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New archaeocyath genus from the early Cambrian of the western Anti-Atlas, Morocco

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KEY WORDS
Archaeocyatha,
Carinacyathidae,
early Cambrian,
Morocco,
western Anti-Atlas,
Issafen Formation,
Tata Group,
Fouanou Syncline,
new genus,
new species.

ABSTRACT
A new archaeocyathan genus had been discovered in the Issafen Formation of the Tata Group, in the western Anti-Atlas of Morocco. It had been identified and assigned to the family Carinacyathidae, which was previously known to have existed in Mongolia, Russia and Morocco during the later early Cambrian. This newly described genus and species is named: *Fouanoucyathus tafraoutiensis* El Bakhouch & Kerner, n. gen., n. sp. This discovery improves significantly our understanding of the morphological evolutionary history among archaeocyaths as well as of the archaeocyath diversification in the western Anti-Atlas of Morocco.

MOTS CLÉS
Archaeocyatha,
Carinacyathidae,
Cambrien inférieur,
Maroc,
Anti-Atlas occidental,
Formation d'Issafen,
Groupe de Tata,
Synclinal de Fouanou,
genre nouveau,
espèce nouvelle.

RESUMÉ
Genre nouveau d'archéocyathes de la Formation d'Issafen (Groupe de Tata), Anti-Atlas occidental, Maroc.
Un genre nouveau d'archéocyathes a été découvert dans la Formation d'Issafen (Groupe de Tata), dans l'Anti-Atlas occidental du Maroc. Ce genre a été identifié et rattaché à la famille des Carinacyathidae, qui est présente en Mongolie, en Russie et au Maroc au cours du Cambrien inférieur. Ce genre et espèce nouvellement décrit est nommé: *Fouanoucyathus tafraoutiensis* El Bakhouch & Kerner, n. gen., n. sp. Cette découverte pourrait améliorer considérablement notre compréhension des caractéristiques morphologiques, de l'histoire évolutive des archéocyathes de même que la diversité de cette faune dans l'Anti-Atlas occidental du Maroc.

INTRODUCTION

Archaeocyatha is a group of sessile, filter-feeding animals that underwent rapid evolution in the early Cambrian. They are the earliest major metazoan builders of Cambrian reefs (Kerner & Debrenne 2013). These remarkable organisms have been documented on all continents, although those of South America occur in allochthonous blocks in Upper Carboniferous-Lower Permian tillites (Stone *et al.* 2012; González *et al.* 2013). Archaeocyatha constitute a unique class within the phylum Porifera, representing the earliest aspiculate calcified sponges. Their calcareous skeletons are found within Cambrian strata that are themselves calcareous in composition. The classification of the archaeocyaths relies heavily on skeletal ontogeny, a process governed by the sequence of emergence and the level of complexity of skeletal elements (Kerner *et al.* 2011b). Furthermore, the global evolution of archaeocyaths reached its zenith during the Botoman age but experienced a dramatic decline by the end of the early Cambrian (end of the Toyonian). This biological event is tentatively linked to the global anoxia (the Sinsk Event) and the global regression that affected platformal marine ecosystems, particularly impacting sessile organisms such as archaeocyaths and other sponges (Zhuravlev & Wood 1996; Gandin & Debrenne 2010).

The lower Cambrian deposits in Morocco are well exposed across the Anti-Atlas and High Atlas mountains. The marine platform of the Anti-Atlas formed part of the northern margin of the Gondwana supercontinent (Álvaro *et al.* 2014). Microbial reefs (dominated by stromatolites) remained unaffected until early Cambrian Stage 3 (Atdabanian and equivalents). The base of the fossiliferous Tata Group is characterized by a sudden replacement of the stromatolite-dominated microbial consortium by calcimicrobial reefs with archaeocyaths and shelly metazoans (Hupé 1960; Schmitt & Monninger 1977; Destombes *et al.* 1985; Debrenne & Debrenne 1995; Álvaro *et al.* 2006; Álvaro & Debrenne 2010; Clausen *et al.* 2014; Azizi *et al.* 2022). The first appearance of archaeocyaths on the Moroccan margin can be related to sea-level fluctuations, transitioning from shallow water conditions to deeper open sea (Debrenne 2007; Álvaro & Debrenne 2010). The Atdabanian-Botoman interval demonstrates a significant increase in the complexity of marine ecosystems, characterized by the establishment of multiple microbial-archaeocyathan reef barriers consisting of various types of bioconstructions, including skeletal bioherms, biostromes, and mud-mounds of varying sizes and diversity of archaeocyaths (Álvaro & Debrenne 2010).

Moreover, the archaeocyathan fauna in Morocco remains largely unexplored and requires further examination. Research on this particular fauna dates back to the early 20th century, marked by the groundbreaking contributions of Russo (1927), Bourcart &Le Villain (1927, 1931), Neltner (1929) and Roch (1927, 1930). The most recent works on Moroccan archaeocyaths were published during the second part of the 20th century by F. Debrenne and M. Debrenne. Their studies were based on fossils collected by the mapping geologists of the "Service géologique du Maroc" (Debrenne 1964), private collections (Debrenne *et al.* 1992), and from some of the typical localities they revisited in 1963 and 1973 (Debrenne & Debrenne 1978, 1995).

Here a new genus *Fouanoucyathus* El Bakhouch & Kerner, n. gen. is described in details, along with the type species, *F. tafraoutiensis* n. gen., n. sp.

