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Raphaël VASSEUR &
Bernard LATHUILIÈRE



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Toarcian corals from Western Tethys (except Thecosmiliidae)

Raphaël VASSEUR
Bernard LATHUILIÈRE
Université de Lorraine, CNRS, lab. GeoRessources, UMR 7359,
BP 70239, 54506 Vandoeuvre-lès-Nancy cedex (France)
raphael.vasseur@univ-lorraine.fr
bernard.lathuiliere@univ-lorraine.fr

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ABSTRACT
In the Late Liassic, the Western Tethys was the cradle of coral diversity known in the Middle and Late Jurassic. This is revealed by the revised and expanded taxonomy of coral faunas from the Pliensbachian and Toarcian stages, based mainly on direct collections from the Moroccan Lias (Middle and High Atlas). The present taxonomic study of non-thecosmiliid Toarcian corals describes 36 species distributed among 28 genera and 13 identified families. It includes a new genus, *Eobracthelia* n. gen. – the first known Aplosmiliidae Fromentel, 1861 – and four new species: *Koilocoenia atlasica* n. sp. (a small Actinastreidae Alloiteau, 1952 without a columella), *Eobracthelia costata* n. gen., n. sp. (a plocoid Aplosmiliidae without a lamellar columella), *Dermosmilia praecox* n. sp. (the first *Dermosmilia* Koby, 1884 with rare joining septa), and *Diplocoenia elmii* n. sp., a cerioid Stylinidae Orbigny, 1851 colony with a plocoid appearance. Special attention was given to species variability in order to correct the overestimation of species numbers published in the literature over the past century, which resulted from an excessively typological descriptive approach. This taxonomic revision helps to better document changes in diversity related to the Pliensbachian-Toarcian boundary, as well as the subsequent anoxic event during the Early Toarcian. It now becomes possible to understand how environments dominated by lithiotids gave way to true coral reefs in which meandroid corals played a leading role. The conquest of deeper environments continued with the development of the first Caryophylliidae Dana, 1846, with the genus *Thecocyathus* Edwards & Haime, 1848.

KEY WORDS
Morocco,
corals,
scleractinians,
Toarcian,
Lias,
Jurassic,
crisis,
new combinations,
lectotypifications,
new genus,
new species.

RÉSUMÉ
Coraux toarciens de l'Ouest Téthysien (Thecosmiliidae exceptés).
Au Lias supérieur, l'Ouest Téthysien a été le berceau de la diversité des coraux connue au Jurassique moyen et supérieur. C'est ce que révèle la taxinomie révisée et augmentée des faunes de coraux des étages Pliensbachien et Toarcien réalisée principalement à partir de collectes directes dans le Lias marocain (Moyen Atlas et Haut Atlas). La présente étude taxinomique de coraux toarciens non thécosmilidés décrit 36 espèces distribuées parmi 28 genres et 13 familles identifiées. Elle inclut un nouveau genre : *Eobracthelia* n. gen., le premier Aplosmiliidae Fromentel, 1861 connu et quatre nouvelles espèces : *Koilocoenia atlasica* n. sp. (un petit Actinastreidae Alloiteau, 1952 sans columelle), *Eobracthelia costata* n. gen., n. sp. (un Aplosmiliidae plocoïde sans columelle lamellaire), *Dermosmilia praecox* n. sp. (le premier *Dermosmilia* Koby, 1884 avec des septes peu jointifs) et *Diplocoenia elmii* n. sp., une colonie de Stylinidae Orbigny, 1851 cérioïde d'apparence plocoïde. Une attention particulière a été apportée à la variabilité des espèces afin de corriger la surestimation du nombre d'espèces publiées dans la littérature lors du dernier siècle en raison d'une approche descriptive exagérément typologique. Le nettoyage taxinomique permet de mieux documenter les changements de diversité liés à la limite Pliensbachien-Toarcien mais aussi à l'évènement anoxique qui a suivi au Toarcien inférieur. On peut désormais comprendre comment les environnements dominés par les lithiotides ont laissé la place à de vrais récifs coralliens où les coraux méandroïdes ont pris une part prépondérante. La conquête des environnements plus profonds se poursuit avec le développement des premiers Caryophylliidae Dana, 1846 représentés par le genre *Thecocyathus* Edwards & Haime, 1848.

MOTS CLÉS
Maroc,
coraux,
scléractiniaires,
Toarcien,
Lias,
Jurassique,
crise,
lectotypifications,
combinaisons nouvelles,
genre nouveau,
espèces nouvelles.

INTRODUCTION

Liassic times are usually considered a period of weak reefal development for corals (e.g. Leinfelder *et al.* 2002; Kiessling 2009 with ref.). The expression of "reef eclipse" has even been used (Stanley 2001). In this context the Toarcian occupies a special place because it recorded the recovery of corals following the multi-phased Pliensbachian-Toarcian (Pli-To) extinction event, with a first extinction phase corresponding to the Pli-To boundary and a second extinction phase during the Jenkyns event (JE) (Vasseur 2018; Vasseur *et al.* 2021; Vasseur & Lathuilière 2021; Stone 2024).

Preceded by Le Maitre (1935, 1937), Beauvais (1986b) produced the most important monograph on Liassic corals of Morocco, her article represents the richest work to approach the Liassic diversity and Morocco appears as the most significant record of diversity for this time, as it may have served as a refugium for many organisms during this period (Stone 2024). However, the taxonomic methodologies employed by Beauvais, along with those of Alloiteau, Fromentel, and Ferry, exhibit a clear bias toward excessive splitting and a systematic underestimation of intraspecific variability. For this reason, to clarify the responses of corals to the Pliensbachian-Toarcian biological crisis we decided to go back to the field in the frame of R. Vasseur's PhD thesis (Vasseur 2018). For the Pliensbachian stage, coral systematic have already been published (Vasseur & Lathuilière 2021) and the present work compiles the corrected data concerning the corals in the Toarcian stage except the Thecosmiliidae which, in view of their importance in terms of evolution and biodiversity, will be the subject of a separate study.

MATERIAL AND METHODS

The present monograph results from a data gathering of a three-year PhD study (2015-2018) with five field missions in Morocco. The material provided by S. Elmi (see Elmi *et al.* 2002) and previously described by Lathuilière (2011) has also been included in this study. In addition, the document integrates revised descriptions from the literature (collections of the Muséum national d'Histoire naturelle [MNHN] in Paris, for instance *Ellipsoidastraea* from Algeria depicted by Alloiteau 1957). This work provides updated descriptions of Tethyan Toarcian coral faunas, with arguments and figurations. Descriptions are based on macroscopic and microscopic observations of whole samples, polished sections and thin sections that have been produced by the thin section platform in GeoRessources lab or by the first author with the precious help of the association Terrae Genesis.

In total, 36 species are described. They are distributed in 28 genera and 13 identified families. Although we tend to lump taxa to correct the species overestimation caused by earlier typological approaches that ignored intraspecific variability, this effort is partly offset by the large volume of field-collected material, which has led to the recognition of new species and genera.

Abbreviations

Abbreviations and symbols used in the descriptions

s.l.	*sensu lato*;
s.s.	*sensu stricto*;
AM	Amellagou, Gueris Valley, Morocco;
BSP	Paleontological collections of the Museum of Münich;

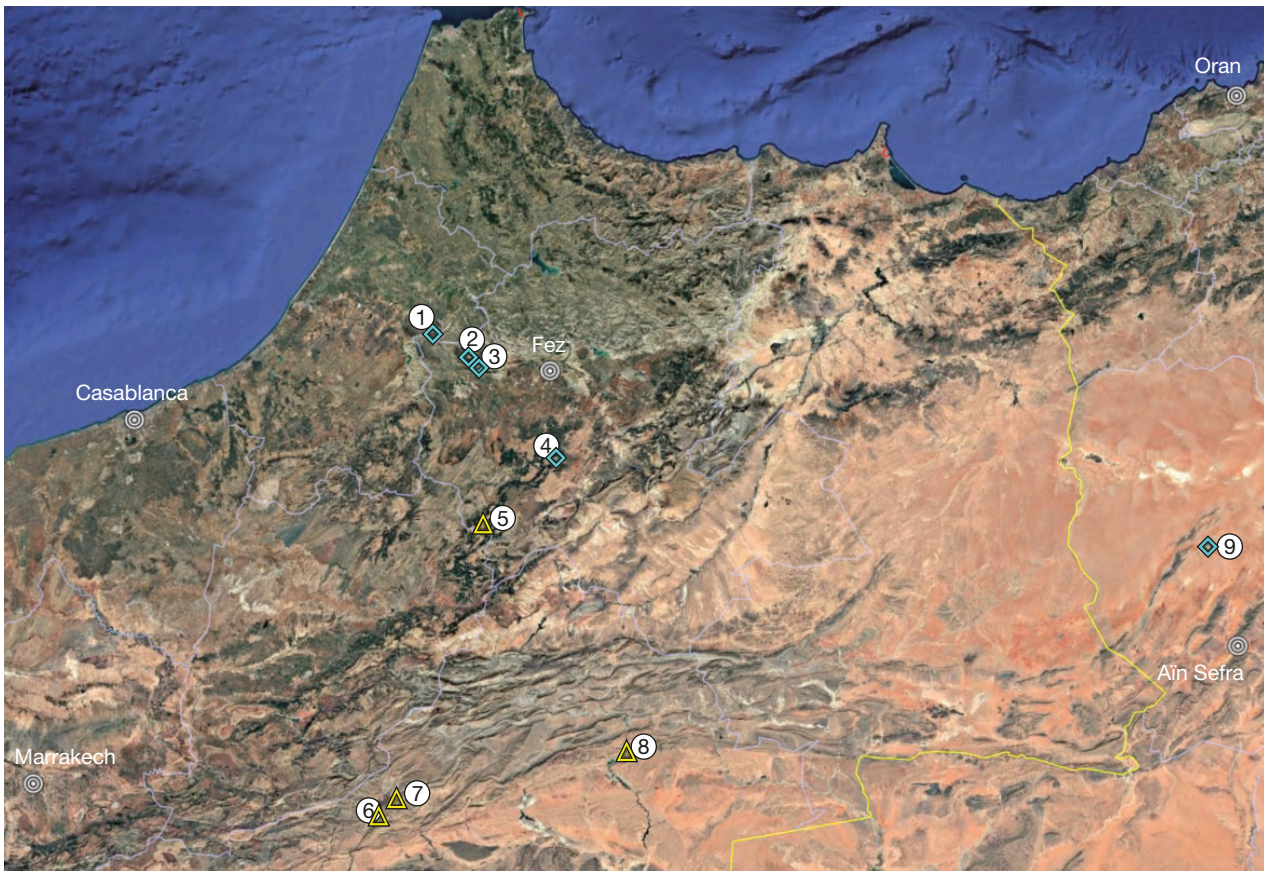

Fig. 1. — Geographic location map of the different identified sampling zones of the African samples used in this study. Yellow triangles correspond to sampling zones of new material collected for this study and blue diamonds correspond to material from museum collections. Sites: **1**, Jebel Outita; **2**, Moulay Idriss; **3**, Moussaoua pass; **4**, Dayet Ifrah; **5**, Aïn Leuh; **6**, Aguerd Izegzawne; **7**, Jebel Toksine; **8**, Aït Athmane; **9**, Aïn Ben Khelil – Raha Zerga. The frontier between Morocco and Algeria is materialized by a **yellow line**.

CPUN	Collections paléontologiques universitaires de Nancy/ Universitary Palaeontological Collections of Nancy; Morrocan specimens should be ultimately housed in Rabat, Morocco;
ENSG	École nationale supérieure de Géologie, Nancy;
JE	Jenkyns event;
LB	Louise Beauvais;
MAN	Muséum Aquarium de Nancy/Museum Aquarium of Nancy;
MGUW	Geological Museum of Wrocław University;
MHNG	Muséum d'Histoire naturelle de Genève/Natural History Museum of Geneva;
MNHN	Muséum national d'Histoire naturelle de Paris/Natural History Museum of Paris;
MNHN.F	MNHN, collections de Paléontologie/Fossil collection;
BIOB-PB	Bonn Institute for Organismic Biology – Section Palaeontology, University of Bonn (previousely IPB).

GEOLOGICAL SETTING

New material used in this study has been collected in the field in different outcrops located in Figure 1.

Corals in the Lower Toarcian (pre-JE) of Jebel Toksine, Morocco

The corals studied in Jebel Toksine (31°37'39"N, 5°50'48"W) come from: 1) a reworked assemblage of corals, sponges and lithiotids in a tidal channel found in an oolite bed (31°37'39"N, 5°50'48"W); or 2) a lithiotid dominated rudstone approximatively 2 meters above the channel ([1] and [2] are both from the upper lithiotid units on South side of Jebel Toksine described by Brame *et al.* (2019); and 3) from a floatstone to rudstone, sometimes packstone level with lithiotids and other large bivalves corresponding to the lower lithiotid unit described by Brame *et al.* (2019) and divided in four lithiotid packages (31°37'46"N, 5°50'45"W). The upper lithiotid unit is approximately 10-15 m below the onset of the Jenkyns event.

For further details, see Brame *et al.* (2019: chapter 4), Krencker *et al.* (2022) and Stone (2024: chapter 4).

Bioherm in the Middle Toarcian of Aguerd Izegzawne

Located in the High Atlas, this early Middle Toarcian bioconstruction made of microbialite and corals (31°43'34"N, 5°44'50"W) is formed in an inner ramp environment. It is a part of a sedimentary sequence described by Krencker *et al.* (2015). This reef corresponds to an average position of 190m (Bifrons zone) in the section of Krencker *et al.* (2015). The coral part of the framework is mostly constituted of phaceloids in the centre and platy, massive forms on the flanks. It contains *Thecosmilia* Edwards & Haime, 1848, *Isastrea* Edwards &

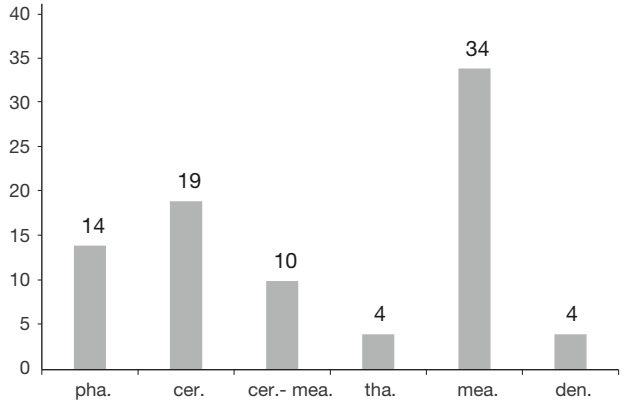

Fig. 2. — Countings of corals according to their colonial structure in the bioherm of Aïn Leuh (Syncline of Awragh-Afennourir, Middle Atlas).

Haime, 1851, *Latiastrea* Beauvais, 1964, *Stylosmilia* Edwards & Haime, 1848 and unidentified Actinastreidae.

Biostromes of the Middle Toarcian of Aït Athmane

Located in the upper part of the Aït Athmane Formation, in the Ziz Valley, High Atlas, Morocco (see Krencker *et al.* 2014), these biostromes (32°3'48"N, 4°21'30"W) developed in a marly environment. They consist of decimeter-scale alternations between marly layers and floatstone-type limestone beds with small phaceloid colonies (*Placophyllia* Orbigny, 1849), cerioid colonies (Actinastreidae), and phacelo-meandroid colonies (*Latomeandra* Orbigny ms in Edwards & Haime, 1849), as well as larger, flattened, meandroid colonies (*Microphyllia* Orbigny, 1849 and *Vallimeandropsis* Beauvais, 1966) that dominate the biomass. This facies indicates a relatively deep carbonate ramp environment, as evidenced by the flattened morphology of meandroid forms and the fine matrix in the interbeds.

Bioherm of the Upper Toarcian of Amellagou

This large bioherm is located in the upper part of the grey marls of the Upper Toarcian of Amellagou (31°59'2"N, 5°2'58"W), in the High Atlas of Morocco (Agoudim b Formation, see Pierre 2006). It formed in an external depositional setting. Solitary *Thecocyathus mactra* (Goldfuss, 1826), typical of deeper environments, were found in the marly levels beneath the bioconstruction. However, the bioherm is dominated by cerioid forms (*Ampakabastraea* Alloiteau, 1858, *Isastrea*) and cerio-meandroid forms in dome-shaped colonies (*Latiastrea*). Meandrioid and phaceloid forms are less abundant, and no thamnasteroid, plocoid, or solitary forms were observed. The massive shapes structure the base of the reef while branched shapes seem to establish mostly on the top of the bioconstruction. A specimen of *Complexastrea* Orbigny, 1849 has been found in a breccia level a few meters below the construction (probably not in a life position).

Bioherm of the Upper Toarcian of Aïn Leuh – syncline of Awragh – Afennourir

This bioherm, located in the Middle Atlas (33°11'31"N, 5°21'6"W), is described in Elmi *et al.* (2002) and El Hammichi *et al.* (2002). The structure is positioned fairly distally on an open carbonate ramp (El Hammichi *et al.* 2002). Counting data (Fig. 2) reveal a predominance of meandroid specimens (*Microphyllia* and *Vallimeandropsis*), with 34 specimens out of a total of 86 along a counting line, whose flattened colonial morphology is consistent with a construction submerged at depth. Additionally, the presence of thecideid brachiopods and bryozoans encrusting some *Thecosmilia* just below the bioconstruction suggests a relatively shaded environment. Cerioid forms are the second most abundant (19/86 specimens), followed by phaceloid forms (14/86), cerio-meandroid forms (10/86), thamnasterioid forms (4/86), and dendroid forms (4/86). Plocoid forms are represented only by one single colony of *Eobracthelia costata* n. gen., n. sp. in this bioherm, although some species of *Diplocoenia* Fromentel, 1857 may be morphologically similar. Numerous solitary corals from the genera *Montlivaltia* Lamouroux, 1821 and *Proleptophyllia* Alloiteau, 1952 were found in the levels beneath the reef. Immediately above the bioherm, alternations of storm-deposited bioclastic beds 15 to 20 cm thick are observed, containing reworked corals in interbeds ranging from 15 to 60 cm in thickness.

It is worth to note that Stone (2024) described Toarcian reefs that have not been seen and sampled by the authors of this study, nevertheless we took in consideration the corals identifications.

