorsal suture are no longer present, while the centrodorsal becomes extremely low, and its basal

part is strongly concave. *Loriolicrinus* is recorded in Crimea, France, Germany, and Portugal (Fig. 6).

8.2.4. *Argoviacrinus*

The last thiolliericrinid crinoid that appeared in the Oxfordian was *Argoviacrinus* Hess and Spichiger, 2001. Hess and Spichiger (2001) documented the calyx of an aberrant individual (*Argoviacrinus rarissimus* Hess and Spichiger) from the middle Oxfordian of Switzerland (Fig. 6). This crinoid had a comatulid-like cup (radial articular facets and development of basals), the centrodorsal (although considerably higher) of a thiolliericrinid (presence of cirri), and the circular column of a cyrtocrinid (rimmed, granulose symplectial facet). Somewhat similar stem facets also occur in the Cyclocrinidae, a group of uncertain affinities represented by columnals only (e.g., Hess and Messing, 2011; Salamon *et al.*, 2021). Thiolliericrinids typically have a truncated conical or discoidal centrodorsal with a distinct synarthrial facet. In contrast, *Argoviacrinus* has a high, stem-like centrodorsal with a cryptosymplectial facet superimposed on a cryptosynarthry, hence, it is not entirely certain that *Argoviacrinus* belongs to the Thiolliericrinidae. *Argoviacrinus rarissimus* has not been documented outside of Switzerland.

8.2.5. *Heberticrinus* and *Umbocrinus*

Heberticrinus includes forms that appeared during the Tithonian (Late Jurassic), and their last occurrences are known from the Berriasian (Lower Cretaceous) (Fig. 6). They had large and convex centrodorsals. In the case of Cretaceous forms, the centrodorsal became unnaturally high. In *Heberticrinus* Klikushin, 1987, the disappearance of the fossae and basals and the decrease of the relative size of radials, are distinct, in which the principal morphological types can be determined according to the form and size of the centrodorsal. The absence of the fossae and basals is also observed in the Cretaceous representatives of *Loriolicrinus* (see Fig. 5).

Klikushin (1987) claimed that *Heberticrinus* was derived from *Umbocrinus* Klikushin, 1987. Indeed, the cups of both forms are similar, especially their centrodorsals, which are large and strongly convex. But there are differences between them. In *Umbocrinus*, the radials are large and exposed externally, whereas in *Heberticrinus*, they are obscured by the upper edge of the centrodorsal. Additionally, in *Umbocrinus*, the fossae near the radial-centrodorsal suture are present, whereas in *Heberticrinus*, they are not known to any of the representatives. Moreover, *Heberticrinus*

appeared much earlier (in the early Tithonian) than *Umbocrinus* (in the late Berriasian), so its origin status is still an open question (see Fig. 5).

Heberticrinus has been recorded in the Caucasus, Crimea, Czech Republic, France, Portugal, and Romania; while *Umbocrinus* is known only from Crimea (see Fig. 6).

8.2.6. *Conoideocrinus*

Conoideocrinus Klikushin, 1987 possesses a conical and moderately high centrodorsal with a flat base and pronounced fulcral ridge. It is the second representative of the Cretaceous thiolliericrinids, next to *Umbocrinus*, in which basals are visible. These features make it morphologically similar to the Jurassic *Burdigalocrinus*, as already noted by Klikushin (1987), who considered *Conoideocrinus* as a descendant of *Burdigalocrinus*. The only difference is related to the presence of cirrus sockets in *Burdigalocrinus*; the centrodorsal of *Conoideocrinus* is devoid of them. *Conoideocrinus* was recorded in the Berriasian of Crimea.

9. Conclusions

In the Bajocian strata of northwestern Algeria, Africa, crinoid remains consisting of columnals, and centrodorsal of a thiolliericrinid crinoid (Thiolliericrinidae) are recorded. The documented centrodorsal is truncated conical, 5-sided, with 10 columns of 1–3 large cirrus sockets separated by distinct ridges, typical of *Solanocrinites*, a stemless comatulid crinoid (Comatulida). At the same time, the African specimen has a facet to the stem, thus enabling its assignment as a thiolliericrinid. It is named *Copernicrinus zamorae* gen. et sp. nov. and represents the oldest thiolliericrinid ever documented. Additionally, it is the first stalked comatulid observed on the African continent. Of all the thiolliericrinids, the most similar to *Copernicrinus* is *Thiolliericrinus*, which is treated as a descendant of the latter.

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Availability of data and materials

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

Authors' contributions

Conceptualization: M.A.S. and B.J.P.; methodology: M.A.S., M.B., F.M., M.A., I.B., S.J., M.K., and B.J.P.; investigation and resources: M.A.S., M.B., F.M., M.A., I.B., S.J., M.K., and B.J.P.; data curation: M.A.S.; writing of preparing the original draft: M.A.S. and B.J.P.; writing of reviewing and editing: M.A.S., M.B., F.M., M.A., I.B., S.J., M.K., and B.J.P.; visualization: M.A.S., M.B., F.M., M.A., I.B., S.J., M.K., and B.J.P.; supervision: M.A.S. and B.J.P.; project administration: M.A.S. and B.J.P.; funding acquisition: M.A.S., B.J.P., and M.K. All authors read and approved the final proof.

Declaration of competing interest

No potential conflict of interest was reported by the authors.

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