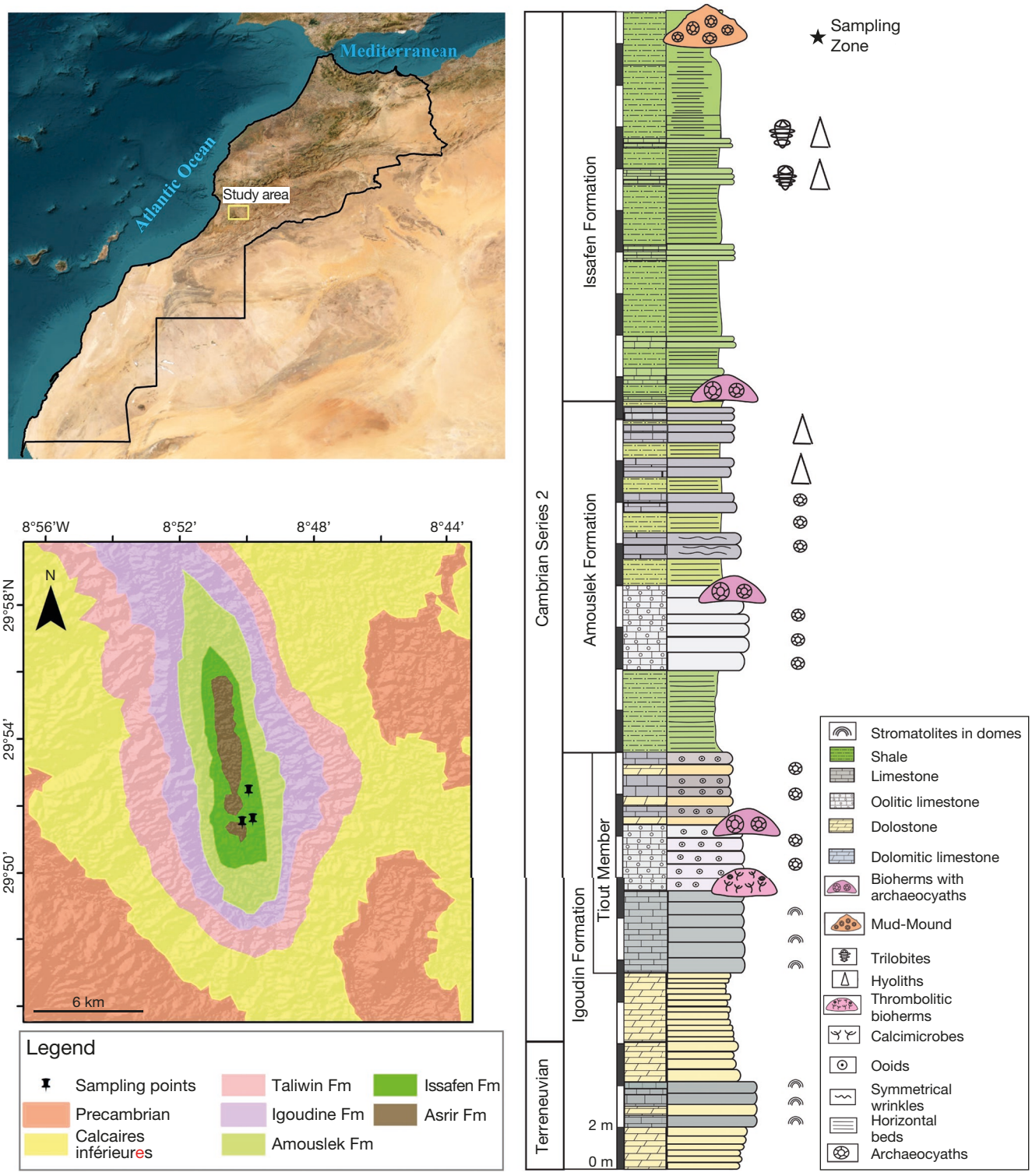

FIG. 1. — **A**, Studied area in the Anti Atlas Mountains within Morocco; **B**, simplified geological map of the Fouanou Syncline with location of the studied section (redrawn and modified after Geological Map of Morocco, TAFRAOUT sheet, scale 1/100 000); **C**, lithostratigraphy of the studied section in the Fouanou Syncline.

GEOLOGICAL SETTING AND STRATIGRAPHY

The Anti-Atlas Mountains are a northeast-trending belt in the central Morocco (Fig. 1A, B). They are bounded in the north by the South Atlas Fault (SAF), and in the south by the Tindouf Basin. Palaeozoic strata are well exposed on the southern slope of the Anti-Atlas, resting on the Precambrian Pan-African orogen (Destombes *et al.* 1985; Geyer & Landing 1995). The Palaeozoic cover comprises a mixed siliciclastics-carbonates with a thickness of about 1800 m. They were

deposited on the northern Gondwana margin and where it directly underlain by volcanics and volcaniclastics of the Ediacaran Ouarzazate Supergroup (577-560 Ma), which are approximately 2000 m thick (Thomas *et al.* 2004; Walsh *et al.* 2012). The lower Cambrian succession of the western Anti-Atlas has been subdivided into two extensive groups: the Taroudant and Tata groups, which together formed the early Cambrian carbonate platform dominated by dolostones and limestones. The Taroudant Group (1000 m thick) consists of the Adoudou and Lie de Vin formations. The overlying Tata Group, with a thickness of approximately 1000 m, is widely exposed in the western Anti-Atlas Souss Basin and was described mainly in the Taroudant area, in the Amouslek, Tiout and Tazemmourt sections (Álvaro *et al.* 2006), and within the Issafen and Fouanou synclines (Benssaou & Hamoumi 2001, 2004; Azizi *et al.* 2022; 2023). The Tata Group is divided into four distinct formations: the Igoudine, Amouslek, Issafen, and Asrir formations (Fig. 1B, C). The Igoudine Formation ("*calcaires supérieurs*" *sensu* Choubert [1952]), has a thickness range of 20-220 m and consists of dolomitized limestone (dominated in its lower part) and massive to bedded black ooid limestone. The latter package is overlain by the fossiliferous Tiout Member, representing the initial shift from microbial consortia, dominated by stromatolites, to shelly metazoan-thrombolite consortia rich in fossils of the Atdabanian stage (unnamed Cambrian Stage 3), such as archaeocyaths, chancelloriides, hyoliths, calcimicrobes and trilobites (Hupé 1960; Schmitt & Monninger 1977; Destombes *et al.* 1985; Debrenne & Debrenne 1995; Álvaro *et al.* 2006; Álvaro & Debrenne 2010; Clausen *et al.* 2014; Azizi *et al.* 2022). The Amouslek Formation ("*formation schistocalcaire*" *sensu* Choubert [1952]) has a thickness range of 20-220 m and consists of variegated shale together with microbial-archaeocyathan bioherms, biostromes and reef complexes with diverse archaeocyath assemblages (Debrenne & Debrenne 1995; Álvaro *et al.* 2006; Álvaro & Debrenne 2010). This formation is succeeded by the fossiliferous Issafen Formation, which is approximately 400 m thick and consists of green shale interbedded with nodular limestones as well as microbial-archaeocyathan bioherms, biostromes and numerous mud-mound complexes (Debrenne & Debrenne 1995; Álvaro *et al.* 2006; Álvaro & Debrenne 2010). The overlying Asrir Formation was originally designated as "*grès terminaux*" by Choubert (1952) but later renamed as the Asrir Formation (Choubert 1963). It consists mainly of a heterolithic succession dominated by sandstones with abundant thin volcanic ash interbeds, localized channel conglomerates and nodular carbonates.

The Cambrian Series 2 interval is well represented in the western Anti-Atlas, particularly in the Fouanou Syncline. Here we have conducted detailed logging of a representative section that includes the Igoudine and Amouslek formations (Fig. 1C). The stratigraphic succession in this region exhibits sedimentary facies that closely resemble those found in the reference sections of the Tiout and Amouslek areas, as previously described by Álvaro *et al.* (2006) and Álvaro & Debrenne (2010).