Description of coral assemblages from Toarcian:

The Pre-JE Toarcian

Pre-JE Toarcian correspond to the time interval between the two main events identified in the multi-phased Toarcian extinction. It is a period of marine eutrophication, increased sedimentation and multiphased recovery (Vasseur 2018; Stone 2024) following the Pli-To transition collapse, when lithiotid bivalves seem to recover faster than corals and sponges thanks to their ability to thrive in nutrient-rich, murky waters and increasing influx of siliciclastics and nutrients. This peculiarity allowed them to weather the climatic changes at the start of the Toarcian and reestablish biostromes quickly (Stone 2024).

No actual reef has been observed in situ within the Pre-JE Toarcian levels by the authors, making it difficult to assess the dominant forms in terms of volume within the assemblages. However, the different Pre-JE Toarcian faunal assemblages described by the authors are perfectly consistent with the observations of coral assemblages made by Stone (2024) in Morocco (Aguerd Izegzawn, Toumiline, Jebel Toksine and Tilout). Both assemblages are constituted mostly of new taxa (i.e. unknown up until pre-JE Toarcian) with a continuity in the Middle-Upper Jurassic (*Eocomoseris* Melnikova, Roniewicz & Löser, 1993, *Periseris* Ferry, 1870, Comoseridae Fromentel, 1861, Actinastreidae, *Stylosmilia, Ampakabastraea, Thecosmilia*, *Latiastrea*, possibly *Isastrea* and an unidentified Synastreidae Alloiteau, 1952) and a few taxa inherited from the Lower Jurassic (*Archaeosmiliopsis* Melnikova, 1975, *Haimeicyclus* Alloiteau, 1957, *Hispaniastraea* Tùrnsek & Geyer, 1975, *Icaunhelia* Beauvais, 1958, *Phacelostylophyllum* Melnikova, 1972 and *Thecactinastraea* Beauvais, 1986b). Taxa with Triassic

roots are rare in these assemblages. This suggests a transitional state for this period, characterized by simultaneous extinction events and radiation phenomena.

Taxa with high levels of integration are more abundant in terms of species diversity than during the Pliensbachian (see Vasseur *et al.* 2021). They are also quantitatively more significant in the lithiotid-poor biostrome of Aguerd Izegzawn despite solitary and phaceloid species keep dominating in biomass in lithiotids-corals assemblages of Jebel Akenzoud and Tilout (see Stone 2024).

Based on morphological considerations that have been developed in detail in the literature (Barnes 1973; Coates & Oliver 1973; Geister 1984; Coates & Jackson 1987; Lathuilière 2000b; Rosen 2000; Gill *et al.* 2004; Cipriani *et al.* 2019) the question of photosymbiosis remains open for Pre-OAE Toarcian assemblages (Vasseur 2018; Vasseur *et al.* 2021). The highly-integrated forms are rare (meandroid form, the only present-day colonial structure that is exclusively photosymbiotic, is absent from sampling). Also, the rare solitary corals that flourished during the Early Toarcian do not provide more arguments for photosymbiosis, neither by their size nor by their growth rate, which is often unknown. It appears at first sight that pre-TOAE Toarcian coral communities could presumably be constituted by azooxantellate forms as well as zooxantellate forms in proportions that we cannot estimate.

Moreover, the Pre-TOAE Toarcian contains the last significant assemblages of lithiotid bivalves observed before their decline during the anoxic event, as documented by Brame *et al.* (2019), Posenato *et al.* (2018) and Stone (2024).

The Post-JE Toarcian

The post-JE Toarcian correspond to a recovery period following the multi-phased perturbations that took place between both the Pli-To boundary and the Jenkins event itself (Vasseur 2018; Stone 2024). Lithiotid bivalves from the genera *Cochlearites* Reis, 1903, *Lithiotis* Gümbel, 1871, and *Lithioperna* Accorsi Benini, 1979, which were unique to the Early Jurassic, went extinct at the Jenkins event and left vacant the ecological niches for the development of scleractinians corals waiting in their shadow. These corals started to develop during the carbon isotope recovery, especially phaceloid and meandroid forms that became dominant in biomass (probably due to their special ability to cope with turbid waters and high rates of sedimentation, e.g. Vasseur 2018 and Stone 2024).

The Post-JE Toarcian is characterized by large reefs, where high-integrated forms significantly outcompete phaceloid forms in both biomass and diversity (see Vasseur *et al.* 2021). The majority of the genera that make up the diversity of these assemblages persist and diversify throughout the Middle and Upper Jurassic (e.g. *Isastrea*, *Thecosmilia*, *Diplocoenia*, *Latomeandra*).

Meandroid forms are highly diversified and represent one of the dominant groups in terms of both biomass and number of specimens (Vasseur 2018; Vasseur *et al.* 2021) particularly in two large reefs sampled in Morocco: the Middle/Upper Toarcian of Aït Atmane in the Ziz Valley and the Upper Toarcian of Aïn Leuh in the Middle Atlas.

The size and importance of high-integrated forms (particularly meandroid forms) and bioconstructions, along with their paleo-bathymetric positioning, strongly support the photosymbiotic nature of the assemblages in the Middle and Upper Toarcian. Genera that flourished in the Toarcian and were key players in Bajocian reefs, such as *Periseris* or *Isastrea*, are also classically considered autotrophic (Lathuilière 2000b).

SYSTEMATIC DESCRIPTIONS

We have chosen a presentation of taxa according to their families (Table 1). A classification of families into suborders seems meaningless in the present state of coral taxonomy. Old classifications of Wells (1956) and Alloiteau (1957) never found an agreement for suborders before the first results of molecular phylogenies that produce two large branches (named complex and robust by Romano & Palumbi 1996, see Quek *et al.* 2023). We understand that none of the previous classifications can be used and, if we guess that microstructure is a fruitful track to follow for attaching Mesozoic family branches to the tree, the present state of our knowledge in microstructure and taxonomy of corals does not allow a solid classification at the suborder scale. For each taxon, the present work provides either: 1) a description accompanied by similarities and differences when we describe some specimens sampled in the field or found in collections that do not include the type material of the corresponding species; 2) an amended description when we propose a revision of the type material of a species with or without new specimens attributed to this species; and 3) a description accompanied with a differential diagnosis for the new species described.

Family ACTINASTREIDAE Alloiteau, 1952 (or ASTROCOENIIDAE Koby, 1889?)

REMARK

The legitimacy of the coexistence of these two families needs to be ascertained by a comparison of microstructures and their variability.

Genus *Allocoenia* Etallon, 1859

SPECIES ORIGINALLY INCLUDED. — *A. trochiformis* Michelin, 1844, *A. furcata* Etallon, 1859.

TYPE SPECIES. — *Allocoenia furcata* Etallon, 1859, subsequent designation by Wells (1936).

REMARKS

The differences between the genera *Actinastrea* Orbigny, 1849, *Allocoenia* Etallon, 1859, *Stephanastrea* Etallon, 1864, *Stelidioseris* Tomes, 1893, *Allocoeniopsis* Alloiteau, 1958 and *Chondrocenia* Roniewicz, 1989 remain very difficult and we propose here an assignation to the genus *Allocoenia* for the following reasons:

TABLE 1. — List of taxa described in the present paper and their family assignment.

Species	Family	Figure number
Allocoenia sp.	Actinastreidae	Fig. 3
Allocoenia waltoni Edwards & Haime, 1851	Actinastreidae	Fig. 5
Enallocoenia sp.	Actinastreidae	Fig. 6
Koilocoenia atlasica n. sp.	Actinastreidae	Fig. 7
Koilocoenia faugeresi (Beauvais, 1986)	Actinastreidae	Fig. 8
Lochmaeosmilia radiata (Lamouroux, 1821)	Actinastreidae or Astrocoeniidae ?	Fig. 9
Eobracthelia costata n. sp.	Aplosmiliidae	Fig. 10
Archaeosmiliopsis densa Melnikova, 1975	Archaeosmiliidae	Fig. 11
Thecocyathus mactra (Goldfuss, 1826)	Caryophylliidae	Fig. 12
Trochocyathus provincialis (Alloiteau, 1948)	Caryophylliidae	Fig. 13
Cladophyllia cf. babeana (Orbigny, 1850)	Cladophylliidae	Fig. 14
Dimorpharaea fungiformis (Edwards & Haime, 1851b)	Comoseridae	Fig. 15
Trocharea sp.	Comoseridae	Fig. 16
Trocharea ilerdensis (M. Beauvais *in* Baudrimont & M. Beauvais, 1962), n. comb.	Comoseridae	Fig. 17
Ellipsoidastraea lucasi Alloiteau, 1957	Conophyllidae	Fig. 18
Ellipsoidastraea sp. 1	Conophyllidae	Fig. 19
Dermosmilia praecox n. sp.	Dermosmiliidae	Fig. 20
Proleptophyllia granulum (Fromentel & Ferry, 1866)	Dermosmiliidae	Fig. 21
Thecactinastraea fasciculata (Beauvais, 1986)	Dermosmiliidae	Fig. 22
Thecactinastraea termieri (Beauvais, 1986)	Dermosmiliidae	Fig. 23
Hispaniastraea murciana (Turnšek & Geyer, 1975)	Hispaniastraeidae	Fig. 24
Hispaniastraea ousriorum Boivin *et al.*, 2019	Hispaniastraeidae	Fig. 25
Axosmilia outitensis (Beauvais, 1986)	Pleurosmilliidae	Fig. 26
Placophyllia amnica Melnikova & Roniewicz, 2021	Pleurosmiliidae	Fig. 27
Diplocoenia elmii n. sp.	Stylinidae	Fig. 28
Stylosmilia sp.	Stylinidae	Fig. 29
Haimeicyclus haimei (Chapuis & Dewalque, 1853)	Stylophyllidae	Fig. 30
Axophyllia convergens (Beauvais, 1986), n. comb.	Synastreidae	Fig. 31
Latiastrea cf. *minima* Beauvais, 1964	Synastreidae	Fig. 32
Latomeandra cf. *plicata* (Goldfuss, 1826)	Synastreidae	Fig. 33
Microphyllia cf. *soemmeringii* Münster *in* Goldfuss, 1829	Synastreidae	Fig. 34
Microphyllia sp.	Synastreidae	Fig. 35
Periseris elegantula (Orbigny, 1850)	Synastreidae	Fig. 36
Synastrea agaricites (Goldfuss 1826)	Synastreidae	Fig. 37

The genus *Actinastrea* being the most anciently described was defined in the Late Cretaceous and was used in the most lumping practices (Geyer 1955a). Despite recent revisions (Löser 2012a), the status of the genus remains nomenclaturally problematic in the sense that the currently admitted type species *A. goldfussi* Orbigny, 1850 was not a part of the originally included nominal species (opposition to article 67-2, ICZN). From a taxonomic point of view, it seems that the lectotype of *A. goldfussi* (if, after all, we use it as a reference) and also the lectotype of *Stelidioseris gibbosa* Tomes, 1893 (another probable species of Late Cretaceous and not Liassic) show septal strong granules near the wall. In *Stelidioseris*, these granules have been misinterpreted by Löser (2012a) who considered these septal parts, trabecular in nature and dark in thin section, as lacunae. We cannot assign the Liassic samples to these taxa and prefer to place our samples within *Allocoenia,* a genus that would also deserve a revision.

The groupings proposed by Geyer (1955a) that placed within *Actinastrea* the type species of *Coenastrea* Etallon, 1862 and *Enallocoenia* Orbigny, 1849 seem immoderate. The occurrence of S2 with paliform inner edge, with S3 tending to join on S2 (the septa are free in both latter genera), and calices globally smaller are characteristic for the forms named *Allocoenia* in the present work.

Concerning *Stephanastrea*, the genus was built on the type species *S. ramulifera* Etallon *in* Thurmann & Etallon, 1864, according to a double crown of pali, more confluent septa with strong teeth on distal edges, and a ramose morphology of the colony. If we put apart the morphology of the colony that cannot be denied, these distinctive characters cannot be found on the type material (specimen MJSN S2234). The ramose character seems to be more relevant of a specific rather than generic variation. The nomenclatural priority belongs to *Allocoenia* (1859) against *Stephanastrea* (1864).

Allocoeniopsis is defined by Alloiteau (1958) on the basis of *Stephanocoenia oolitica* Koby, 1905 and distinguished from *Allocoenia* by mean of the structure of the wall. The observation of the type material does not allow such a distinction.

These forms are distinguished from *Koilocoenia* Duncan, 1884 by the occurrence of a styliform columella. Authors have often used *Cyathocoenia* Duncan, 1867 for Actinastreidae without columella but it appears that the type specimen of the type species has a neat columella.

In the end, the genus differs from *Isastrea* by its straight septa with an often marked angle between confluent septa and the presence of a columella.

Allocoenia sp.
(Fig. 3)

Allocoenia sp. 1 – Vasseur 2018: 109-110, fig. 3.2.

Allocoenia sp. – Vasseur & Lathuilière 2021: 1194, fig. 2.

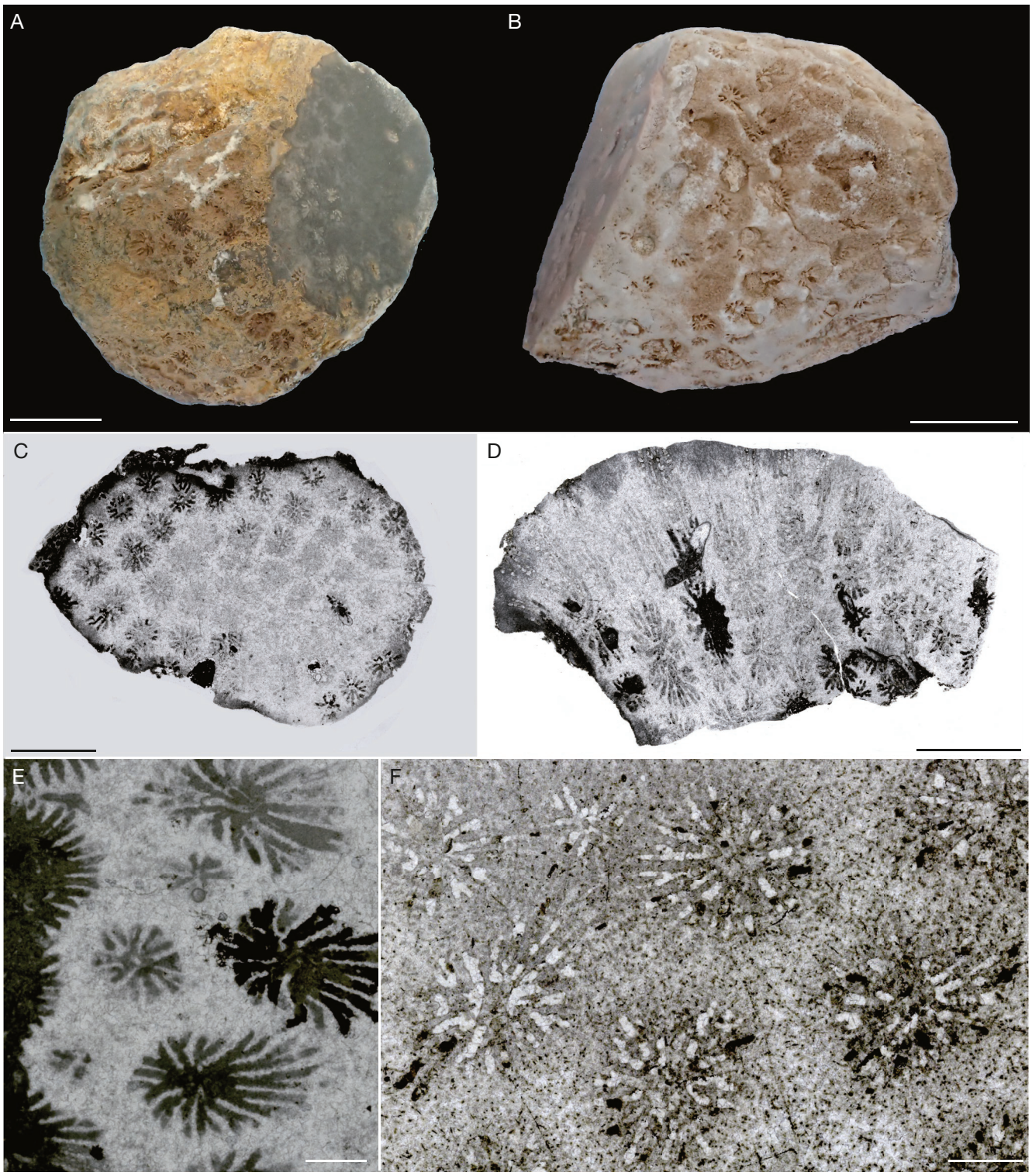

Fig. 3. — *Allocoenia* sp.: **A**, distal view of the specimen CPUN DA0106E2-2 (Toarcian, above Polymorphum zone, Dades Valley between Tillout and Tidrit); **B**, distal view of the specimen CPUN MA0504E7-9 (Toarcian from Taililout Pass, Morocco); **C**, superficial transverse thin section in the specimen CPUN DA0106E2-2 (Toarcian, above Polymorphum zone, Dades Valley between Tillout and Tidrit, Morocco); **D**, oblique thin section in the specimen CPUN DA0106E3-2 (Toarcian, above Polymorphum zone, Dades Valley between Tillout and Tidrit, Morocco); **E**, transverse thin section in the specimen CPUN MA1004E4-11 (Middle/Upper Toarcian from Ain Leuh, Morocco); **F**, transverse thin section in the specimen CPUN 1603A3E5 (Upper Toarcian of Amellagou, Morocco). Scale bars: A, B, 1 cm; C, D, 5 mm; E, F, 1 mm. Photos: R. Vasseur.

Studied samples. — Seven specimens: CPUN 1603A3E5, CPUN DA3005E1, CPUN DA0106E2-2, CPUN MA0504E7-9, CPUN MA1004E4-11, CPUN MA1004E4-28, DA0106E3-2.

Geographic and stratigraphic ranges. — Pliensbachian of Koudiat Ech Chehem (Guigou plateau, Middle Atlas of Morocco) and Toarcian of Amellagou and Dadès Valley (High Atlas of Morocco) and Aïn Leuh (Middle Atlas of Morocco).

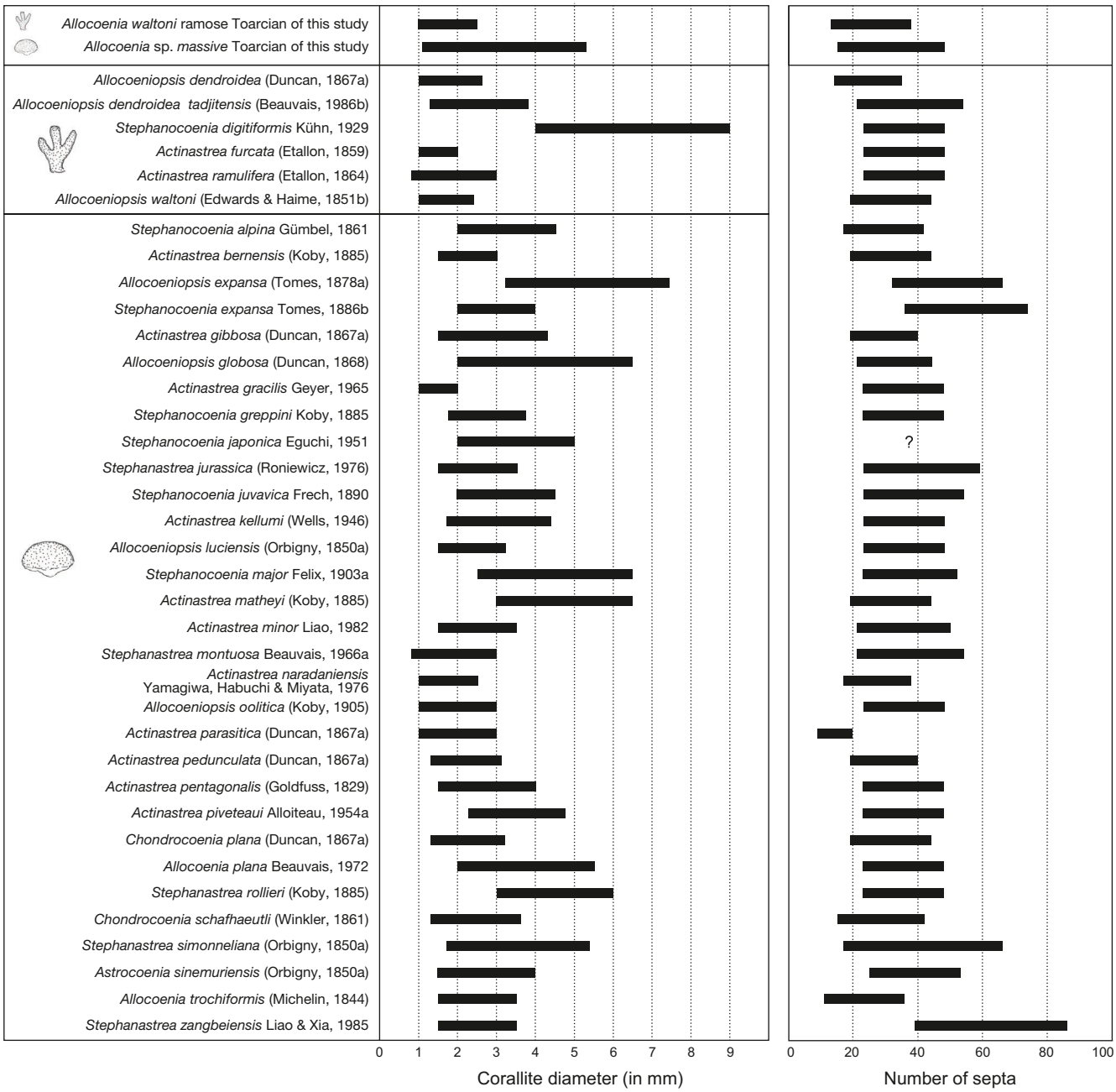

FIG. 4. — Comparison of Triassic and Jurassic species of the genera *Chondrocoenia* Roniewicz, 1989 and *Allocoenia* Etallon, 1859. Binoma are named according to their last combination in the literature. Cretaceous species, octameral or pentameral species, forms without trident junctions of septa, forms clearly plocoid, forms without septal hierarchy and forms with intracalicular increase have been discarded. *S. japonica* Eguchi, 1951 is said to be either massive or ramose. Taxa are in alphabetic order of species names.

DESCRIPTION

Cerioid massive corallum forming small, rounded, pluricentrimetric colonies. The calices are subcircular to polygonal and multiply by extracalicular increase. Radial elements are straight, free or joined, subcompact septa with well-defined but quite irregular trabecular structure producing irregular granules on lateral faces. The inner edge of septa is sometimes swollen or paliform. The septal apparatus is organized in 3 distinct size orders and sometimes the first order septa reach the axial styliform columella. Subordinate septa often join others creating a typical "trident" pattern. Endotheca made of many vesicular dissepiments. Synapticulae not observed. Wall present, of undetermined nature. No holotheca observed.

DIMENSIONS

Calicular diameter: 1.1 to 4.2 mm – distance between calicular centres: 1.5 to 3.5 mm – number of septa: 16 to 32 – septal density: 3 to 5 per 1 mm.

SIMILARITIES AND DIFFERENCES

We have compared with a large number of described nominal species and the intraspecific variation of our specimens encom-

pass the variation range of a large number of them (Fig. 4) with only five specimens. We have hesitated to attribute this taxon to *Allocoenia pentagonalis* Goldfuss, 1829, the most anciently named Kimmeridgian species. We finally kept it distinct considering the high variability (both in measures and symmetry) and the temporal gap between these two taxa associated to a poor documentation about evolutionary variability between Toarcian and Kimmeridgian *Allocoenia*.

Allocoenia waltoni (Edwards & Haime, 1851b) (Fig. 5)

Thamnastraea waltoni Edwards & Haime, 1851b: 120, pl. 25, fig. 4; 1857: t.2, 564. — Tomes 1883: 189.

Thamnastraea (*Centrastræa*) *waltoni* – Fromentel 1861: 217.

non Thamnastrea waltoni – Duncan 1872: 8, pl. 2, fig. 6-9.

Stephanocœnia (*Thamnastrea*) *waltoni* – Koby 1907: 10, pl. 4, fig. 1, 1a.

Allocoeniopsis waltoni – Beauvais 1970a: 40, pl. D, fig. 3. — Negus & Beauvais 1975: 195.

Allocoenia furcata Etallon, 1859: 478/78. — Alloiteau 1957: pl. 12, fig. 9. — Beauvais 1964: 110; 1973: 324. — Roniewicz 1966: 174, pl. 1, fig. 2.

Stephanocoenia furcata – Fromentel 1861: 203. — Koby 1885: 304, pl. 85, fig. 6-8. — Speyer 1913: 244, pl. 24, fig. 53-53a. — Babaev 1965: 48.

Stephanocoenia ?furcata – Fromentel 1865: 22.

Stephanastrea ramulifera Etallon, 1864: 402, pl. 57, fig. 2. — Alloiteau 1957: 60. —? Errenst 1990: 160, pl. 1, fig. 1a-c. — Morsch 1995: 52, pl. 7, fig. 1; 1996: 676, pl. 83, fig. 1a-e.

Astrocoenia carrapateirensis Koby, 1904: 52, pl. 14, fig. 10-13.

Astrocoenia cesaredensis Koby, 1904: 53, pl. 14, fig. 9.

Actinastrea furcata – Geyer 1955a: 321. — Rosendahl 1985: 33.

Actinastrea cf. *furcata* – ?Prinz 1991: 192, pl. 7, fig. 2. — Nose 1995: 108. — Nose & Leinfelder 1997: 1759.

Actinastrea ramulifera – Fezer 1988: 87. — Geyer 1954: 129, pl. 9, fig. 1-2; 1955a: 321, pl. 3, fig. 6; 1955b: 181. — Frajová 1957: 53. — Veselinovic 1963: 298. — ? Rosendahl 1985: 32. — Reiff 1988: 359. — Prinz 1991: 188, pl. 6, fig. 4, text fig. 24. — Lauxmann 1991: 111, pl. 1, fig. 2.

non Actinastrea ramulifera – Ljuljeva & Permyakov 1980: 118, pl. 39, fig. 10-11, pl. 40, fig. 2. — Liao & Xia 1985: 128, pl. 1, fig. 1, 7; 1994: 88, pl. 11, fig. 7-9. — Liao & Deng 2013: 112, pl. 48, fig. 4-6.

Stephanocoenia? pentagonalis – Becker 1875: 147, pl. 39, fig. 2.

Stephanocoenia ramulifera – Koby 1885: 303, pl. 88, fig. 5-8; 1904: 55, pl. 14, fig. 3. — ?Zuffardi-Comerci 1959: 226, pl. 2, fig. 6.

Actinastrea cf. *ramulifera* – ?Prinz 1986: 739, fig. 6a, f. — Helm *et al.* 2003: 82.

Stylastraea dendroidea – Tomes 1884a: 371.

Astrocoenia dendroidea – Duncan 1867:22, pl. 9, fig. 10-11.

Allocoeniopsis dendroida – Beauvais 1976: 49, pl. 9, fig. 3, pl. 10, fig. 3-4.

Allocoeniopsis dendroidea tadjitensis Beauvais, 1986b: 31.

Allocoenia sp. 2 – Vasseur 2018: 112, fig. 3.3.

TYPE MATERIAL. — **Holotype. England •** By monotypy; near Bath; Bathonian Great Oolite sumset; collection Walton Sedgwick Museum Cambridge n°J5848; Walton leg.

STUDIED SAMPLES. — Four specimens: CPUN A116-1, A116-2, A116-3; CPUN A122 from Upper Toarcian of Amellagou (High Atlas of Morocco).

DESCRIPTION

Cerioid ramose colony of which approximately 1 cm wide branches are covered by subcircular calices multiplying by intercalicular budding. Radial elements are straight or wavy, subcompact septa, free or joined by their inner edges. The septal apparatus is organized in three distinct size orders (it is probably hexameral) and sometimes the first order septa reach the axial styliform columella. Subordinate septa often join others creating a typical "trident" pattern ("fused triplet" according to Veron [2000: 278]). Lateral faces hold strong granules sometimes large and rounded, sometimes sharp, irregularly distributed. A styliform columella sometimes appear at the axis of the corallites. Endotheca made of vesicular dissepiments. Wall probably parathecal.

DIMENSIONS

Calicular diameter: 1 to 1.5 mm – distance between calices centres: 1 to 2.7 mm – number of septa: 14 to 24 – septal density: approximately 5 for 1 mm.

SIMILARITIES AND DIFFERENCES

Astrocoenia delemontana Koby, 1885 has been synonymized with the present species however it does not show the typical "trident" pattern made by subordinate septa. In addition, Koby already noticed the proximity with *Astrocoenia crassoramosa* (Michelin, 1844), which is the type species of the genus *Enallocoenia*. *Astrocoenia schardti* Koby, 1885 seems to show the same absence of "trident" pattern as for *A. delemontana* (it is also compared with *A. crassoramosa* by Koby) and is possibly decameral. *Allocoenia* sp. described before is not ramose.

Genus *Enallocoenia* Orbigny, 1849

SPECIES ORIGINALLY INCLUDED. — *Astrea crassoramosa* Michelin, 1843.

TYPE SPECIES. — *Astrea crassoramosa* Michelin, 1843 (Michelin 1843: 109, pl. 25, fig. 2), by monotypy.

REMARKS

The differences between the genera *Coenastrea* and *Enallocoenia* being unclear at this day, we merge here these taxa under the genus *Enallocoenia* following the position of Lathuilière (2017 in Corallosphere).

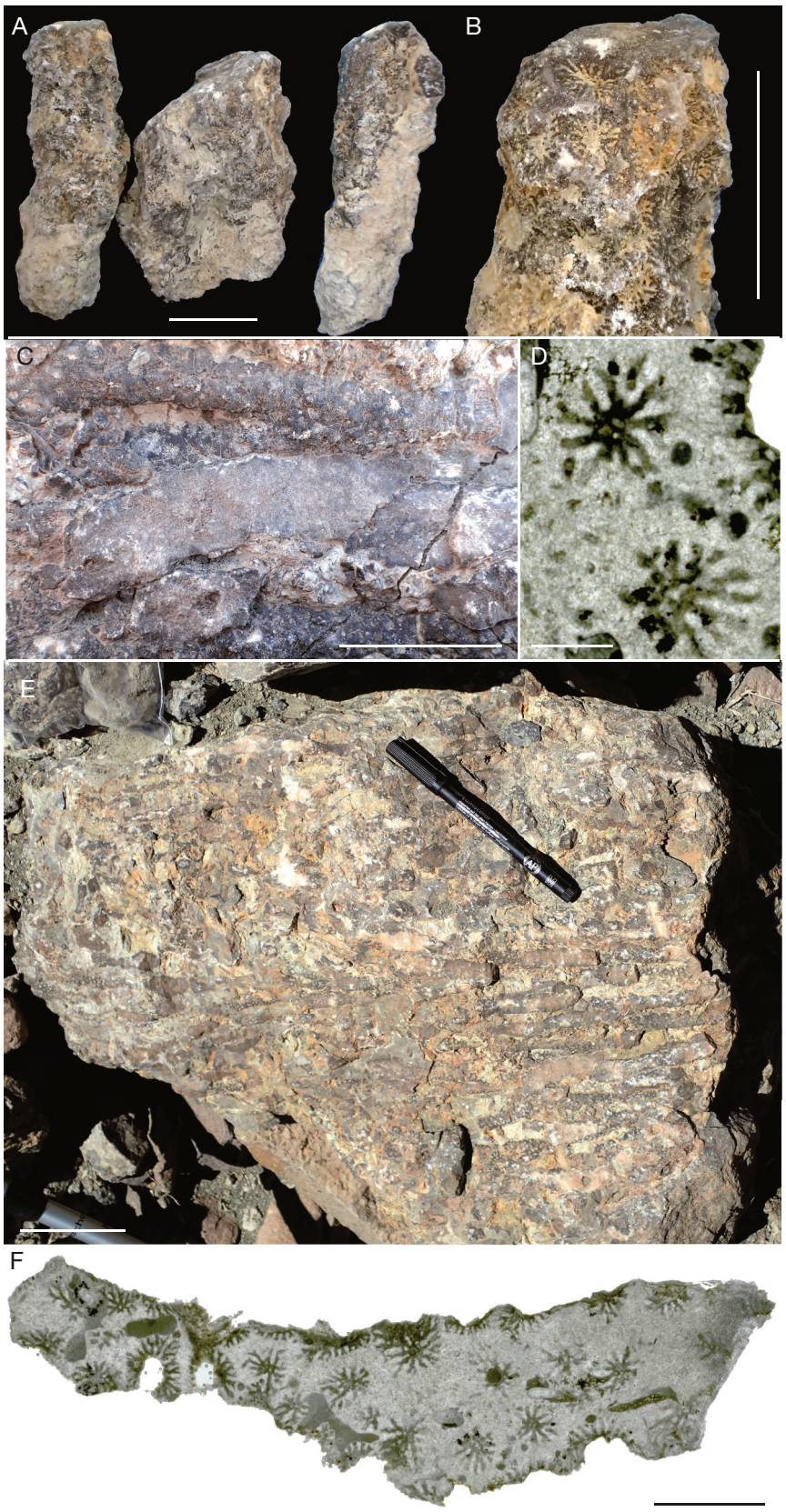

Fig. 5. — *Allocoenia waltoni* Edwards & Haime, 1851b, Upper Toarcian from Amellagou, Morocco: **A**, distal view of the specimens CPUN A116-1, 2 and 3; **B**, detail of the surface of the specimen CPUN A116-1; **C**, specimen pictured in the field (Amellagou); **D**, detail of two calices of specimen CPUN A116-1 in transverse thin section; **E**, specimen pictured in the field (Amellagou); **F**, transverse thin section in the specimen CPUN A116-1. Scale bars: A, B, 1 cm; C, 2 mm; D, 1 mm; E, 6 cm; F, 4 mm. Photos: R. Vasseur.

Actinastrea and all the similar genera differ from *Enallocoenia* by the presence of paliform inner edge of S2 septa with S3 often joining on it (septa are free in the present genus) and globally smaller calices.

Enallocoenia differs from *Koilocoenia* by the presence of a styliform columella See *Koilocoenia* for its relationship to *Cyathocoenia*.

Enallocoenia sp.
(Fig. 6)

Enallocoenia sp. 1 – Vasseur 2018: 189, fig. 3.35.

Studied samples. — CPUN 1603A8-17; CPUN 1603A9-1; CPUN A137; CPUN MA1004E4-29 from Middle/Upper Toarcian of Amellagou and Aïn Leuh (Morocco).

Description
Cerioid massive corallum forming small, rounded, pluricentrimetric colonies. The calices are subcircular to polygonal and multiply by extracalicular budding. Radial elements are subconfluent, straight, free or rarely joined, subcompact septa with well-defined and regular trabecular structure producing quite regular granules on lateral faces. The inner edge of septa is rarely swollen or paliform. The septal apparatus is organized in 3 distinct size orders and sometimes the first-order septa reach the axial styliform columella. Endotheca made of vesicular dissepiments. Synapticulae not observed. Wall present, septoparathecal, incomplete. No holotheca observed.

Dimensions
Calicular diameter: 1.8 to 5.4 mm – distance between calices centres: 2.6 to 4.3 mm – number of septa: 36 to 45 – septal density: 4 to 5 per 1 mm.

Similarities and differences
In comparison with other species of the genera *Coenastrea* and *Enallocoenia* our specimens have more numerous septa. The closest species in this respect are *C. thurmanni* Etallon, 1860 and *C. martis* Etallon, 1864, possibly two synonyms from the Kimmeridgian. However, both species are ramose.

Despite similarities with *Isastrea*, we discard this assignation because of the presence of a rather styliform columella, the confluence of septa and the intercalicular budding.

Genus *Koilocoenia* Duncan, 1884

Species originally included. — *Phyllocoenia decipiens* Laube, 1865.

Type species. — *Phyllocoenia decipiens* Laube, 1865 (Laube 1865: 264, pl. 6, fig. 1a, 1b), by original designation.