MATERIAL AND METHODS

Fossil material

The fossils of the new were collected from carbonate mud mounds, oriented in a northeasterly direction and located above the shale interval of the Issafen Formation. The age of this formation aligns with the Moroccan Banian stage, which is equivalent of the Botoman stage (Álvaro *et al.* 2006) within the Fouanou Syncline.

Data acquisition

For the analysis, selected samples were sawn and thin-sectioned with precision to create both transverse and longitudinal sections of archaeocyath skeletons (cups). This allowed us to closely examine the morphological features of archaeocyathan skeletal structures. We carried out precise measurements of these various structures using a specialized software, *Annotate-on* version 1.9.55 (RECOLNAT [ANR-11-INBS-0004] (Hays & Kerner 2020; Gourraud *et al.* 2021; Pignal *et al.* 2024). We photographed of the thin sections using a digital camera (Axiocam erc5s) in combination with a binocular magnifier, while sections themselves were pictured using an EPSON EXPRESSION 10000 XL scanner.

Identification

The morphological examination of archaeocyaths specimens was based on prior research conducted on this fauna, summarized in Debrenne *et al.* (2015). We also made use of a digital identification database created with Xper3 (Kerner *et al.* 2021), available at http://archaeocyatha.identificationkey.org/mkey.html (Kerner *et al.* 2011a). During this examination, we have focused on detailed morphology of archaeocyath cup structures.

Abbreviations

Collection acronyms

FO.IS	Fouanou Syncline (FO) of the Issafen Formation (IS);
AA-FOU-CI	Indeterminate collection (CI) from the Fouanou Syncline (FOU) of the Ait Abdellah region (AA).

Archaeocyaths measurements

D	cup diameter;
OW	outer wall;
IW	inner wall;
Int	intervallum width;
IS	interseptal width;
N	number of septa;
RK	radial coefficient = N/D;
GPC	general porosity coefficient = porosity coefficient IW/ porosity coefficient OW;
IC	ratio of sides of interseptal loculi in transverse section = int/IS expressed as 1/x;
n	number of perforation rows per intersept;
d	perforation diameter;
l	lintel width (horizontal distance between two adjacent perforations);
t	wall/septa thickness;
d/l	porosity coefficient = perforation diameter / lintel width.

SYSTEMATIC PALAEONTOLOGY

The classification used to describe this genus is founded on the research conducted by Debrenne *et al.* (2015).

The material, collected belonging to this new species is referenced as FO.IS4, FO.IS8, FO.IS10 and FO.IS24; and it is securely housed at the MHNM (Natural History Museum of Marrakech) with the following designations, respectively: AA-FOU-CI-1, AA-FOU-CI-2, AA-FOU-CI-3, and AA-FOU-CI-4. Table 1 depicted the summary of the sampled material.

Table 1. — Geographical data for sampling points.

Sample number	Museum references	Field references	Grid reference
no. 1	AA-FOU-CI-1	FO.IS4	29°51'30.27"N, 8°50'7.47"W
no. 2	AA-FOU-CI-2	FO.IS8	29°51'35.07"N, 8°49'48.59"W
no. 3	AA-FOU-CI-3	FO.IS10	29°51'35.07"N, 8°49'48.59"W
no. 4	AA-FOU-CI-4	FO.IS24	29°52'26.61"N, 8°49'56.12"W

Order AJACICYATHIDA Bedford & Bedford, 1939
Suborder AJACICYATHINA Bedford & Bedford, 1939
Superfamily ETHMOPHYLLOIDEA Okulitch, 1937
Family CARINACYATHIDAE Krasnopeeva, 1953

Genus *Fouanoucyathus* El Bakhouch & Kerner, n. gen.

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ETYMOLOGY. — Named after the Fouanou Syncline where the specimen was discovered.

TYPE SPECIES. — *Fouanoucyathus tafraoutiensis* El Bakhouch & Kerner, n. sp., Early Cambrian (Cambrian age 4 or Botoman), Issafen Formation, Fouanou Syncline, Ait Abdellah, western Anti-Atlas, Morocco.

DIAGNOSIS. — Outer wall with several vertical rows of horizontal to upwardly projecting slightly S-shaped canals; inner wall with one vertical row of horizontal to upwardly S-shaped canals per intersept, septa completely porous, linked by synapticulae.

DISCUSSION

Fouanoucyathus El Bakhouch & Kerner, n. gen. is the only carinacyathid genus with synapticulae, it differs to *Carinacyathus* in the shape of canals on the outer wall (S-shaped but not straight), absence of supplementary bracts externally and the appearance of the inner wall (S-shaped but not straight, horizontal to upwardly but not downwardly plus no additional bracts on central cavity side). *Hupercyathelus* differs in possessing an outer wall with downwardly projecting canals and bearing supplementary independent microporous sheath externally and an inner wall with several rows of canals. *Porocyathellus* differs in possessing several rows of canals on the inner wall. *Vologdinocyathellus* differs in possessing an inner wall with straight canals.

Fouanoucyathus tafraoutiensis El Bakhouch & Kerner, n. gen., n. sp. (Figs 2-5)

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ETYMOLOGY. — Named after Tafraout, the city from where the specimens were collected.

TYPE LOCALITY. — Tafraout, Morocco.

TYPE AGE. — Early Cambrian (Cambrian age 4 or Botoman).

TYPE MATERIAL. — **Morocco** • 1 specimen; western Anti-Atlas, Tata Group, Issafen Formation, Tafraout, section FO.IS8; holotype: AA-FOU-CI-2 • 3 specimens; western Anti-Atlas, Tata Group, Issafen Formation, Tafraout; paratypes: AA-FOU-CI-1 from section FO.IS4; AA-FOU-CI-3 from section FO.IS10; AA-FOU-CI-4 from section FO.IS24.

MEASUREMENTS. — See Table 2.

DIAGNOSIS. — Intervallum 4-9 mm wide; outer wall with 3 to 5 vertical rows of canals per intersept; septa completely porous; some synapticulae grouped into synapticular tabulae (Fig. 2F, 3B, D); in cups of diameter 22-50 mm.

DESCRIPTION

Cup conical, diameter 22-50 mm with intervallum 4-9 mm wide, outer wall with 3-5 rows of canals (diameter 0.09-0.2 mm, lintels 0.06-0.07 mm, porosity coefficient 1.3-3.3), wall thickness (0.2-0.3 mm). Inner wall with one row of straight canal per intersept (diameter 0.4-0.7 mm, lintels 0.11-0.23 mm, porosity coefficient 1.9-6.4), wall thickness (0.6-1.2 mm).