Remarks
This genus correspond to the conceptual genus *Cyathocoenia* Duncan, 1867 that is supposed to be distinguished among the family of the Actinastreidae by the lack of columella in the axis of the calices (For instance see the revision by Melnikova (1968)) . It appears that the type specimen of *Cyathocoenia incrustans* Duncan, 1867, the type species of the genus, shows a distinct styliform columella. *Koilocoenia* has no columella and similar characters as we can see from the revision of the type material by Cuif (1973).

Koilocoenia atlasica n. sp.
(Fig. 7)

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Cyathocoenia sp. 1 – Vasseur 2018: 161, fig. 3. 23.

Type material. — **Holotype. Morocco** • 1 specimen; Amellagou (High Atlas); 31°59'4"N, 5°2'57"W; Upper Toarcian, Lower Jurassic; Vasseur Leg.; CPUN A128-1.
Paratypes. Morocco • 6 specimens; Amellagou (High Atlas); 31°59'4"N, 5°2'57"W; Upper Toarcian, Lower Jurassic; Vasseur Leg.; CPUN 1603A8-4, CPUN 2603A1-9, CPUN A130, CPUN A135, CPUN A142-1, CPUN A142-3.

Type age and locality. — Morocco, Amellagou (High Atlas); Upper Toarcian, Lower Jurassic.

Studied samples. — CPUN 1603A8-4; CPUN 2603A1-9; CPUN A128; CPUN A130; CPUN A135; CPUN A142-1; CPUN A142-3 from Upper Toarcian of Amellagou (High Atlas of Morocco).

Differential diagnosis. — Differs from *Koilocoenia decipiens* (Laube, 1865) which have septa of equal length (according to the original figure and description of Laube), trabecular detachments at the inner edge of septa and tabular dissepiments (see Cuif 1973). Differs from *Koilocoenia faugeresi* described herein by its smaller calice diameters and number of septa and also by a more discrete ornamentation on lateral faces of septa. We found no corresponding morphometric dimensions in Triassic species described under the name *Cyathocoenia,* the closest species are *C. paradoxa* Melnikova, 1968 and *C. minor* Melnikova, 1975 but they both have a higher number of septa.

Etymology. — The species name refers to the Atlas mountains where the specimens were found.

Description
Cerioid massive corallum forming small, rounded, pluricentrimetric colonies. The calices are subcircular to polygonal and multiply by extracalicular budding. Radial elements are straight, free or joined, subcompact septa with well-defined but quite irregular trabecular structure producing tiny irregular granules on lateral faces. The inner edge of septa is sometimes swollen or paliform. The septal apparatus is organized in two distinct size orders. No axial structure. Endotheca made of vesicular dissepiments. Synapticulae not observed. Wall present, it seems septothecal. No holotheca observed.

Dimensions
Calicular diameter: 1.2 to 1.6 mm – distance between calices centres: 1.2 to 2.2 mm – number of septa: 14 to 22 – septal density: 5 to 6 per 1 mm.

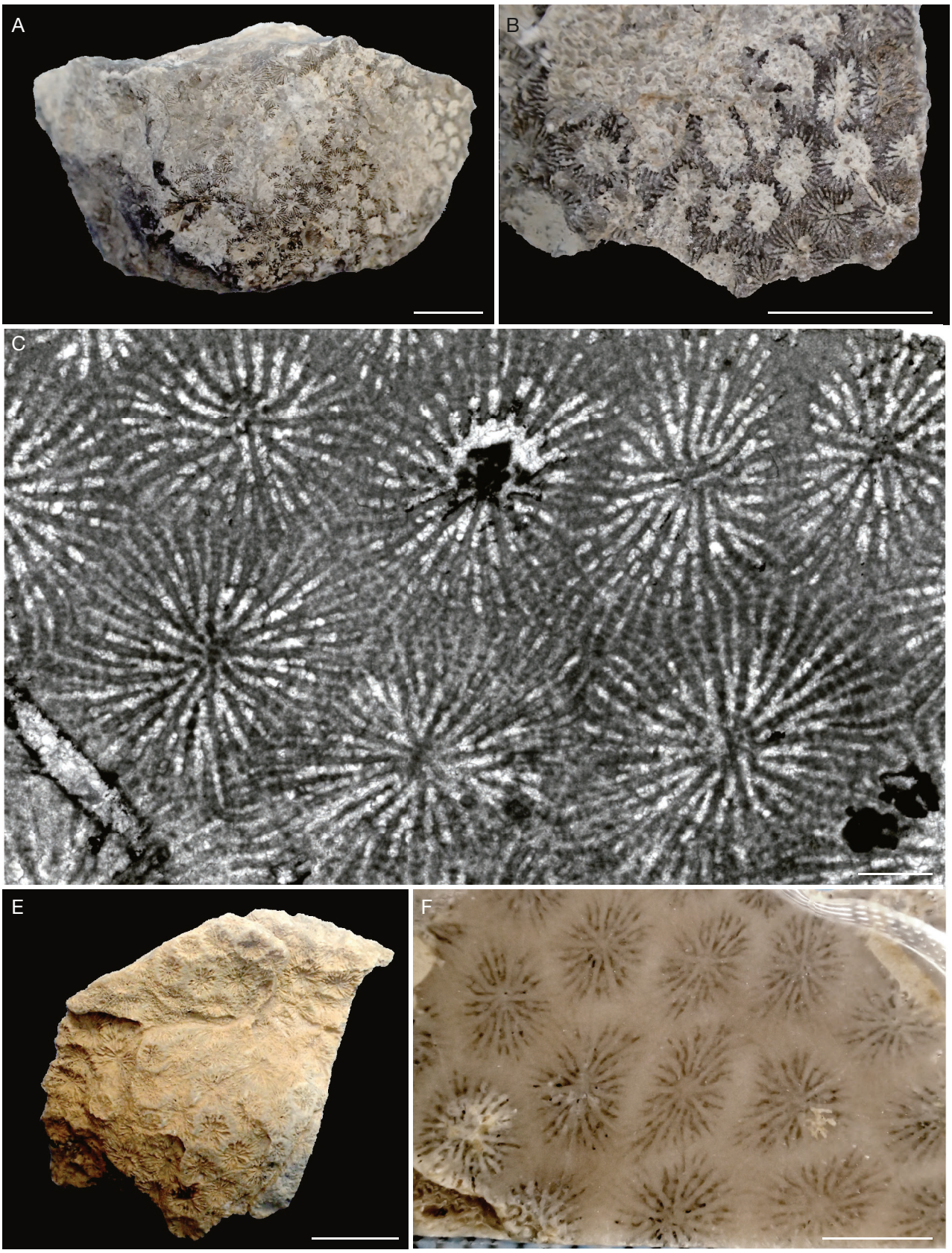

Fig. 6. — *Enallocoenia* sp.: **A**, distal view of the specimen CPUN 1603A9-1 (Upper Toarcian from Amellagou, Morocco); **B**, distal view of the specimen CPUN 1603A9-1 (detail); **C**, superficial transverse thin section in the specimen CPUN A137 (Upper Toarcian from Amellagou, Morocco); **D**, distal view of the specimen CPUN MA1004E4-29 (Middle/Upper Toarcian of Aïn Leuh, Morocco); **E**, transverse polished section in the specimen CPUN MA1004E4-29. Scale bars: A, B, D, 1 cm; C, 1 mm; E, 4 mm. Photos: R. Vasseur.

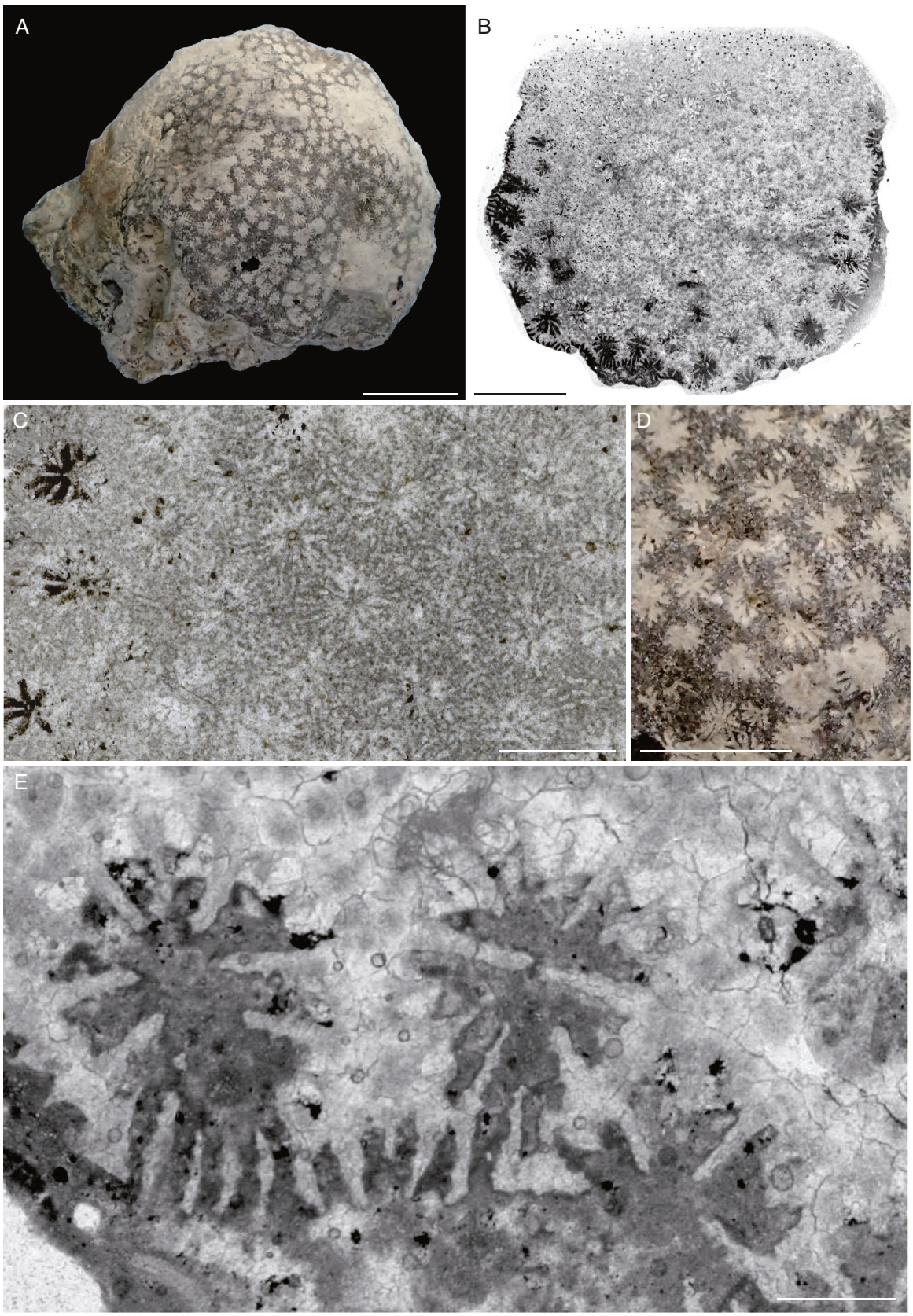

FIG. 7. — *Koilocoenia atlasica* n. sp., Upper Toarcian from Amellagou, Morocco: **A**, distal view of the holotype CPUN A128-1; **B**, transverse thin section of the paratype CPUN A142-1; **C**, transverse thin section of the paratype CPUN 1603A8-4; **D**, detail in distal view of the holotype CPUN A128-1; **E**, detail in transverse thin section of the paratype CPUN A142-1. Scale bars: A, B, 1 cm; C, 2 mm; D, 5 mm; E, 0.5 mm.

Koilocoenia faugeresi (Beauvais, 1986)
(Fig. 8)

Isastrocoenia? faugeresi Beauvais, 1986b: 39, pl. 9, fig. 3, txt-fig. 28.

Cyathocoenia faugeresi – Vasseur 2018: 158, fig. 3.22.

Type material. — **Holotype**. **Morocco** • 1 specimen; Bab-Tisra, 34°10'47"N, 5°42'0"W (based on nearby landmark, PaleoDB collection 33615); Upper Toarcian to Aalenian, Lower to Middle Jurassic; Faugères Leg.; MNHN.F.R11631.

Studied samples. — The holotype MNHN.F.R11631; CPUN 1603A8-5; CPUN 1603A8-9 from Upper Toarcian of Amellagou (Morocco).

Description
Cerioid massive corallum forming small, rounded, pluricentrimetric colonies. The calices are subcircular to polygonal and multiply by extracalicular budding. Radial elements are straight, free or joined, subcompact septa with well-defined but quite irregular trabecular structure producing tiny irregular granules on lateral faces. The inner edge of septa is sometimes swollen or paliform. The septal apparatus is organized in three distinct size orders and sometimes the first-order septa join each other in the centre of the calix in depth. No columella but the projection of trabeculae from the inner edges of septa sometimes looks like a weak papillose axial structure in distal view. Endotheca made of vesicular dissepiments. Synapticulae are not excluded but not clearly identified. Wall present, it seems septothecal and incomplete (porous). No holotheca observed.

Dimensions
Calicular diameter: 1.5 to 4.2 mm – distance between calices centres: 1.8 to 4.5 mm – number of septa: 28 to 40 – septal density: 5 to 7 per 1 mm.

Similarities and differences
In comparison to *Koilocoenia atlasica* n. sp. described before, *K. faugeresi* has higher calice diameters and number of septa and also a more marked ornamentation on lateral faces of septa that sometimes creates synapticulae. If we exclude from the genus *Cyathocoenia* all the nominal species with a columella, *K. faugeresi* differs from all the other Triassic and Liassic *Cyathocoenia* species by larger calices and a higher number of septa. *C. gerthi* has similar dimensions but presents an axial structure made by the junction of curved septa. Differs from *Koilocoenia decipiens* which have septa of equal length (according to the original figure and description of Laube), trabecular detachments at the inner edge of septa and tabular dissepiments (see Cuif 1973).

Genus *Lochmaeosmilia* Wells, 1943

Species originally included. — *L. trapeziformis* (Gregory, 1900); *L. koniakensis* (Ogilvie, 1897); *L. aethiopica* Wells, 1943.

Type species. — *Stylosmilia trapeziformis* Gregory, 1900, by original designation.

Remarks
This taxon differs from the genus *Apocladophyllia* Morycowa and Roniewicz, 1990 which increases by dichotomous division and possesses an essential columella. We place here *Aggomorphastraea* Alloiteau, 1958 in synonymy with *Lochmaeosmilia* considering the discriminant characters presented by Alloiteau (1958: 96): the porous nature of septa is interpreted as controlled by diagenesis based on the thin sections in the holotype (see specimen MNHN.F.M05009). Synapticulae are mentioned as absent in the description of *Aggomorphastraea barrabei* Alloiteau, 1958 but present as a discriminant character of the sub-genus. The synapticular ring presented in fig. 14 p. 97 is exaggerated regarding the thin sections, we interpret this as the consequence of a local rejuvenescence pattern, absent in other parts of the colony. The columella appears highly variable in structure, cited as spongy, papillose or absent. Gregory (1900) described an intracalicular budding for *L. trapeziformis* but this character has been erroneously changed subsequently by Wells (1943). In their study of topotypical material, Pandey & Fürsich (1993) reaffirmed the intracalicular budding as a character of this genus. In both cases, apophyses (cross tubules of Wells 1943) are observed.

We attribute with doubt this taxon to the family Actinastreidae Alloiteau, 1952 which did not contain phaceloid forms until now. The septal structures, joining patterns of septa and corallite sizes are compatible with the family.

Lochmaeosmilia radiata (Lamouroux, 1821)
(Fig. 9)

Eunomia radiata Lamouroux, 1821: 83, pl. 81, fig. 10-11. — Lamouroux *et al.* 1824: 382. — Bronn 1825: 42, pl. 4, fig. 13; 1837: 252, pl. 16, fig. 23. — Defrance 1826: 393. — Holl 1843: 414. — Morris 1843: 36. — Edwards & Haime 1849: 260. — *pars* Orbigny 1850: 321. — Lathuilière 2011 *in* Corallosphere.

Tubipora or *Eunomia* sp. – Phillips 1829: 149.

Favosites radiata – Blainville 1830: 367, pl. 13, fig. 4; 1834: 403, pl. 64, fig. 4.

Lithodendron eunomia Michelin, 1846: 223, pl. 54, fig. 6.

non *Calamophyllia luciensis* Orbigny, 1850: 321.

Calamophyllia radiata – Edwards & Haime 1851b: 81; 1851a: 111, pl. 22, fig. 1; 1857: 346. — Fromentel 1861: 136. — Eichwald 1865-1868: 143. — Tomes 1881: 157; ?1883: 182. — Koby 1884b: 187, pl. 56, fig. 1; 1907: 28. — *non* Speyer 1926: 259.

non *Calamophyllia radiata* ? – Achiardi 1880: 266.

non *Calamophyllia* cf. *radiata* – Speyer 1913: 221.

Lochmaeosmilia radiata – Alloiteau 1957: 173, pl. 6, fig. 17, pl. 16, fig. 5; 129, pl. 17, fig. 5. — Beauvais 1967: 29; 1971: 2; 1972a: 54; 1986a: 207, pl. 24, fig. 3; 1988: 157; 1989: 1090. — Ljuleva & Permyakov 1980: 92 pl. 17, fig. 1, 2.

Lochmaeosmilia besavoensis Alloiteau, 1958: 69, pl. 9, fig. 8, pl. 13, fig. 7.

non *Cladophyllia radiata* – Kolosváry 1961: 220, pl. 3, fig. 17-18.

Aggomorphastraea sp.1 – Vasseur 2018: 106 – 108, fig.3.1.