Septa are perced by numerous vertical pore rows, with the number varying from 6 to 21 rows; (perforation diameter 0.14-0.22 mm, lintels 0.17-0.34 mm) (Fig. 2C, 3B). Some synapticulae grouped into synapticular tabulae.

RK 1.4-2.3. IC 1/4,0-1/9,0. GPC 1.1-1.9

REMARKS

The canals on the inner wall for this new taxon are quite regular in size and shape (Fig. 5B) and their direction varies from horizontal to upward with all the intermediate directions. Septa are completely porous (6-21 rows) and their pores have round to slightly longitudinally elongate shape (Fig. 3C).

CONCLUSION

New finds of archaeocyaths in the Fouanou Syncline of the western Anti-Atlas, Morocco provide a fresh insight into archaeocyath assemblages of northern Gondwana by revealing the presence of a new genus possessing synapticulae among a

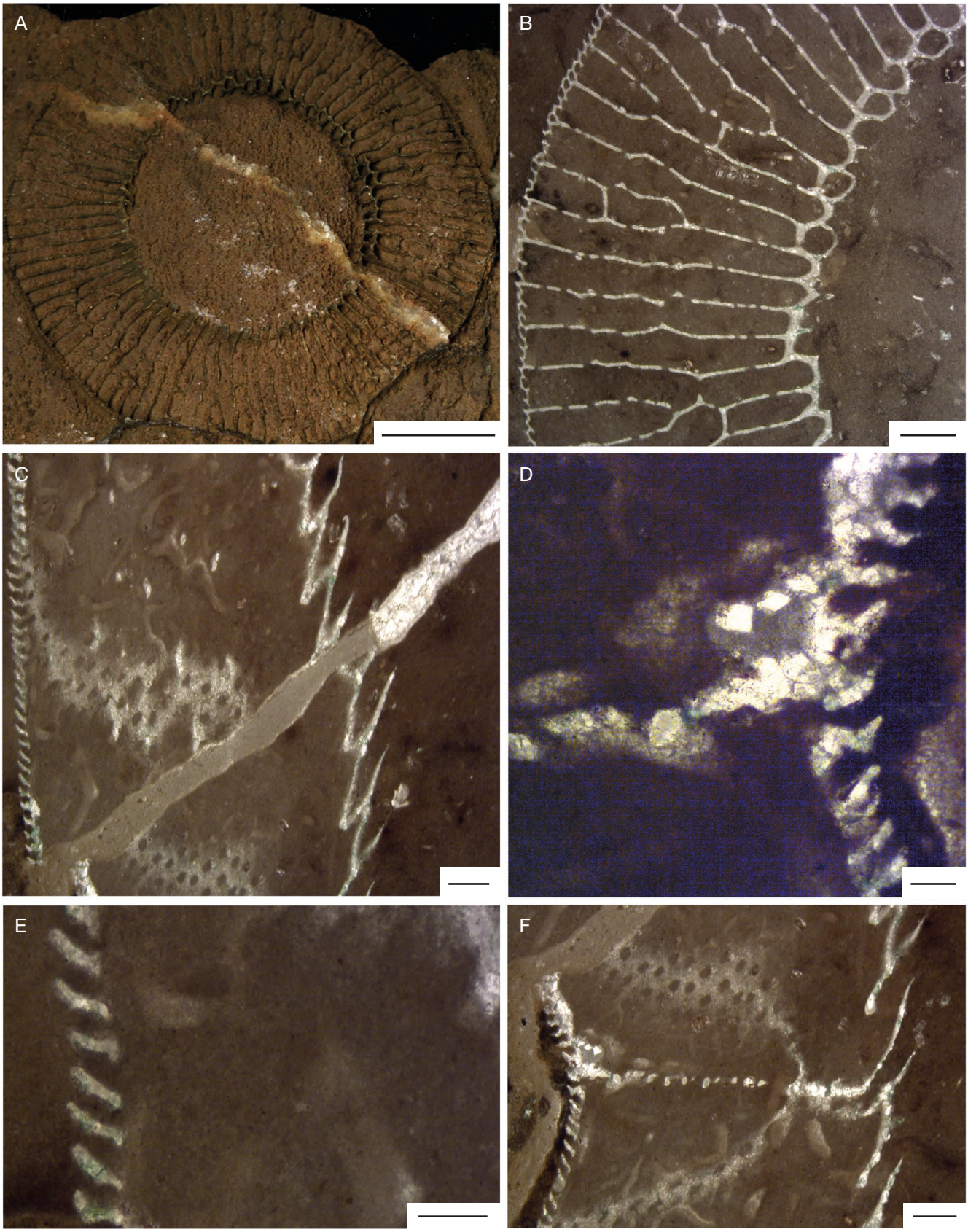

FIG. 2. — *Fouanoucyathus tafraoutiensis* El Bakhouch & Kerner, n. gen., n. sp., holotype AA-FOU-CI-2 from section FO.IS8: **A**, transverse view of specimen prior to preparation; **B**, transverse section showing wall and septal porosity (inner wall at right); **C**, detail of longitudinal section showing the outer and inner walls with canals and septal porosity; **D**, detail of longitudinal section showing inner wall porosity (central cavity at right); **E**, detail of longitudinal section showing outer wall porosity (intervallum at right); **F**, longitudinal section showing wall, septal porosity and a synapticular tabulae (inner wall at right). Scale bars: A, 9 mm; B, 0.5 mm; C, E, F, 1 mm; D, 0.2 mm.