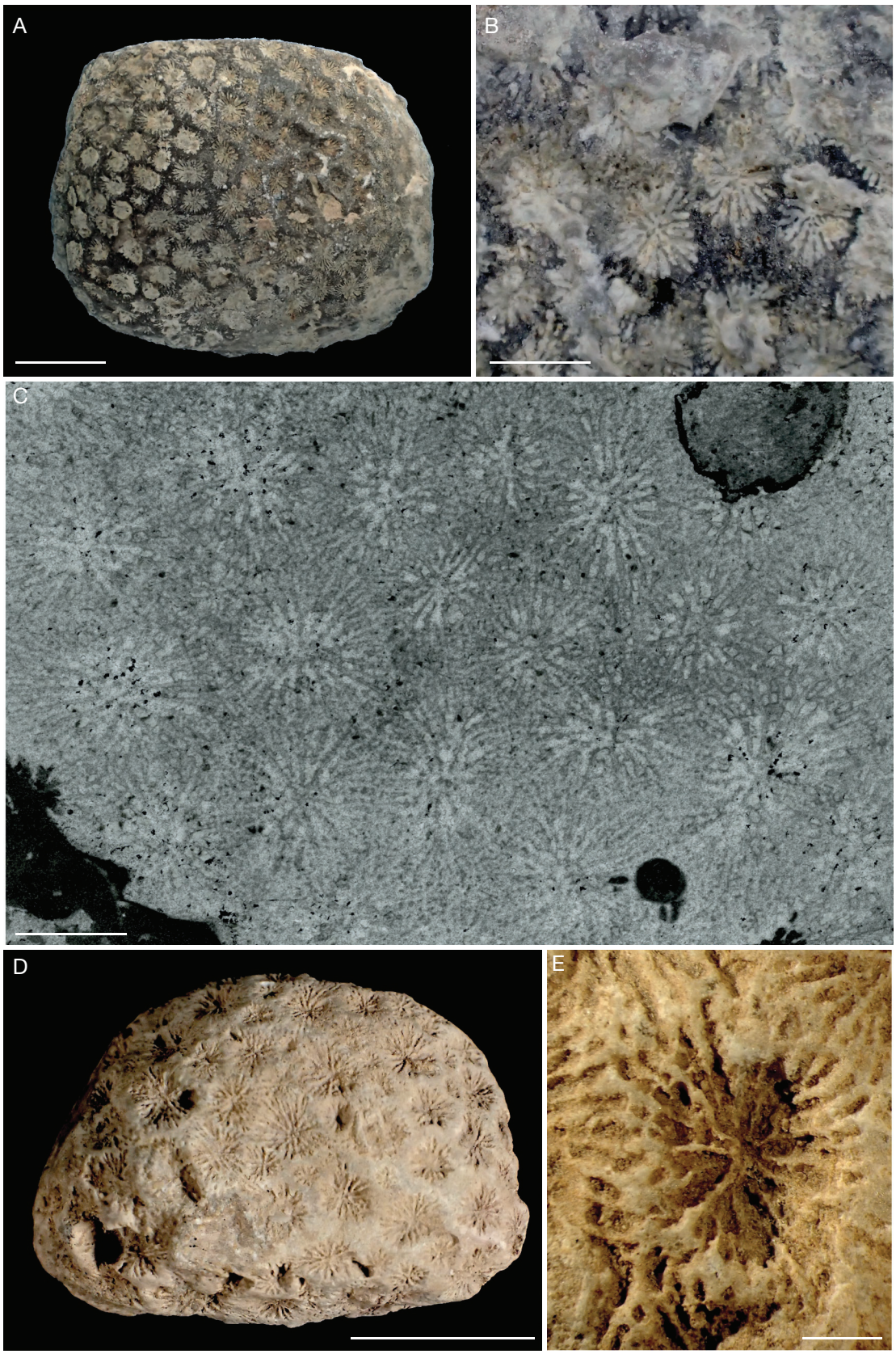

Fig. 8. — *Koilocoenia faugeresi* (Beauvais, 1986): **A**, distal view of the specimen CPUN 1603A8-9 (Upper Toarcian from Amellagou, Morocco); **B**, distal view of the specimen CPUN 1603A8-5 (Upper Toarcian from Amellagou, Morocco); **C**, transverse thin section of the specimen CPUN 1603A8-9 (Upper Toarcian from Amellagou, Morocco); **D**, distal view of the holotype MNHN.F.R11631 (Upper Toarcian-Aalenian from Bab Tisra, Morocco); **E**, detail of one calix of the holotype MNHN.F.R11631 (Upper Toarcian-Aalenian from Bab Tisra, Morocco). Scale bars: A, 1 cm; B, C, 2 mm; D, 1 cm; E, 1 mm. Photos: R. Vasseur.

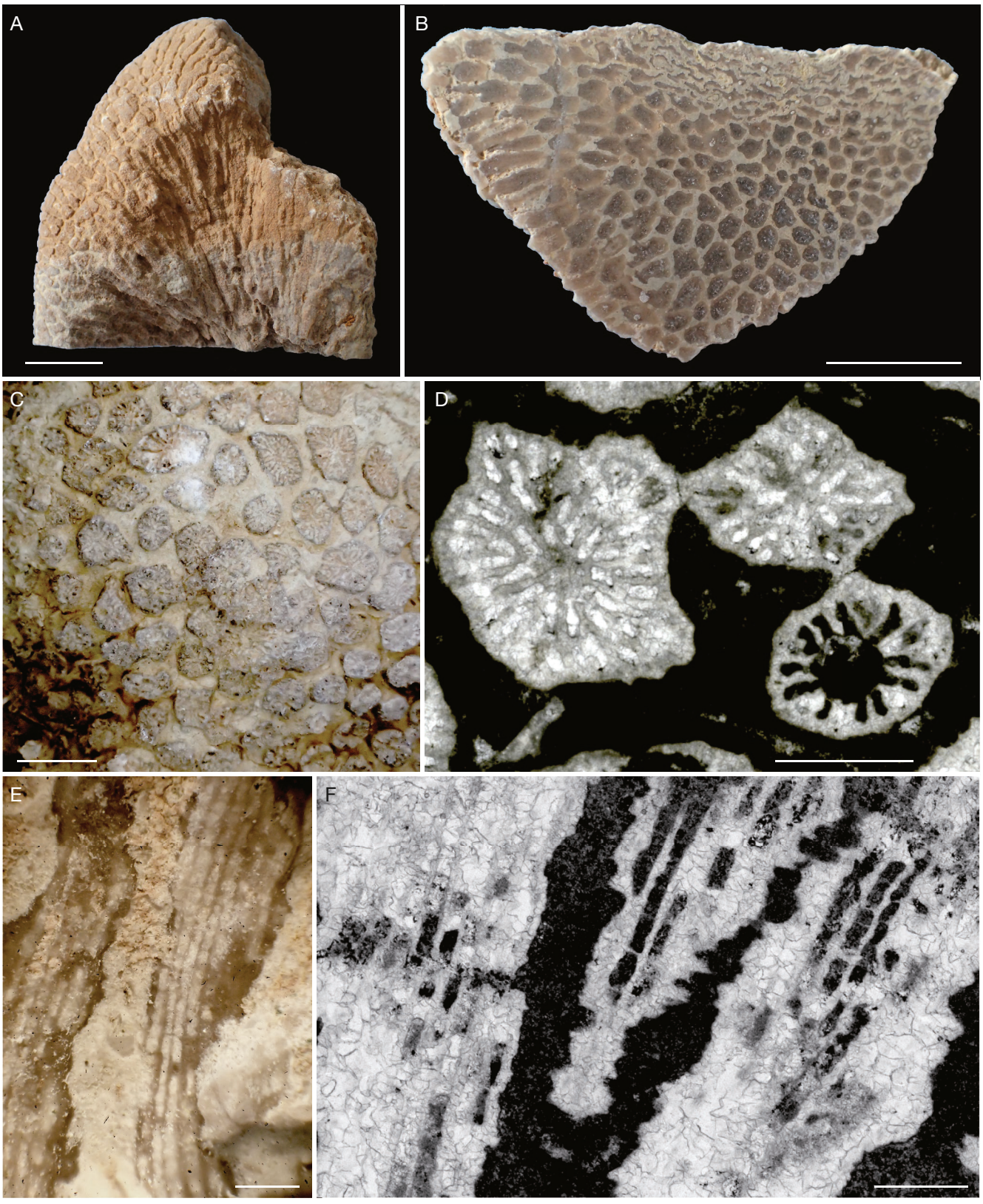

Fig. 9. — *Lochmaeosmilia radiata* (Lamouroux, 1821), Middle/Upper Toarcian from Aïn Leuh, Morocco: **A**, lateral view of the specimen CPUN MA1004E5-2; **B**, transverse/oblique section in the specimen CPUN MA1004E5-2; **C**, detail in distal view of the specimen CPUN MA1004E5-2; **D**, detail in transverse thin section of the specimen CPUN MA1004E5-2; **E**, detail in longitudinal view of granulated septal structure in the specimen CPUN MA1004E5-2; **F**, transverse thin section of the specimen CPUN MA1004E5-2. Scale bars: A, B, 2 cm; C, 5 mm; D, 1.5 mm; E, F, 1 mm. Photos: R. Vasseur.

TYPE MATERIAL. — **Neotype**. **France** • Designated by Alloiteau (1957: 173); 1 specimen; Cormelles near Caen (Normandy); Middle Jurassic, Late Bathonian; Hébert leg.; MNHN.F.R10931.

STUDIED SAMPLES. — Six specimens: CPUN MA1004E5-2, MA1004E4-18; CPUN MA0804E2-9, MA0804E2-10, MA0804E2-11, MA0804E2-12.

AGE AND LOCALITIES OF EXAMINED MATERIAL. — Bioherm of Middle/Upper Toarcian from Aïn Leuh (Middle Atlas, Morocco).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION. — Middle/Upper Toarcian of Middle Atlas (Aïn Leuh) and High Atlas (Amellagou) of Morocco. Bathonian of Normandy and Saint-Gaultier (France), Bathonian of Bath (England), Dogger (Callovian?) of Crimea, Bajocian of Switzerland, Bathonian of Thailand. According to Beauvais (1986a; 1988) the species occurs also in the Dogger of India.

AMENDED DESCRIPTION

Phaceloid colony with subparallel, close calices multiplying by intracalicular increase. Calices present irregular shapes due to apophyses and the space between the calices is strongly conserved (which is unusual in phaceloid corals). Radial elements are straight or slightly curved, sometimes wavy costosepta, often joined or contratingent, with a trabecular structure. Lateral faces are regularly granulated and the distal edge is ornamented with small teeth. Costal part is short. Endotheca made of vesicular dissepiments. A parietal spongy columella generally appears at the axis of the calix, joined by some first orders septa. Epicostal wall, often eroded and regularly horizontally wrinkled. Synapticulae possibly present but rare. Some calices show rejuvenescence.

REMARKS

The figuration of Ljuleva & Permyakov (1980) corresponds to photographs from Edwards & Haime plates and not to the material of Crimea.

Edwards & Haime (1857) placed *Calamophyllia luciensis* Orbigny, 1850 in synonymy with *E. radiata*. Considering the lectotype MNHN.F.R54524, this synonymy is clearly incorrect and *C. luciensis* should probably be included in *Enallhelia* Orbigny, 1849.

DIMENSIONS

Calicular diameter: 1.3 to 3.2 mm – Distance between calices centres: 1.9 to 3.8 mm – Septal density: 5 to 6 for 1 mm – number of septa: 22 – 29.

SIMILARITIES AND DIFFERENCES

L. trapeziformis Gregory, 1900 and *L. aethiopica* Wells, 1943 differ from this species by smaller calices and number of septa. *Calamophyllia guebhardi* Koby, 1905, cited only once, is probably synonym of *L. trapeziformis*.

L. nodosa Alloiteau, 1958, the type species of the genus *Calamoseris* Alloiteau, 1952 does not belong to *Lochmaeosmilia* because it is pennular and lacks apophyses.

L. barrabei Alloiteau, 1958, the type species of *Aggomorphastraea* (synonymized with *Lochmaeosmilia* in this study) has bigger calices and more septa.

Family APLOSMILIIDAE Fromentel, 1861

Genus *Eobracthelia* n. gen.

urn:lsid:zoobank.org:act:2845FAAB-9633-441A-8FFA-76D46DF413A8

TYPE SPECIES. — *Eobracthelia costata* n. sp. by present designation.

DIAGNOSIS. — Plocoid Aplosmiliidae with three peculiar characters: the axial structure is variable but not lamellar, the peritheca is costulate and the septa of the last size orders are so thin that some pores can occur.

ETYMOLOGY. — From *Eos* meaning "dawn" in Greek and *Bracthelia*, the oldest genus of the family known until now. *Eobracthelia* appears to be now the most ancient genus of the family Aplosmiliidae.

SIMILARITIES AND DIFFERENCES

Differential characters of the new genus are summarized in Table 2.

Eobracthelia costata n. sp.
(Fig. 10)

urn:lsid:zoobank.org:act:0F46B650-B826-4BBC-915C-9DEEE7E8E28B

Gen. indet. 1 sp. 1 – Vasseur 2018: 202, fig. 3.40.

TYPE MATERIAL. — **Holotype**. **Morocco** • Two pieces from one single colony; Aïn Leuh (Middle Atlas), Al Yabes levels; 33°11'32"N, 5°21'8"W; Middle/Upper Toarcian, interval Gradata zone, Gemma subzone up to basal Meneghini zone according to Elmi *et al.* (2002), Lower Jurassic; Vasseur Leg.; CPUN MA1004E5-3.

TYPE AGE AND LOCALITY. — Morocco, Aïn Leuh (Middle Atlas), Al Yabes levels; Middle/Upper Toarcian, interval Gradata zone, Gemma subzone up to basal Meneghini zone according to Elmi *et al.* (2002), Lower Jurassic.

STUDIED SAMPLES. — Only the holotype.

DIFFERENTIAL DIAGNOSIS. — Plocoid Aplosmiliidae with three peculiar characters: the axial structure is variable but not lamellar, the peritheca is costulate and the septa of the last size orders are so thin that some pores can occur.

ETYMOLOGY. — The species name refers to the presence of costae.

DESCRIPTION

Plocoid massive colony with circular to elliptical calices multiplying by extracalicular budding. Radial elements are straight, curved or wavy costosepta, free or joined, subcompact, highly unequal with inner edge often swollen, which suggest the presence of auriculae rather massive in shape. A radial symmetry can be observed, either sixfolded (in most cases), or eightfolded, depending of the calices. The first order septa sometimes join a parietal axial structure of variable aspect: papillose, spongy or styliform, which is not present everywhere. Lateral faces of septa hold small, irregular granules and the S1 are sometimes cuneiform. Endotheca made of vesicular dissepiments. No synapticulae. Wall parathecal and costulate peritheca.

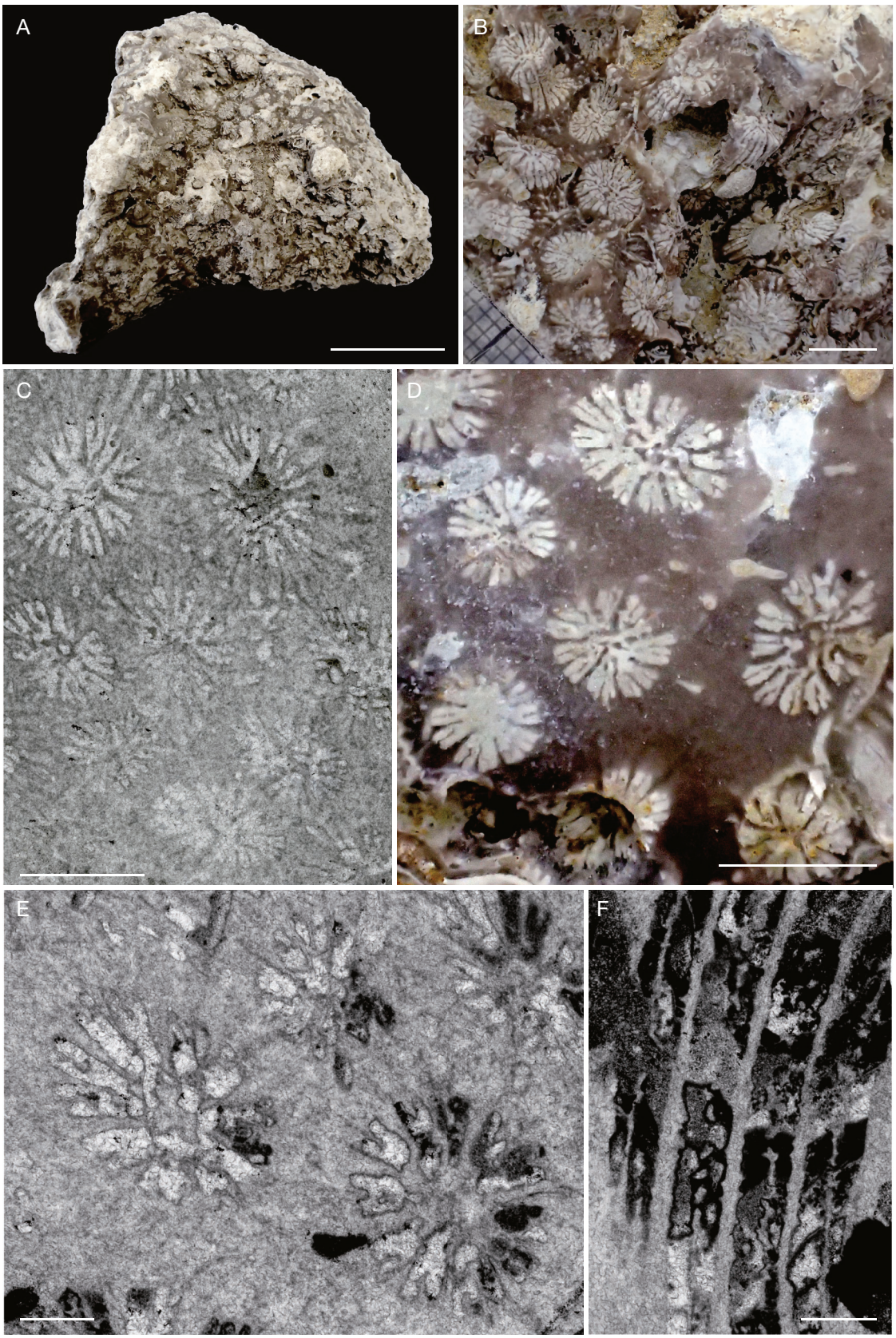

Fig. 10. — *Eobracthelia costata* n. sp., Middle/Upper Toarcian from Aïn Leuh, Morocco: **A**, distal view of the holotype CPUN MA1004E5-3; **B**, distal view of the holotype CPUN MA1004E5-3 (detail); **C**, transverse thin section of the holotype CPUN MA1004E5-3; **D**, distal view of the holotype CPUN MA1004E5-3 (detail); **E**, transverse thin section of the holotype CPUN MA1004E5-3; **F**, longitudinal thin section of the holotype CPUN MA1004E5-3. Scale bars: A, 4 cm; B, D, 5 mm; C, 4 mm; E, F, 1 mm. Photos: R. Vasseur.