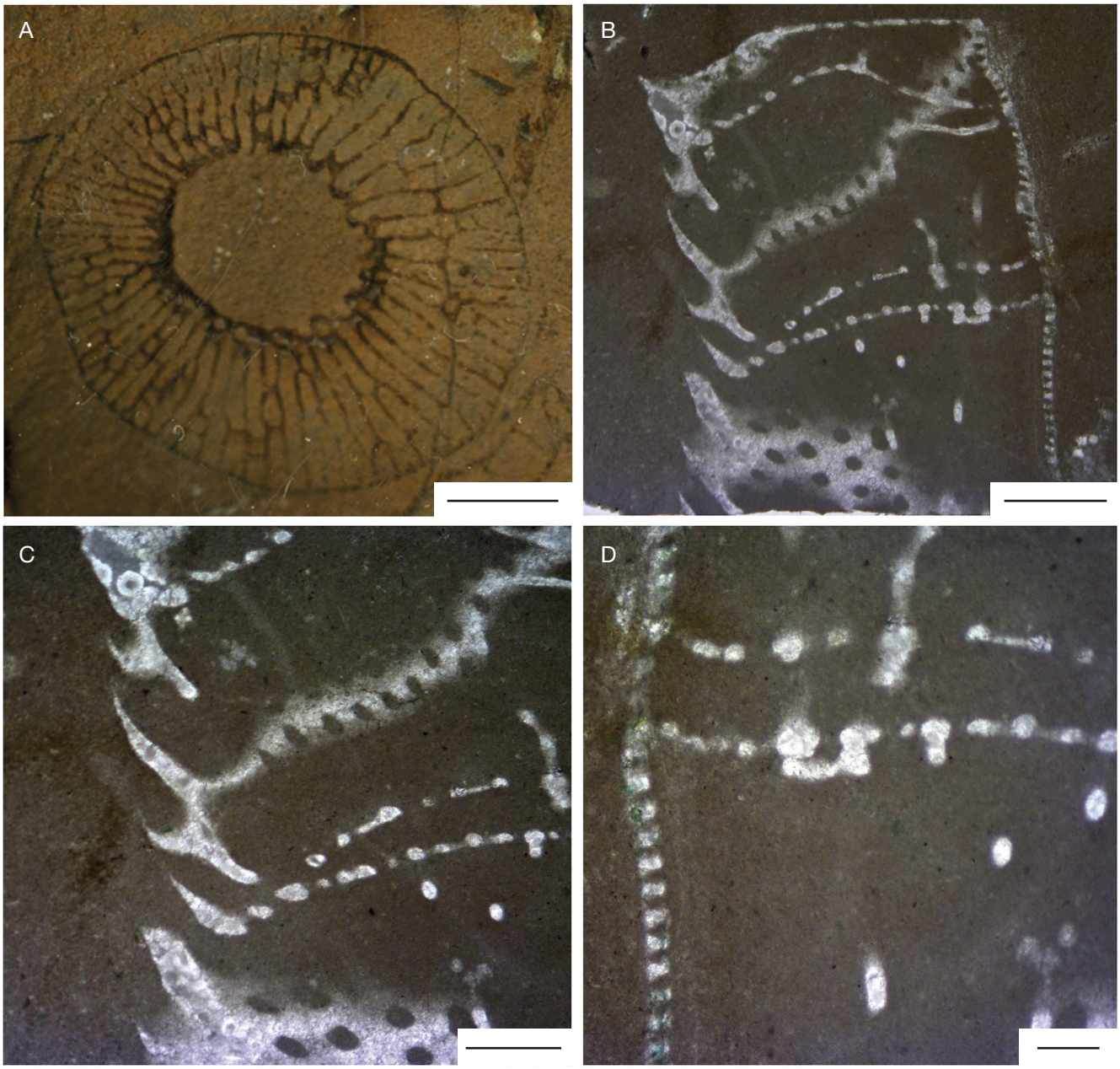

FIG. 3. — *Fouanoucyathus tafraoutiensis* El Bakhouch & Kerner, n. gen., n. sp., paratype AA-FOU-CI-3 from FO.IS10: **A**, transverse view of specimen prior to preparation; **B**, detail of longitudinal section showing walls, septal porosity and synapticular tabulae (inner wall at left); **C**, detail of longitudinal section showing inner wall canals (central cavity at left); **D**, detail of longitudinal section showing outer wall canals and synapticular tabulae (intervallum at right). Scale bars: A, 8.5 mm; B, 2 mm; C, 1 mm; D, 0.5 mm.

TABLE 2. — Measurements of *Fouanoucyathus tafraoutiensis* El Bakhouch & Kerner, n. gen., n. sp.

Coll. no.,	Cup					Outer wall					Inner wall					Septa					
Specimen	D	int	RK	GPC	IC	n	d	l	t	d/l	n	d	l	t	d/l	N	IS	n	d	l	t
AA-FOU-CI-1 FO.IS4	50	4	1.4	1.4	1/4.0	3-5	0.1	0.07	0.2	1.4	1	0.45	0.23	0.6	1.9	<70	1	6	0.19	0.17	0.3
AA-FOU-CI-2 FO.IS8	40	9	1.9	1.9	1/9.0	4	0.2	0.06	0.3	3.3	1	0.7	0.11	1.2	6.4	74	0.9	21	0.22	0.34	1.4
AA-FOU-CI-3 FO.IS10	22	6-8	2.3	1.6	1/6.0-1/8.0	3	0.09	0.07	0.2	1.3	1	0.4	0.19	0.9	2.1	51	0.8-1	12	0.14	0.17	1.2
AA-FOU-CI4 FO.IS24	32	5-7	2.1	1.1	1/5.0-1/7.0	3-4	0.12	0.06	0.3	2	1	0.4	0.17	0.8	2.3	<66	1	8	0.19	0.30	0.6