TABLE 2. — Comparison of different genera close to *Eobracthelia* among Aplosmiliidae.

		Eobracthelia	***Bracthelia***	***Ogilvinella***	***Bodeurina***	***Astreoidogyra***	***Diplocoeniella***
Nomenlature	authors/year	n. gen.	Beauvais & Beauvais, 1975	Eliášová, 1976	Beauvais, 1980	Ricci *et al.*, 2018	Morycowa, 1997
	synonyms	–	*Ironella* Starostina & Krasnov, 1970 *non* Cobb, 1920 *Starostinia* Doweld, 2014 *Pseudironella* Sikharulidze, 1979	*Ogilviella* Eliášová, 1973 *non* Lentz, 1968 ?*Lamnastrea* Reig Oriol, 1997			
	species	*E. costata* n. sp.	*B. abkhazica* (Lebanidze, 1980) *B. arabica* (El-Asaad, 1991) *B. collignoni* Beauvais & Beauvais, 1975 *B. giseldonensis* (Krasnov & Starostina, 1970) *B. rutimeyeri* (Koby 1889) *B. tosaensis* (Eguchi, 1951)	*O. elegans* Eliasova, 1973, *O. jurassica* (Geyer, 1954) *O. morycowae* Kolodziej, 2003	*B. languedociencis* Beauvais, 1980	*A. giadae* Ricci, Lathuilière & Rusciadelli, 2018	*D. gerochi* Morycowa, 1997
Morphology	Colonial structure	Mostly plocoid	Plocoid	Plocoid	Plocoid	Astreoid	Astreoid
	Axial structure	Variable, from absent to spongy or styliform	Variable (absent, parietal, sublamellar)	Lamellar columella	Absent	Lamellar columella	Styliform columella
	Septal structure	Minor septa subcompact	Compact	Compact	Compact	Compact	Compact
	Endotheca	Dissepimental	Dissepimental	Dissepimental	Tabular	Dissepimental	Tabuloid to dissepimental
	Peritheca	Costate	Dissepimental granulose	Dissepimental	Dissepimental	Dissepimental	Costate
Biostratigraphy	FAD	Toarcian	Bathonian	Kimmeridgian	Kimmeridgian-Tithonian interval	Kimmeridgian-Tithonian interval	Upper Barremian
	FAD reference	This paper	Beauvais & Beauvais 1975	Rosendahl 1985	Beauvais 1980	Ricci *et al.* 2018	Morycowa 1997
	LAD	Toarcian	Albian	Tithonian Berriasian interval/ ?Campanian	Kimmeridgian-Tithonian interval	Kimmeridgian-Tithonian interval	Lower Aptian
	LAD reference	This paper	Sikharulidze 1979	Eliášová 1976/? Reig Oriol 1997	Beauvais 1980	Ricci *et al.* 2018	Morycowa 1997

DIMENSIONS

Calicular diameter: 2.8 to 5.6 mm – distance between calices centres: 3.6 to 4.5 mm – number of septa: approximately 31 – septal density: 5 to 7 per 2 mm.

Family ARCHAEOSMILIIDAE Melnikova, 1975

Genus *Archaeosmiliopsis* Melnikova, 1975

SPECIES ORIGINALLY INCLUDED. — *Archaeosmiliopsis densus* Melnikova, 1975.

TYPE SPECIES. — *Archaeosmiliopsis densus* Melnikova, 1975 (Melnikova 1975b: 113, pl. 2, fig. 1), by monotypy.

REMARKS

This genus differs from the genus *Icaunhelia* by its phaceloid form.

Archaeosmiliopsis densa Melnikova, 1975 (Fig. 11)

Archaeosmiliopsis densus Melnikova, 1975b: 113, pl. 2, fig. 1. — Melnikova *in* Turnšek & Kosir 2000: 85, pl. 1, fig.1-2. — Vasseur 2018: 129, fig. 3.10.

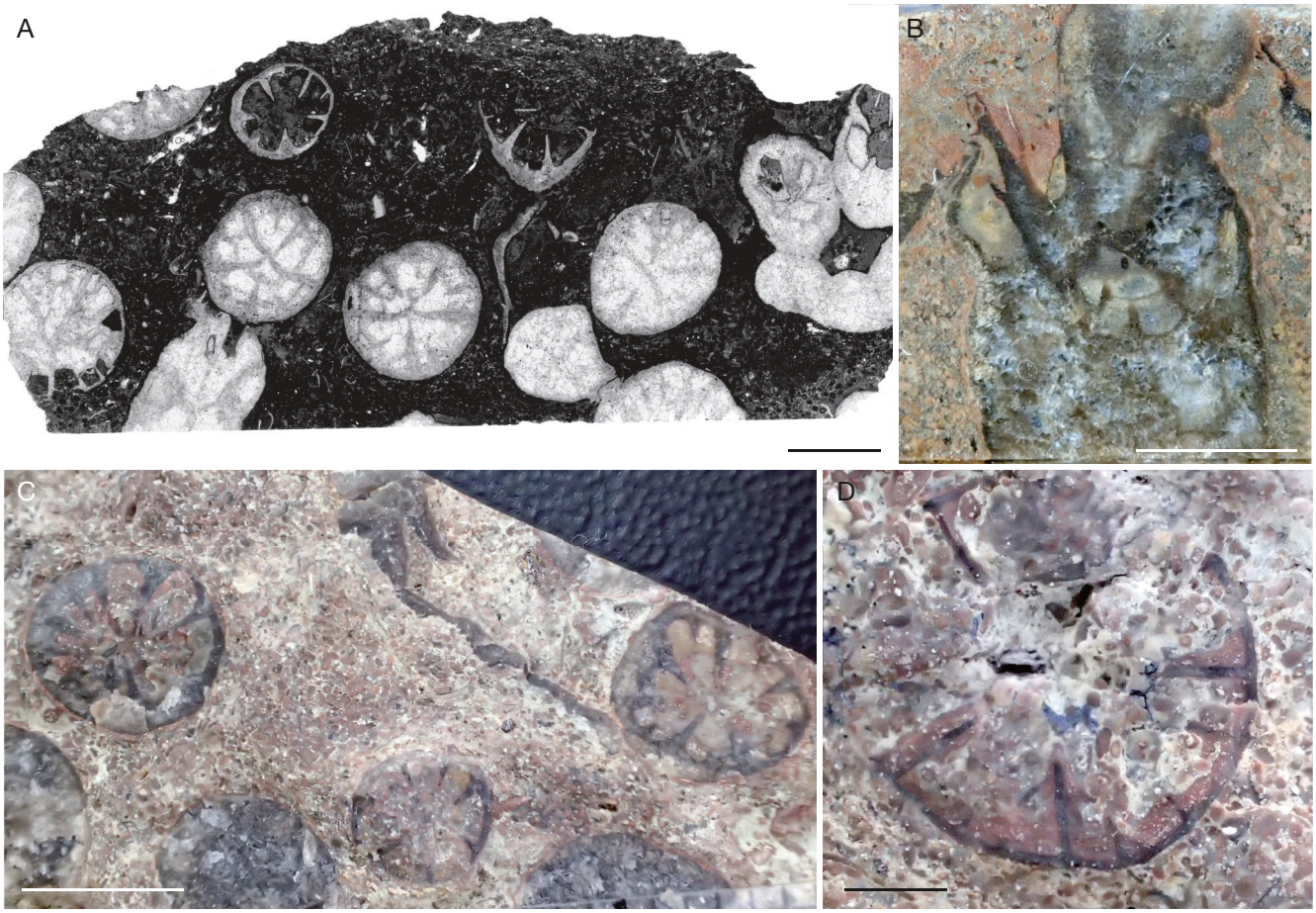

Fig. 11. — *Archaeosmiliopsis densa* Melnikova, 1975, Toarcian above *Polymorphum* Zone, Dades Valley between Tillout and Tidrite, Morocco: **A**, transverse thin section in sample CPUN DA0106E2-1; **B** longitudinal section of a calix in sample CPUN DA0106E2-1; **C**, distal view of the colony CPUN DA0106E2-1; **D**, detail of a very distal part of a corallite showing the link between the septa and the wall in the specimen CPUN DA0106E2-1. Scale bars: A, B, 4 mm; C, 5 mm; D, 2 mm. Photos: R. Vasseur.

Phacelostylophyllum ramosum – Beauvais 1986b: 11, pl. 2, fig. 2.

Archaeosmiliopsis densa – Melnikova & Roniewicz 2021: 483, fig. 9 a1.

Type material. — **Holotype**. **Tadjikistan** • 1 specimen by original designation and 5 topotypes described and figured in Melnikova (1975b); Say Sedek creek Alichur Valley, SE Pamirs; Pliensbachian (previously assigned to Hettangian – Sinemurian and corrected in Melnikova & Roniewicz 2021), Early Jurassic; ZPAL IGD no. 3634.

Studied samples. — CPUN DA0106E2-1 from Lower Toarcian (Polymorphum zone) of Dades Valley (High Atlas of Morocco).

Geographic and stratigraphic ranges. — Pliensbachian of Say Sedek creek, Alichur Valley, SE Pamirs (Tadjikistan), Lias of Krim mountain (Slovenia) and Lower Toarcian (Polymorphum zone) of Dades Valley (High Atlas of Morocco).

Description

Phaceloid coral building a 10 to 20 cm sized colony, with subcylindrical corallites. Septa organized in two or three distinct size orders, wedge-shaped, thickening from the centre to the periphery of the calix. They are straight or curved, free in distal view although facing S1 septa sometimes reach each other in depth. Septa grow by successive stereomal deposits on a thin and straight frame in continuity with the epithecal wall, conferring a "gloves fingers" structure with smooth lateral faces typical of the Archaeosmiliidae family. The septal apparatus is generally constructed on a basis of five or six S1, revealing a six-folded symmetry in the latter case. Endotheca made of tabular and vesicular dissepiments.

Dimensions

Calicular diameter: 3.3 (perhaps 2 mm ?) to 9.1 mm – distance between corallites centres: 3.1 to 10.6 mm – number of septa: 10 to 20 – septal density: 2 to 4 for 2 mm.

Similarities and differences

Archaeosmiliopsis densa is the only species in the genus.

Family Caryophylliidae Dana, 1846

Genus *Thecocyathus* Edwards & Haime, 1848

Species originally included. — *T. tintinnabulum* (Goldfuss, 1826) and *T. mactra* (Goldfuss, 1826).

TYPE SPECIES. — *Cyathophyllum tintinnabulum* Goldfuss, 1826 (Goldfuss 1826: 56, pl. 16 fig. 6 a, b), by subsequent designation of Edwards & Haime (1850: XIV).

Thecocyathus mactra (Goldfuss, 1826) (Fig. 12)

Cyathophyllum mactra Goldfuss, 1826: 56, pl. 16, fig. 7. — Quenstedt 1856: 317, pl. 43, fig. 38; 1879: 582, pl. 164, fig. 45-55.

Cyathophyllum tintinnabulum Goldfuss, 1826: 56, pl. 16, fig. 6a, b. — Quenstedt 1879: 578, pl. 164, fig. 40-43.

Fungia mactra – Blainville 1830: 303.

Thecocyathus mactra – Edwards & Haime 1848b: 318; 1851b: 24; 1857: 49. — Orbigny 1850: 259. — Fromentel 1861: 81. — Fromentel & Ferry 1865: 32, pl. 1, fig. 2. — Delbos Koechlin-Schlumberger 1866: 305. — Bölsche 1866: 441. — Moesch 1867: 70; 1874: 20. — Dumortier 1864: 317, pl. 12, fig. 6-7. — Branco 1879: 16. — Koby 1881a: 14, pl. 3, fig. 3-7. — Meyer 1888: 42, pl. 6, fig. 18-20. — Lissajous 1912: 179, pl. 18, fig. 57-58. — Charles 1948: 58. — Alloiteau 1952: 644, pl. 1, fig. 7. — Guérin 1954: 14.

Cyclolites mactra – Bronn 1848: 374. — Quenstedt 1852: 657, pl. 59, fig. 14-15; 1867: 789, pl. 76, fig. 14-15.

Thecocyathus mactrus – Vaughan & Wells 1943: pl. 41, fig. 1, 1ab. — Wells 1956: 421, fig. 322-2.

Thecocyathus cf. *mactrus* – Negus 1991: 256.

Thecocyathus tintinnabulum – Edwards & Haime 1848b: 317; 1851b: 24; 1857: 48. — Orbigny 1850: 259. — Fromentel 1861: 81. — Bölsche 1866: 442. — Negus 1991: 256, tab. 1.

Cyclolites tintinnabulum – Quenstedt 1852: 657, pl. 59, fig. 11; 1856: 292, pl. 41, fig. 51; 1867: 789, pl. 76, fig. 11.

TYPE MATERIAL. — **Lectotype**. **Germany** • 1 specimen (initial syntype) in Bonner Institut für Organismische Biologie (BIOB), Abt. V Paläontologie/Sect. V Palaeontology & Goldfuß-Museum (BIOB-PAL); collected near Banz, Bamberg; Lias, Lower Jurassic; Goldfuss Leg.; BIOB-PB-Goldfuss-193B (**here designated**) (see Fig. 12).
Paralectotypes. **Germany** • 4 specimens (initial syntypes) in Bonner Institut für Organismische Biologie (BIOB), Abt. V Paläontologie / Sect. V Palaeontology & Goldfuß-Museum (BIOB-PAL); collected near Banz, Bamberg; Lias, Lower Jurassic; Goldfuss Leg.; BIOB-PB-Goldfuss-193A, 193C, 193D and 193E.

STUDIED SAMPLES. — Lot MNHN.F.M03354, MNHN.F.C05113 (13 specimens), batches 20, 25, 38, and some without numbers (62 specimens, MAN – collections ENSG), CPUN AM16100, CPUN AM16101.

GEOGRAPHIC AND STRATIGRAPHIC RANGES. — Toarcian of Lorraine and Jura (France), Upper Toarcian of Amellagou (High Atlas of Morocco), Western Europe.

DESCRIPTION
Discoidal to cupuloid solitary coral sometimes distorded, with axially depressed calicular surface and attachment scars on lower face. Radial elements are compact, straight, exert costosepta. Lateral faces seem to hold granules and the distal edge hold big rounded teeth corresponding to trabeculae, which also project as pali at the inner edge of septa. No endotheca. Large papillose columella, made of homogeneous prismatic rods similar to pali. An epitheca with concentric bulges covers the lower side of the corallite. In our samples, the basal angle is generally rather obtuse.

DIMENSIONS
Calicular diameter: 4 to 15 mm – corallum high: 3 to 5 mm – number of septa: 47 to 86 – septal density: 4 to 6 for 2 mm.

SIMILARITIES AND DIFFERENCES
The comparison with other Jurassic nominal species suggests some possible synonymies that cannot be verified without examination of the type material: *Thecocyathus* ? *grenieri* (Fromentel, 1861); *T.* ? *grosgogeati* Fromentel, 1861; *T. mactraeformis* Kolosváry, 1954a; *T. moorei* Edwards & Haime, 1851b; *T. pusillus* Koby, 1904; *T. quenstedti* Fromentel & Ferry, 1865a; *T. tuberculata* (Tomes, 1878b). The latter, the only Liassic one, is the most probable synonym because of a distinction based only on the smaller size of the corallum (which actually corresponds to our smaller specimens), a more rugose epitheca and pali the margin of which are much more tubercular according to Tomes (1886b).

REMARKS
The species was occasionally named *T. mactrus*, which is grammatically incorrect because "mactra" is a name (meaning "kneading trough") and not an adjective. Consequently, there is no need to find a Latin termination appropriate to the genus gender.

Some photographs of the type material provided by Dr. Georg Heumann and Manuel Kunz from Bonner Institut für Organismische Biologie (BIOB) in Bonn allowed to include these specimens in the present figuration and to compare it with our own specimens (see Table 3).

Genus *Trochocyathus* Edwards & Haime, 1848b

SPECIES ORIGINALLY INCLUDED. — 30 species (see Edwards & Haime 1848b: 301).

TYPE SPECIES. — *Turbinolia mitrata* Goldfuss, 1826 subsequent designation by Edwards & Haime (1850: XIV).

Trochocyathus provincialis Alloiteau, 1948 (Fig. 13)

Trochocyathus provincialis Alloiteau, 1948: 2, pl. 1, fig. 1, 2, 3.

Trochocyatus provincialis – Alloiteau *in* Charles 1948: 58, pl. 1, fig. 1, 2, 3.

TYPE MATERIAL. — **Lectotype** (**here designated**). **France • 1 specimen**; Dardennes; Jurassic, Liassic, Toarcian according to Alloiteau (1948) or possibly Aalenian according to Charles (1948), in the definition anterior to 1962 as the boundary between the two stages was redefined in 1964 after the Jurassic Congress in Luxembourg (see Maubeuge 1964); collected before 1948, R-P. Charles Leg.; MNHN.F.A26691.
Paralectotype (**here designated**). **France • 1 specimen**; same data as the lectotype; MNHN.F.C05033.

RESIDUAL SYNTYPE. — The syntypes included three samples but one of them (MNHN.F.C05034) is different, and is not considered here. This last one should be excluded, and a lectotype is designated herein.



Fig. 12. — *Thecocyathus mactra* (Goldfuss, 1826): **A**, distal view of *T. mactra* specimen MNHN.F.M03354 (Upper Liassic from Salins, Jura, France); **B**, basal view of *T. mactra* specimen MNHN.F.C05113 (Toarcian from Besançon, France); **C**, distal oblique view of the specimen CPUN AM16100 (Toarcian from Amellagou, Morocco); **D**, batch of *T. mactra* specimens without number (MAN – collections ENSG; Toarcian from Pont-à-Mousson, Lorraine, France); **E**, distal view of the lectotype BIOB-PB-Goldfuss-193B (Lower Jurassic from Banz, Germany); **F**, basal view of the lectotype BIOB-PB-Goldfuss-193B; **G**, lateral view of the lectotype BIOB-PB-Goldfuss-193B; **H**, distal view of the paralectotype BIOB-PB-Goldfuss-193A (Lower Jurassic from Banz, Germany); **I**, basal view of the paralectotype BIOB-PB-Goldfuss-193A; **J**, lateral view of the paralectotype BIOB-PB-Goldfuss-193A. Scale bars: A, B, 4 mm; C, D, 5 mm; E-I, 2 mm; J, 3 mm. Photos: A-D, R. Vasseur; E-J, M. Kunz.

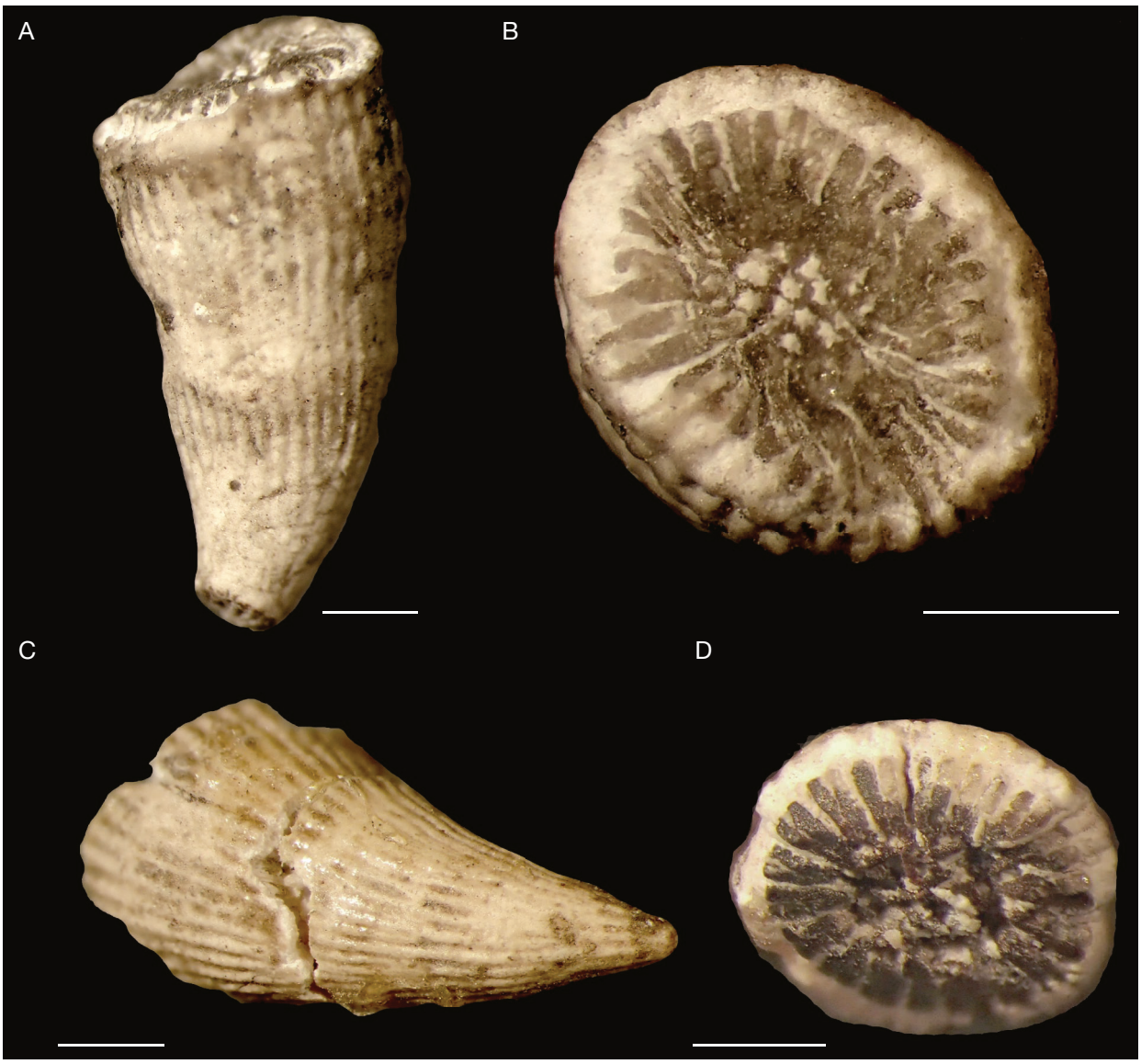

Fig. 13. — *Trochocyathus provincialis* Alloiteau, 1948, Toarcian or Aalenian from Dardennes, Provence, France: **A**, **B**, lectotype MNHN.F.A26691 in lateral (**A**) and distal (**B**) views; **C**, paralectotype MNHN.F.C05033 in lateral (**C**) and distal (**D**) views. Scale bars: 1 mm. Photos: R. Vasseur.

Description

Small conical, curved solitary coral (horn shaped) with costulate external surface visible from the most proximal part up to the distal edge. Radial elements are bicuneiform, straight or wavy, free costosepta organized in two distinct size orders that alternate from one septum to the next. Some septa join an axial papillose columella made of large beams in form of stars in transverse section. No endotheca observed. Wall apparently septothecal.

Dimensions

Calicular diameter: approximately 3 mm – calicular height: approximately 6 mm – number of septa: 36 – septal density: 5 for 1 mm.

Similarities and differences

Most of the Jurassic *Trochocyathus* species have at least 48 septa, except *T. proximus* (Fromentel & Ferry, 1865a) with 26 septa and *T. calcar* (Fromentel & Ferry, 1865a) with 27 to 40 septa. The latter Bajocian species is undoubtedly the closest to *T. provincialis*. However, costae are observed in the proximal part in *T. provincialis* and not in *T. calcar*. The general shape seems also different. For these reasons we keep *T. provincialis* as a separate species. A synonymy is not excluded but requires a population approach to evaluate the strength of these characters to discriminate the two species.

Family Cladophyllidae Morycowa & Roniewicz, 1990

Genus *Cladophyllia* Edwards & Haime, 1851

Species originally included. — A list of 11 species is given in Edwards & Haime (1851b: 81)

Type species. — *Lithodendron dichotomum* Goldfuss, 1826: 44, pl. 13, fig. 3a, b, by subsequent designation of Wells (1933: 172).

TABLE 3. — Dimensions of syntypes of *Thecocyathus mactra* (Goldfuss, 1826), compared to other observed specimens. The specimen BIOB-PB-Goldfuss-193E is too poorly preserved to provide informations.

	Diameter (mm)	Septal density per 2 mm	Number of septa
Non-type specimens	4-15	4-6	47-86
Syntype 1	12.9	5	*c.* 82
Syntype 2	7	6	*c.* 60
Syntype 3	unknown	5	unknown
Syntype 4	unknown	4-5	unknown

Cladophyllia cf. ***babeana*** (Orbigny, 1850) (Fig. 14)

Eunomia babeana Orbigny, 1850: 292. — Cottreau 1910: 113, t.6.

?*Madrepora flexuosa* – Smith 1816: 30, fig. 5.

Cladophyllia babeana – Edwards & Haime 1851b: 81; 1851a: 113, pl. 22, fig. 2; 1857: 366. — Tomes 1881: 158. — Meyer 1888: 22, pl. 4, fig. 8-10. — Beauvais 1971: 2. — Lathuilière 2000a: 56, fig. 5.1-5.11. — Lathuilière *et al.* 2023: 23, fig. 4 (a-c).

Cladophyllia babeaui – Fromentel 1861: 145.

Cladophyllia babeauana – Ferry 1861: 23.

?*Cladophyllia babeana* – Tomes 1883: 182; 1884b: 711. — Beauvais 1967: 12.

Cladophyllia choffati Koby, 1884b: 179, pl. 57, fig. 4. — Lissajous 1912: pl. 18, fig. 56. — Wullschleger 1966: 146, fig. 31. — Beauvais 1966: 991, pl. 1, fig. 4.

Cladophyllia ? *babeana* – Wells 1956: 400, fig. 295-3.

?*Cladophyllia* aff. *choffati* – Bendukidze 1960: 23, pl. 1, fig. 6.

Cladophyllia (*Aplophyllia*) *babeauana* – Wullschleger 1966: 148, fig. 33-34.

Cladophyllia babeana var. *minor* – Beauvais 1967: 12, pl. 1, fig. 5. — Negus & Beauvais 1975: 195, pl. 1, fig. 3. — Negus 1991: 252, tab. 1.

Stylosmilia fromenteli – Beauvais 1967 : 11, pl. 1, fig. 2.

Cladophyllia minor – Morycowa & Roniewicz 1990: 171, fig. 1, pl. 15, fig. 1-3, pl. 16, fig. 1, 2. — Roniewicz & Stolarski 1999: 135, fig. 2a.

?*Cladophyllia minor* – Pandey & Fürsich 2005: 17, pl. 5, fig. 3-4.

Cladophyllia sp. – Lathuilière 2011: 535, pl. I, fig. 1-2.

TYPE MATERIAL. — **Lectotype**. **France** • Rolampont; 47°56'56"N, 5°17'45"E (based on nearby landmark); Bajocian, Middle Jurassic; Orbigny Leg.; MNHN.F.R09168.

STUDIED SAMPLES. — CPUN MAM1; CPUN MA1004E4-4, 26 ; CPUN MA1004E5-9,10 (5 specimens) from Upper Toarcian of Aïn Leuh (Middle Atlas of Morocco).

GEOGRAPHIC AND STRATIGRAPHIC RANGES. — Jurassic of France, Luxembourg, Switzerland, Slovakia, United Kingdom and Morocco (Middle Atlas).

DESCRIPTION

Phaceloid corallum, only rare branches with large angle connections. No costae, but can be imitated by microbioerosional processes. Corallites circular in outline. Septa compact, joined, straight or tortuous, smooth or finely ornamented. Inner edge with teeth often joining the styliform columella. Septal apparatus with irregular hexameral symmetry, including S1 and S2 of similar sizes and smaller S3. Endotheca made of quite numerous vesicular dissepiments. Wall of unknown nature. A wrinkled epitheca *l.s.* covers the external part of the corallites.

DIMENSIONS

Calicular diameter: 4.2 to 6 mm – number of septa: approximately 24 to 30 – septal width: 100-260 µm for the S1-S2 80-120 µm for the S3.

REMARK

There is no evidence of the septal budding in the studied samples. In the corallite centres there are some kind of trabecular detachments, unorthodox for *Cladophyllia babeana*. These reasons justify the *cf.* attribution to the species *babeana*.

SIMILARITIES AND DIFFERENCES

As possible synonyms we listed *C. choffati* Koby, 1884; *C. dichotoma*; *C. conybearii* Edwards & Haime, 1851b; *C. corallina* Koby, 1888; *C. ramea* Koby, 1884b ; *C. excelsa* Koby, 1888; *C. rollieri* Koby, 1888; *C. thurmanni* Etallon, 1864. Presently we keep the reference to *C. babeana* for which the intraspecific variability is well documented and due to the stratigraphical proximity. The history of the genus variability remains unknown after the Bajocian. We cannot exclude an iterative evolution between *C. babeana* and the type species of the Kimmeridgian (*C. dichotoma*).

Family COMOSERIDAE Fromentel, 1861

Genus *Dimorpharaea* Fromentel, 1861

SPECIES ORIGINALLY INCLUDED. — *D. convexa* Fromentel, 1861; *D. koechlini* (Haime *in* Edwards, 1860).

TYPE SPECIES. — *Microsolena koechlini* Haime *in* Edwards, 1860, designated by Gregory (1900) that is today a junior synonym of *D. expansa* (Etallon, 1859), *non D. expansa* Tomes, 1886, *non D. expansa* Solomko, 1888.

Dimorpharaea fungiformis (Edwards & Haime, 1851b) (Fig. 15)

Thamnastrea fungiformis Edwards & Haime, 1851b: 141, pl. 30, fig. 4; 1857: 576. — Fromentel 1861: 212. — Tomes 1882: 439.

pars. *Synastraea jurensis* Orbigny, 1850: 293 (only specimen MNHN.F.R54657).

Thamnastraea fungiformis? – Reuss 1867: 18.

?*Thamnastraea defranciana* – Reuss 1867: 16, pl. 4, fig. 4.

?*Cyclolites lycetti* – Duncan 1872: 23, pl. 3, fig. 7-9.

?*Dimorphastraea dubia* – Tomes 1878b: 305.

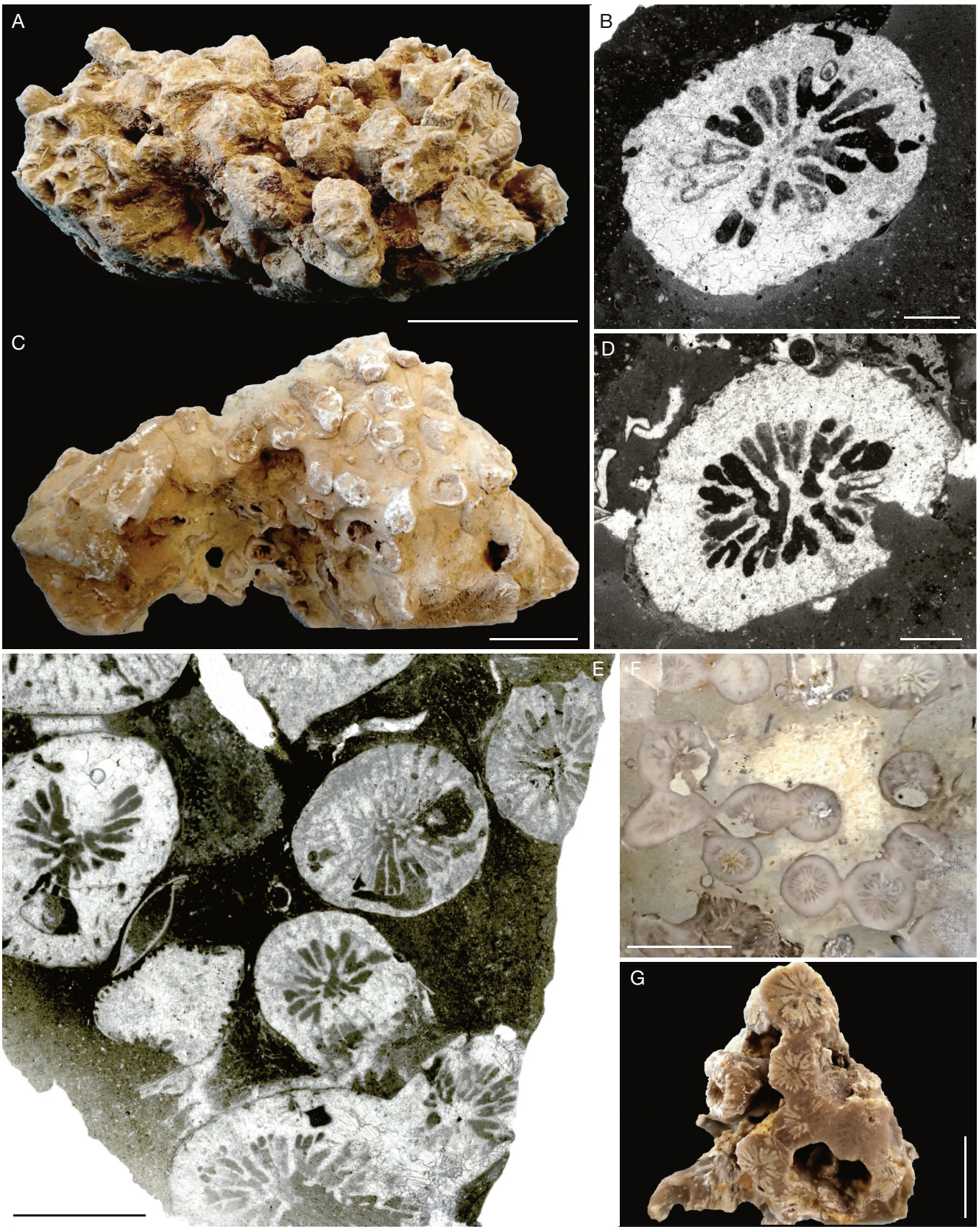

FIG. 14. — *Cladophyllia* cf. *babeana* (Orbigny, 1850), Middle/Upper Toarcian from Aïn Leuh, Morocco: **A**, lateral view of the specimen CPUN MA1004E5-9; **B**, transverse thin section of one calix in the specimen CPUN MAM 1; **C**, distal view of the specimen CPUN MA1004E4-4; **D**, transverse thin section of one calix in the specimen CPUN MAM 1; **E**, transverse thin section of the specimen CPUN MA1004E4-4; **F**, transverse section of the specimen CPUN MA1004E4-4; **G**, transverse polished section in the specimen CPUN MA1004E5-9. Scale bars: A, C, 2 cm; B, D, 1 mm; E, 4 mm; F, 1 cm; G, 0.5 mm. Photos: R. Vasseur.

Thamnastraea fromenteli Tomes 1878b: 304.

Dimorpharaea fromenteli – Tomes 1882: 446.

? *Dimorpharaea lycetti* – Tomes 1882: 444; 1890: 306.

Oroseris contorta Tomes, 1882: 441, pl. 18, fig. 17; 1890: 306.

Oroseris concentrica Tomes, 1882: 441.

Dimorpharaea lentiformis Koby, 1907: 49, pl. 3, fig. 15-21. — Beauvais 1972a: 73, pl. D, fig. 4-7. — Lebanidze 1991: 359.

Dimorpharaea contorta – Beauvais 1971: 3.

Dimorpharaea aff. *contorta* – Beauvais 1972b: 33, pl. 2, fig. 2-3.

Dimorpharaea pedunculata Tomes, 1882: 445.

Dimorphastraea lehmani Beauvais, 1967: 39, pl. 2, fig. 4, pl. 4, fig. 7.

Dimorpharaea fungiformis – Beauvais 1970a: 68, pl. A, fig. 1, pl. E, fig. 5; 1971: 2. — Negus 1991 : 252, tab. 1. — Kutz *et al.* 2020: 29, fig. 22.

Dimorpharaea lehmani – Lathuilière 2000b: 154.

TYPE MATERIAL. — **Lectotype**. **England •** 1 specimen; Charlcomb, Inferior Oolite; J.6115 Sedgwick Museum, fixation by inference of a holotype before 2000 by Beauvais (1970a: 68, pl. A, fig. 1, pl. E, fig. 5), art. ICZN 74.6.

STUDIED SAMPLE. — CPUN MA1004E5-6 from Upper Toarcian of Aïn Leuh (Middle Atlas of Morocco).