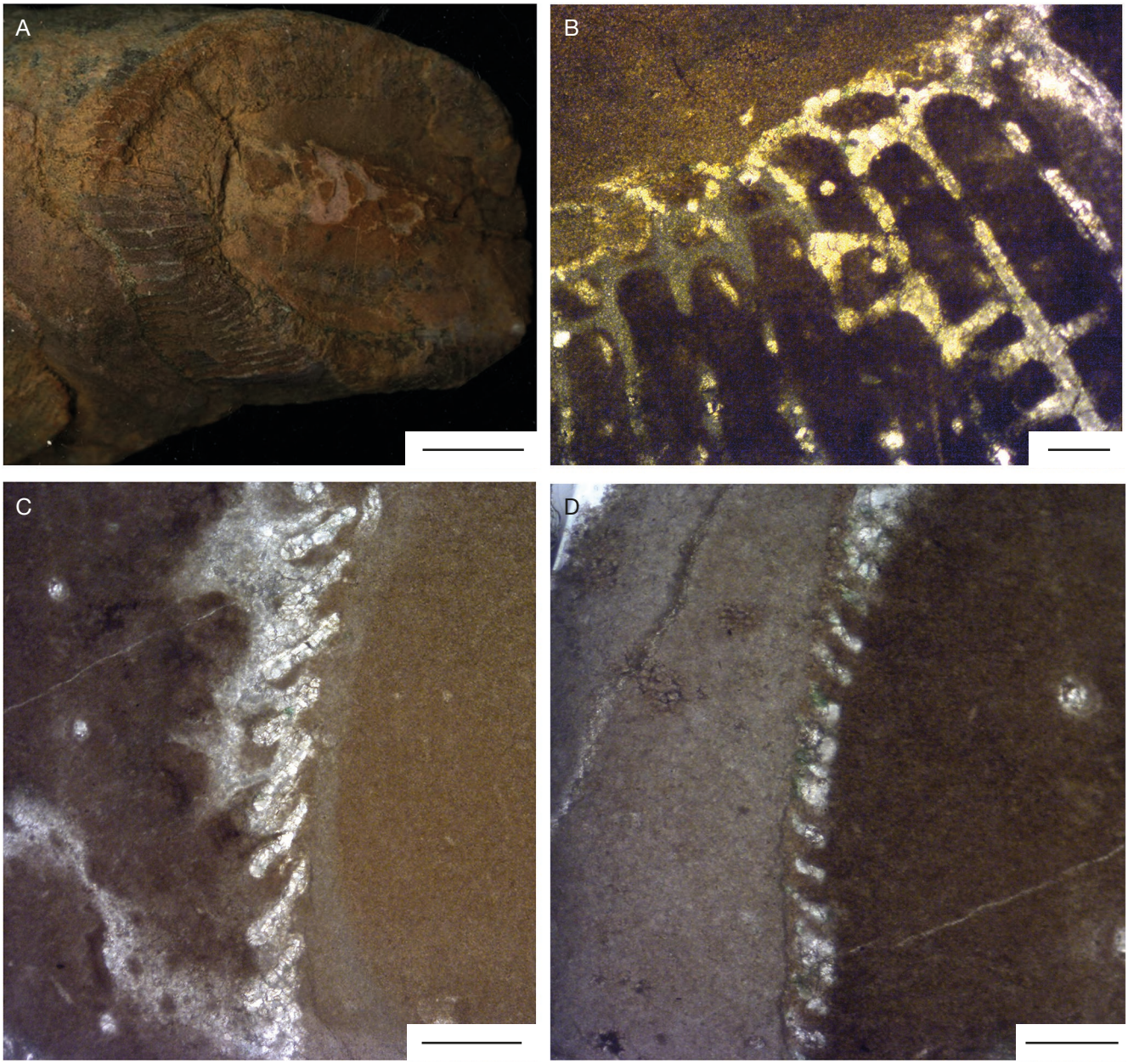

FIG. 4. — *Fouanoucyathus tafraoutiensis* El Bakhouch & Kerner, n. gen., n. sp., paratype AA-FOU-CI-4 from FO.IS24: **A**, transverse view of specimen prior to preparation; **B**, detail of transverse section showing inner wall porosity and synapticulae (central cavity at upper left); **C**, detail of longitudinal section showing septal porosity and inner wall canals (central cavity at right); **D**, detail of longitudinal section showing outer wall canals. Scale bars: A, 7.5 mm; B, 0.3 mm; C, 1 mm; D, 0.6 mm.

previously unreported characteristic within the family Carinacyathidae. This observation further expands our knowledge on archaeocyathan diversity. Once again, archaeocyathan palaeocommunities of Morocco are dominated by species with porous septa and synapticulae instead of pectinate tabulae typical of archaeocyaths in other principal areas of their diversification. This fact is related either to the phenomenon of the first founder combining these features or to an adaptation of archaeocyaths to local environmental conditions. Reaching a conclusion between these two assumptions requires a further study.

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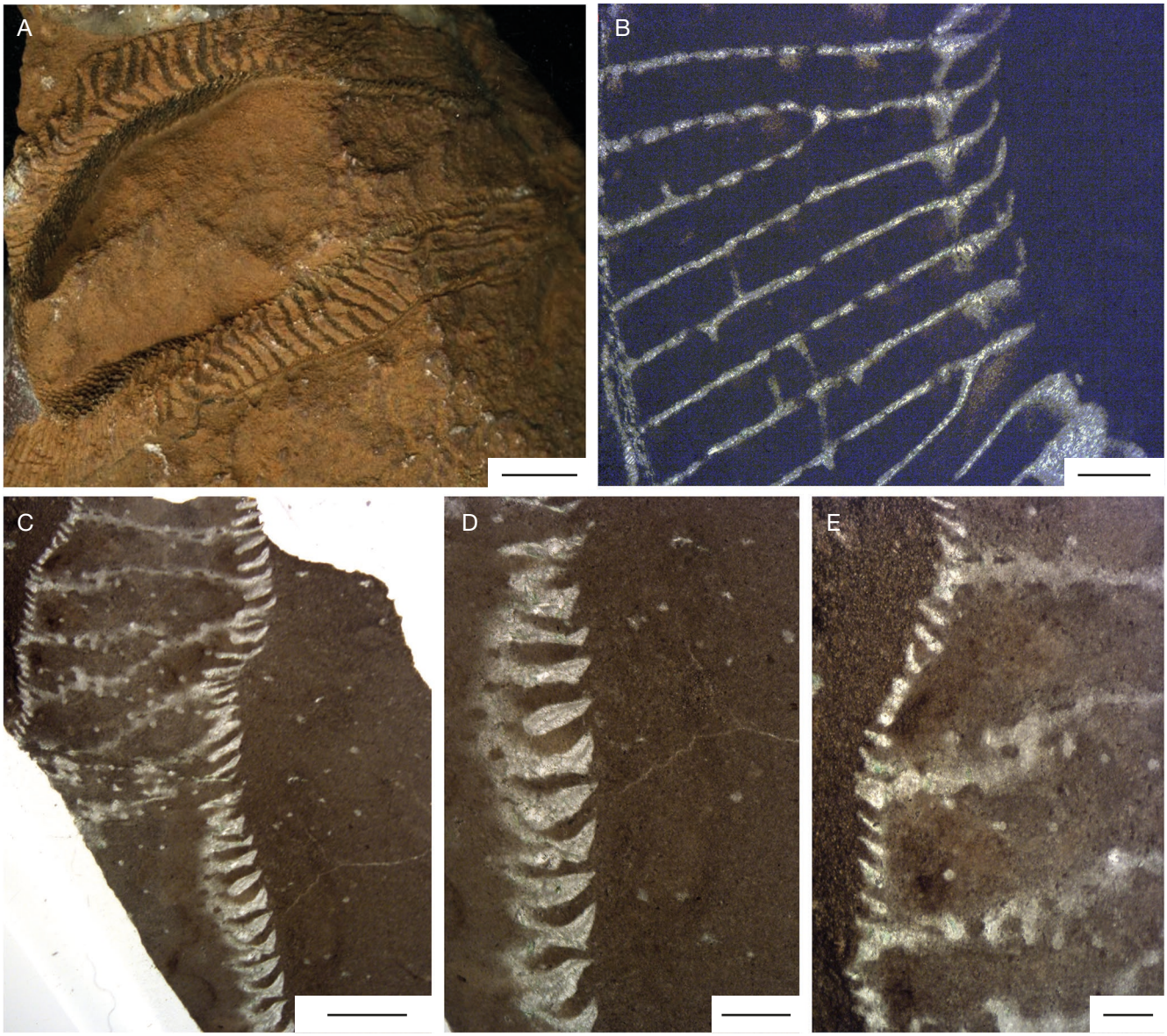

FIG. 5. — *Fouanoucyathus tafraoutiensis* El Bakhouch & Kerner, n. gen., n. sp., paratype AA-FOU-CI-1 from section FO.IS4: **A**, longitudinal view of specimen prior to preparation; **B**, oblique transverse section showing details of walls and septa porosity; **C**, longitudinal section (inner wall at right); **D**, detail of **C** showing inner wall porosity (central cavity at right); **E**, detail of **C** showing outer wall porosity. Scale bars: A, 4 mm; B, 0.4 mm; C, 1.5 mm; D, 1 mm; E, 0.3 mm.

REFERENCES

ÁLVARO J. J. & DEBRENNE F. 2010. — The Great Atlasian Reef Complex: An early Cambrian subtropical fringing belt that bordered West Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology* 294 (3-4): 120-132. https://doi.org/10.1016/j.palaeo.2009.11.022

ÁLVARO J. J., CLAUSEN S., EL ALBANI A. & CHELLAI E. H. 2006. — Facies distribution of the Lower Cambrian cryptic microbial and epibenthic archaeocyathan-microbial communities, western Anti-Atlas, Morocco. *Sedimentology* 53 (1): 35-53. https://doi.org/10.1111/j.1365-3091.2005.00752.x

ÁLVARO J. J., BENZIANE F., THOMAS R., WALSH G. J. & YAZIDI A. 2014. — Neoproterozoic-Cambrian stratigraphic framework of the Anti-Atlas and Ouzellagh promontory (High Atlas), Morocco. *Journal of African Earth Sciences* 98: 19-33. https://doi.org/10.1016/j.jafrearsci.2014.04.026

AZIZI A., EL ALBANI A., EL BAKHOUCHE A., VINN O., BANKOLE O. M., FONTAINE C., HAFID A., KOURAISS K. & EL HARIRI K. 2022. — Early biomineralization and exceptional preservation of the first thrombolite reefs with archaeocyaths in the lower Cambrian of the western Anti-Atlas, Morocco. *Geological Magazine* 160 (3): 428-443. https://doi.org/10.1017/S0016756822001017

AZIZI A., EL ALBANI A. & EL HARIRI K. 2023. — Geochemistry of the early Cambrian succession in the western Anti-Atlas , Morocco : implications on provenance and paleoredox conditions. *Estonian Journal of Earth Sciences* 72 (2): 171-184. https://doi.org/https://doi.org/10.3176/earth.2023.83

BEDFORD R. & BEDFORD J. 1939. — Development and classification of Archaeos (Pleospongia). *Memoirs of Kyancutta Museum* 6: 67-82. https://www.biodiversitylibrary.org/page/62099536

BENSSAOU M. & HAMOUMI N. 2001. — L'Anti-Atlas occidental du Maroc: Étude sédimentologique et reconstitutions paléo-

géographiques au Cambrien inférieur. *Journal of African Earth Sciences* 32 (3): 351-372. https://doi.org/10.1016/S0899-5362(01)90102-2

Benssaou M. & Hamoumi N. 2004. — Les microbialites de l'Anti-Atlas occidental (Maroc) : Marqueurs stratigraphiques et témoins des changements environnementaux au Cambrien inférieur. *Comptes Rendus Geoscience* 336 (2): 109-116. https://doi.org/10.1016/j.crte.2003.10.024

Bourcart J. & Le Villain G. 1927. — Découverte du Cambrien à *Archaeocyathus* de l'Anti-Atlas marocain. *Compte rendu sommaire des séances de la Société géologique de France* 1-2: 10-11

Bourcart J. & Le Villain G. 1931. — La faune des calcaires cambriens de Sidi Mouça d'Aglou (Anti-Atlas marocain). *Notes et Mémoires du Service géologique du Maroc* 15: 1-44

Choubert G. 1952. — Histoire géologique du domaine de l'Anti-Atlas, *in* Choubert G. & Marçais J. (eds), *Géologie du Maroc. 19ème Congrès géologique international, Alger. Monographies régionales, série 3,* 6: 77-194.

Choubert G. 1963. — *Histoire géologique du Précambrien de l'Anti-Atlas*. Service géologique du Maroc, Rabat, 352 p.

Clausen S., Álvaro J. J. & Zamora S. 2014. — Replacement of benthic communities in two Neoproterozoic-Cambrian subtropical-to-temperate rift basins, High Atlas and Anti-Atlas, Morocco. *Journal of African Earth Sciences* 98: 72-93. https://doi.org/10.1016/j.jafrearsci.2014.03.025

Debrenne F. 1964. — Archaeocyatha ; contribution à l'étude des faunes cambriennes du Maroc de Sardaigne et de France. *Notes et Mémoires du Service des Mines et de la Carte géologique du Maroc* 179: 1-370.

Debrenne F. 2007. — Lower Cambrian archaeocyathan bioconstructions. *Comptes Rendus Palevol* 6 (1-2): 5-19. https://doi.org/10.1016/j.crpv.2006.07.003

Debrenne F. & Debrenne M. 1978. — Archaeocyathid fauna of the lowest fossiliferous levels of Tiout (Lower Cambrian, Southern Morocco). *Geological Magazine* 115 (2): 101-119. https://doi.org/10.1017/S0016756800041157

Debrenne F. & Debrenne M. 1995. — Archaeocyaths of the Lower Cambrian of Morocco, *in* Geyer G. & Landing E. (eds), Morocco'95: The Lower-Middle Cambrian Standard of Western Gondwana: Introduction, Field Guide, Abstracts, and Proceedings of the First Conference of the Lower Cambrian Stage Subdivision Working Group and I.G.C.P. Project 366, Ecological Aspects of the Cambrian Radiations. *Beringeria,* special issue 2: 121-145.

Debrenne F., Debrenne M. & Faure-Muret A. 1992. — Faunes d'Archéocyathes de l'Anti Atlas occidental (bordures Nord et Sud) et du Haut Atlas occidental. Cambrien inférieur, Maroc. *Annales de l'Université de Provence Géologie méditerranéenne* 17 (3-4): 177-211. https://doi.org/10.20595/jjbf.19.0_3

Debrenne F., Zhuravlev A. Y. & Kruse P. 2015. — General features of the Archaeocyatha. Systematic descriptions: Archaeocyatha, *in* Selden P. A. (ed.), *Treatise on Invertebrate Paleontology. Part E Revised, Porifera*. Vols 4, 5. University of Kansas Paleontological Institute, Lawrence: 845-1084. https://doi.org/10.17161/dt.v0i.5767

Destombes J., Hollard H. & Willefert S. 1985. — Lower Palaeozoic Rocks of Morocco, *in* Holland C. H. (ed.), *Lower Palaeozoic Rocks of the World*. Volume 4. *Lower Palaeozoic of North Western and West Central Africa*. John Wiley & Sons, United Kingdom: 57-184

Gandin A. & Debrenne F. 2010. — Distribution of the archaeocyath-calcimicrobial bioconstructions on the Early Cambrian shelves. *Palaeoworld* 19 (3-4): 222-241. https://doi.org/10.1016/j.palwor.2010.09.010

Geyer G. & Landing E. 1995. — Morocco'95: The Lower-Middle Cambrian Standard of Western Gondwana: Introduction, Field Guide, Abstracts, and Proceedings of the First Conference of the Lower Cambrian Stage Subdivision Working Group and I.G.C.P. Project 366, Ecological Aspects of the Cambrian Radiations. *Beringeria,* special issue 2: 1-269.

González P. D., Tortello M. F., Damborenea S. E., Naipauer M., Sato A. M. & Varela R. 2013. — Archaeocyaths from South America: review and a new record. *Geological Journal* 48 (2-3): 114-125. https://doi.org/10.1002/gj.2415

Gourraud A., Vignes Lebbe R., Kerner A. & Pignal M. 2021. — Architectural Pattern: Study of orchid architecture using tools to take quick measurements of virtual specimens. *Biodiversity Information Science and Standards* 5. https://doi.org/10.3897/biss.5.75752

Hays L.-M. & Kerner A. 2020. — Virtual Systematics with Annotate: The Mexican archaeocyaths example. *Biodiversity Information Science and Standards* 4. https://doi.org/10.3897/biss.4.59106

Hupé P. 1960. — Sur le Cambrien inférieur du Maroc, *in* Reports of the 21st Session of the International Geological Congress, Part VIII (Proceedings of Section 8), Copenhagen: 75-85.

Kerner K. & Debrenne F. 2013. — The role of Archaeocyatha in Cambrian biostratigraphy and biogeography, in Harper D. A. T. & Servais T. (eds), Early Palaeozoic Biogeography and Palaeogeography. *Geological Society Memoir* 38 (1): 59-66. https://doi.org/10.1144/M38.6

Kerner A., Debrenne F. & Vignes-Lebbe R. 2011a. — Cambrian archaeocyathan metazoans: Revision of morphological characters and standardization of genus descriptions to establish an online identification tool. *ZooKeys* 150: 381-395. https://doi.org/10.3897/zookeys.150.1566

Kerner A., Vignes Lebbe R. & Debrenne F. 2011b. — Computer-aided identification of the Archaeocyatha genera now available online. *Carnets de géologie (Notebooks on Geology)*: 99-102. https://doi.org/10.4267/2042/42329

Kerner A., Bouquin S., Portier R. & Lebbe R. V. 2021. — The 8 years of existence of Xper3: State of the art and future developments of the platform. *Biodiversity Information Science and Standards* 5: e74250. https://doi.org/10.3897/biss.5.74250

Krasnopeeva P. S. 1953. — Features of the Kameshki archaeocyathan assemblage in the facies of effusive-sedimentary deposits exemplified by the archaeocyaths of the western part of Tuva. *Tomskiy Gosudarstvenniy Universitet 124*: 51-62.

Neltner L. 1929. — Sur l'extension du Cambrien dans le sud marocain et la présence dans cette région de plissements précambriens. *Comptes rendus hebdomadaires des séances de l'Académie des sciences* 188: 871-873. https://gallica.bnf.fr/ark:/12148/bpt6k31417/f871.item

Okulitch V. 1937. — Changes in nomenclature of Archaeocyathi (Cyathospongia). *Proceedings of the Geological Society of America* 1936: 358.

Pignal M., Bertin G., Chupin L., Perez Pimparé E., Klasnja S., Vignes Lebbe R. & Dusoulier F. 2024. — Récolnat Annotate-On: a tool to improve your experience with virtual collections. *Adansonia*, sér. 3, 46 (13): 133-148. https://doi.org/10.5252/adansonia2024v46a13. http://adansonia.com/46/13

Roch E. 1927. — Sur l'extrémité orientale des Djebilets (Maroc). *Comptes rendus hebdomadaires des séances de l'Académie des sciences* 185 (2): 137-139. https://gallica.bnf.fr/ark:/12148/bpt6k31384/f137.item

Roch E. 1930. — Études géologiques dans la région méridionale du Maroc occidental. *Notes et Mémoires du Service géologique du Maroc* 9: 386-431.

Russo P. 1927. — Recherches géologiques sur le territoire des Hauts Plateaux (Maroc Oriental). *Annales de l'Université de Lyon* 46: 1-195.

Schmitt M. & Monninger W. 1977. — Stromatolites and thrombolites in Precambrian/Cambrian boundary beds of the Anti-Atlas, Morocco: preliminary results, *in* Flügel E. (ed.), *Fossil Algae*. Springer, Berlin: 80-85. https://doi.org/10.1007/978-3-642-66516-5_8

Stone P., Thomson M. R. A. & Rushton A. W. A. 2012. — An Early Cambrian archaeocyath-trilobite fauna in limestone erratics from the Upper Carboniferous Fitzroy Tillite Formation, Falkland Islands. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 102 (4): 201-225. https://doi.org/10.1017/S175569101101005X

THOMAS R. J., FEKKAK A., ENNIH N., ERRAMI E., LOUGHLIN S. C., GRESSE P. G., CHEVALLIER L. P. & LIÉGEOIS J. P. 2004. — A new lithostratigraphic framework for the Anti-Atlas Orogen, Morocco. *Journal of African Earth Sciences* 39 (3-5): 217-226. https://doi.org/10.1016/j.jafrearsci.2004.07.046

WALSH G. J., BENZIANE F., ALEINIKOFF J. N., HARRISON R. W., YAZIDI A., BURTON W. C., QUICK J. E. & SAADANE A. 2012. — Neoproterozoic tectonic evolution of the Jebel Saghro and Bou Azzer-El Graara inliers, eastern and central Anti-Atlas, Morocco. *Precambrian Research* 216-219: 23-62. https://doi.org/10.1016/j.precamres.2012.06.010

ZHURAVLEV A. Y. & WOOD R. A. 1996. — Anoxia as the cause of the mid-Early Cambrian (Botomian) extinction event. *Geology* 24 (4): 311-314. https://doi.org/10.1130/0091-7613(1996)024<0311:AATCOT>2.3.CO;2

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