DESCRIPTION
Fungiform thamnasterioid colony with calices that do not seem to follow a typical circumoral mode of gemmation given that no clear concentric organization of calices can be identified nor smaller calices from the centre to the periphery of the colony. However, near the colony edge, septa are generally perpendicular to the colony boundary. Radial elements are straight or flexuous, porous biseptal blades with typically microsolenid pennular structures. A weak papillose axial structure made of the projection of septal trabeculae sometimes appear in depth. Endotheca made of thin vesicular dissepiments. Synapticulae present. No wall between the calices. A concentrically wrinkled holotheca covers the base of the colony.

DIMENSIONS
Calicular diameter: 4 to 6 mm – distance between calices centres: 3 to 7 mm – number of septa: 15 to 26 – septal density: 5 per 2 mm – trabecular density: *c.* 6 per 2 mm.

SIMILARITIES AND DIFFERENCES
The existence of one mother corallite bigger than others in the centre of the colony is not a discriminant criterium to distinguish species in the genus *Dimorpharaea* according to Pandey *et al.* (1999). For this reason we synonymized *D. contorta*, *D. fromenteli* and *D. fungiformis*. *D. pedunculata* as well as *D. lehmani* and *D. lentiformis* tend to have a little more septa but could fit within the variability of the species. The dimensions of the type material of *D. lycetti* that has been synonymized by Beauvais (1970a) have never been published.

The distinction between *D. fungiformis* and *S. agaricites* (Goldfuss, 1826) also described in the present work is made only on the septal structure, microsolenid (i.e. regularly porous) in *D. fungiformis* and subcompact in *S. agaricites*.

Genus *Trocharea* Etallon *in* Thurmann & Etallon, 1864

SPECIES ORIGINALLY INCLUDED. — *Trocharea actiniformis* Etallon *in* Thurmann & Etallon, 1864.

TYPE SPECIES. — *Trocharea actiniformis* Etallon *in* Thurmann & Etallon, 1864 (Thurmann & Etallon 1864: 411, pl. 58, fig. 4), by monotypy.

REMARKS
For a discussion about the relationships between *Trochoplegma* Gregory, 1900 and *Trocharea*, see Vasseur & Lathuilière (2021: 1206).

Trocharea ilerdensis
(M. Beauvais *in* Baudrimont & M. Beauvais, 1962), n. comb.
(Fig. 16)

Anabacia ilerdensis M. Beauvais *in* Baudrimont & M. Beauvais, 1962: 272, pl. 4b, fig. 1a, b.

Trochoplegma ? *ilerdensis* – Vasseur 2018: 365, fig. 3.105.

TYPE MATERIAL. — **Syntype**. **Spain •** Number of specimens unknown, 42°11'22"N, 1°14'30"E according to Baudrimont's map, Jurassic, Lias, Toarcian, sampled before 1961, Baudrimont Leg. MNHN.F.A50994.

STUDIED SAMPLE. — MNHN.F.A50994.

DESCRIPTION
Solitary, subhemispherical, possibly free corallum with no holotheca on the basal face. Radial elements are straight or slightly flexuous, free, fenestrate and exert costosepta for which cycles are difficult to decipher. The septal microstructure is typically microsolenid. The distal edge of septa is ornamented by small, very regular trabecular teeth. Numerous synapticulae present. No endotheca observed but the original description mentions rare and very thin dissepiments distributed in the whole interseptal space. No axial structure but a very elongated axial fossa that defines a bilateral symmetry plan. The syntype is strongly affected by *Trypanites* Mägdefrau, 1932 post-mortem bioerosion.

DIMENSIONS
Calicular diameter: 34.4 × 32.2 mm – septal density: 7-8 per 2 mm – number of septa: *c.* 360.

SIMILARITIES AND DIFFERENCES
See Table 4.

REMARK
The species is newly combined with the genus name *Trocharaea* for the following reasons: *Anabacia* d'Orbigny in Edwards &



Fig. 15. — *Dimorpharaea fungiformis* (Edwards & Haime, 1851b), Middle/Upper Toarcian from Aïn Leuh, Morocco: **A**, distal view of the specimen CPUN MA1004E5-6; **B**, proximal view of the specimen CPUN MA1004E5-6; **C**, longitudinal section of the specimen CPUN MA1004E5-6; **D**, transverse thin section of the specimen CPUN MA1004E5-6. Scale bars: A, B, 1 cm; C, 3 mm; D, 4 mm. Photos: R. Vasseur.



Fig. 16. — *Trocharea ilerdensis* (M. Beauvais *in* Baudrimont & M. Beauvais, 1962), n. comb., syntype MNHN.F.A50994, Toarcian from Rio Cullès, Spain: **A**, distal view; **B**, proximal view; **C**, longitudinal polished section; **D**, detail in longitudinal polished section; **E**, detail in transverse polished section. Scale bars: A, B, C, 1 cm; D, E, 1 mm. Photos: R. Vasseur.

TABLE 4. — Comparison of Liassic *Trocharea* Etallon *in* Thurmann & Etallon, 1864 species.

Species of *Trocharea*	Calicular diameter (mm)	Septal density (per 2 mm)	Number of septa	General shape	Age	References
Trocharea ilerdensis (M. Beauvais *in* Baudrimont & M. Beauvais, 1962), n. comb.	34.4	7-8	*c.* 360	Cupolate	Toarcian	This article and Vasseur 2018
Trocharea tenuilamellosa (Gregory, 1900)	24-26	9	> 300	Conical	Pliensbachian	Vasseur & Lathuilière 2021
Trocharea cf. *cupuloides* Fischer, 1969	19.3	6.5	> 136	Discoid	Pliensbachian	Vasseur & Lathuilière 2021
Trocharea sp. 1	20.1	5.5-6	*c.* 160	Fungiform	Pliensbachian	Vasseur & Lathuilière 2021
Trocharea sp. 2	12	8	*c.* 96	Subcylindrical	Pliensbachian	Vasseur & Lathuilière 2021
Trocharea sp.	17	8-9	*c.* 116	Fungiform	Toarcian	This article

Haime, 1849 is an obsolete name replaced by *Chomatoseris* Thomas, 1935, a genus characterized by a downward growth and an automobile behaviour which are absent in the present case.

Trocharea sp.
(Fig. 17)

Microsolena sp. 1 – Vasseur 2018: 248, fig. 3.58.

Trocharea sp. 3 – Vasseur 2018: 361-362, fig. 3.103.

Trocharea sp. 2 – Vasseur & Lathuilière 2021: 1207, fig. 12.

STUDIED SAMPLE. — CPUN MA1004E4-34. Morocco, 1 specimen; Aïn Leuh (Middle Atlas), Couches d'Al Yabès, 33°11'32"N, 5°21'8"W (PaleoDB collection 233562); Middle/Upper Toarcian, interval Gradata zone, Gemma subzone up to Meneghini zone, Lower Jurassic.

DESCRIPTION
Small fungiform corallum with 2 calices of similar diameters, which excludes the possibility of a circumoral mode of budding. Radial elements are straight or flexuous, porous septa or biseptal sheets with typically microsolenid pennular structures. A weak papillose axial structure made of the projection of septal trabeculae seems to appear in depth. Endotheca made of thin vesicular dissepiments. Synapticulae present. No wall between the calices. A thick, concentrically wrinkled holotheca covers the base of the colony. The banding is regular enough to propose an age of six years for the corallum.

DIMENSIONS
Calicular diameter: approximately 17 mm – distance between calices centres: 7 mm –septal density: 8 to 9 per 2 mm – trabecular density: 8 to 9 per 2 mm.

REMARKS
Initially, the sample was attributed to *Microsolena* Lamouroux, 1821 for its colonial character. However, it is worth noting that two calices were already present at the early stages of the colony (Fig. 18B) suggesting that the colony could result from the fusion of two initial planulae of *Trocharea*. In addition, only two corallites constitute the colony after six years of existence (Fig. 18A). The evidence for fusion is poorly documented in the fossil record and we do not discard the possibility of a more widespread phenomenon especially in samples described as small colonies.

SIMILARITIES AND DIFFERENCES
According to the Table 4, the specimen presented in this study corresponds more closely to the *Trocharea* sp. 2 described for the Pliensbachian in Vasseur & Lathuilière (2021). Considering the low number of samples, it is difficult to assess the variability among the genus and to understand how this variability is controlled or not across the Pliensbachian-Toarcian boundary. For these reasons it is difficult to attribute species names to the specimens, this is the reason why we keep some samples in open nomenclature.

Family CONOPHYLLIDAE Alloiteau, 1952

Genus *Ellipsoidastraea* Alloiteau, 1957

SPECIES ORIGINALLY INCLUDED. — *Ellipsoidastraea lucasi* Alloiteau, 1957.

TYPE SPECIES. — *Ellipsoidastraea lucasi* Alloiteau, 1957: 347, pl. 7, fig. 1, by monotypy.

REMARKS
We cannot see the microstructure on our samples although the observation of the micro-morphology of septa point to a clear alternation of the pennular rims on both sides of a single septum. This pattern corresponds to both Procyclolitidae Vaughan & Wells, 1943 and Conophyllidae. The granulae on the distal edges of septa and the papillose structure of the columella point to Conophyllidae.

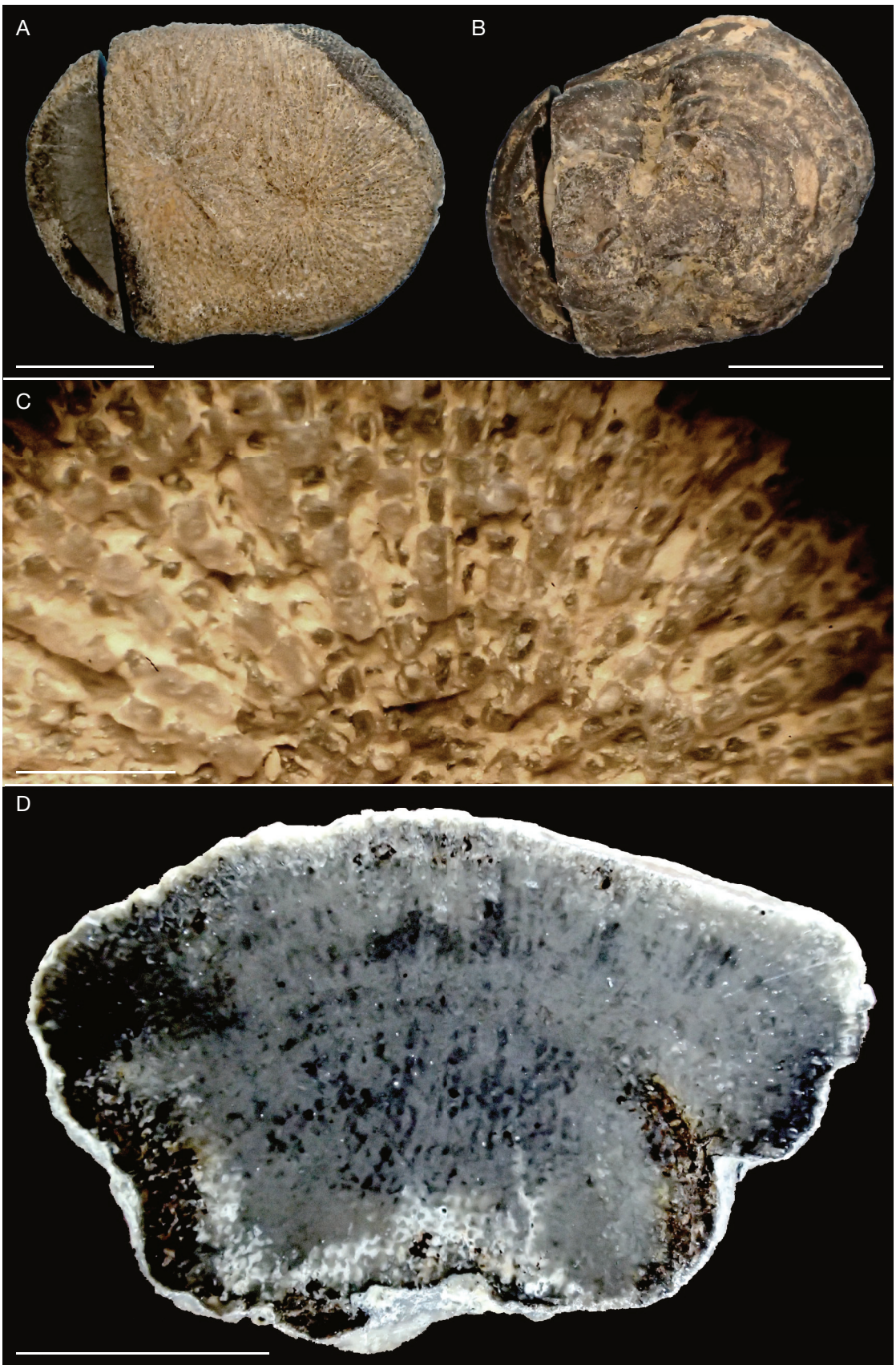

Fig. 17. — *Trocharea* sp., Middle/Upper Toarcian from Aïn Leuh, Morocco: **A**, distal view of the specimen CPUN MA1004E4-34; **B**, proximal view of the specimen CPUN MA1004E4-34; showing the two intial centres of growth and the annual regular concentric banding. **C**, detail in distal view of the specimen CPUN MA1004E4-34; **D**, longitudinal section of the specimen CPUN MA1004E4-34. Scale bars: A, 8 mm; B, 1 cm; C, 1 mm; D, 5 mm. Photos: R. Vasseur.

Ellipsoidastraea lucasi Alloiteau, 1957
(Fig. 18)

Ellipsoidastraea lucasi Alloiteau, 1957: 347, pl. 7, fig. 1. — Vasseur 2018: 184, fig. 3. 33.

Type material. — **Holotype**. **Algeria** • 1 specimen by original designation and many paratypes; Raha Zerga; Toarcian, Lower Jurassic; Lucas Leg.; MNHN.F.J08919.

Studied material. — The holotype and two thin sections from an unidentified paratype.

Amended description
Description (modified from Lathuilière *in* Cairns *et al.* [2012] in Corallosphere): cyclolitoid solitary coral. Circular in outline but a very elongate fossa gives a strong bilateral symmetry. Radial elements are numerous, compact, straight or slightly curved (depending on the angular position to the elongated fossa), with a global thickness rather constant (if the ornamentation is neglected), joined. Ornamentation made of pennulae and more often mi-pennulae. No strict pennular alternation. Synapticulae-like structures probably formed by the junction of pennular rims facing each other on neighbouring septum, vesicular dissepiments numerous. Wall absent or present. Parietal axial structure.

Dimensions
Calicular diameter: 88.4 to 90 mm – septal density: approximately 5 per 2 mm – calicular height: 48 mm.

Remark
The above description is based on the observation of the holotype and on new longitudinal radial sections. There are important discrepancies between the original description by Alloiteau (1957) and with Brede *et al.* (1989) especially with regards to the misinterpretation of septal ornamentation (pennulae, mi-pennulae) and the so-called endotheca and synapticulae. The new sections show that there are no rod-like structures joining neighbouring septa. A distinction is to be done between septal ornamentation and dissepiments.

Similarities and differences
The differences between *E. lucasi* Alloiteau, 1957, *E.* sp. (*sensu* Beauvais 1986b) and the Middle Jurassic species *E. hemispherica* Brede, Hauptmann & Herbig, 1989 are given in Brede *et al.* (1989: 8, table 1). The ratio height/diameter allows a clear distinction.

Ellipsoidastraea sp.
(Fig. 19)

Ellipsoidastraea sp. – Beauvais 1986b: 40, pl. 8, fig. 4a, pl. 9, fig. 4a, b, c. — Vasseur 2018: 187, fig. 3. 34.

Studied samples. — MNHN.F.R11624 and MNHN.F.R11625 (and one thin section apparently from the specimen R11624 and figured in Beauvais [1986b] as *Ellipsoidastraea* sp.).

Geographic and stratigraphic ranges. — Lower Toarcian of Jebel Outita and Moussaoua pass (Morocco).

Amended description
Cyclolitoid solitary coral. Circular in outline but a very elongate fossa gives a strong bilateral symmetry. Radial elements are numerous, compact, straight or slightly curved (depending on the angular position to the elongated fossa), and sometimes joined. Ornamentation made of pennulae and more often mi-pennulae. No strict pennular alternation. Synapticulae present. The edge of pennulae often join the neighbouring septum, vesicular dissepiments numerous. Wall absent or present. No axial structure observed. The lower face is covered by a wrinkled epitheca l.s.

Dimensions
Calicular diameter: 30 to 35 mm – corallite height: 11 to 12 mm – septal density: 5 to 6 per 2 mm.

Family Dermosmiliidae Koby, 1889

Genus *Dermosmilia* Koby, 1884

Species originally included. — *D. crassa* (Orbigny, 1850), *D. laxata* (Etallon, 1864), *D. divergens* Koby, 1884, *D. arborescens* Koby, 1884, *D. corymbosa* Koby, 1884, *D. etalloni* Koby, 1884, *D. rugosa* Koby, 1884.

Type species. — *Dermosmilia divergens* Koby, 1884, by subsequent designation of Wells (1936).

Remarks
The designation by Dacqué (1934), which was proposed in Löser (2002 and 2016) is not valid as Dacqué himself explicitly mentioned (Dacqué 1934: 20) that these designations should not be considered as nomenclaturally valid (ICZN art. 67.5).

Dermosmilia praecox n. sp.
(Fig. 20)

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Dermosmilia sp. 1 – Vasseur 2018: 164, fig. 3.24.

Type material. — **Holotype**. **Morocco** • 1 specimen; Amellagou (High Atlas); 31°59’4”N, 5°2’57”W; Upper Toarcian, Lower Jurassic; Vasseur Leg.; CPUN AM2603A1-1.

Studied samples. — CPUN AM2603A1-1, CPUN AM1603A3E1 from Upper Toarcian of Morocco (High Atlas).

Type locality and age. — Morocco, Amellagou (High Atlas); Upper Toarcian, Lower Jurassic.

Differential diagnosis. — Among the nominal species with close dimensions (*D. simplex* Koby, 1889 and *D. bathonica* Koby, 1907), *D. praecox* is characterized by a high number of corallites in the colony, mostly free septa even in depth and a papillose (rather than spongy) axial structure of septal origin.

Etymology. — The species name refers to the precocious (in latin “*praecox*”) age of this species in comparison to other species of the genus.

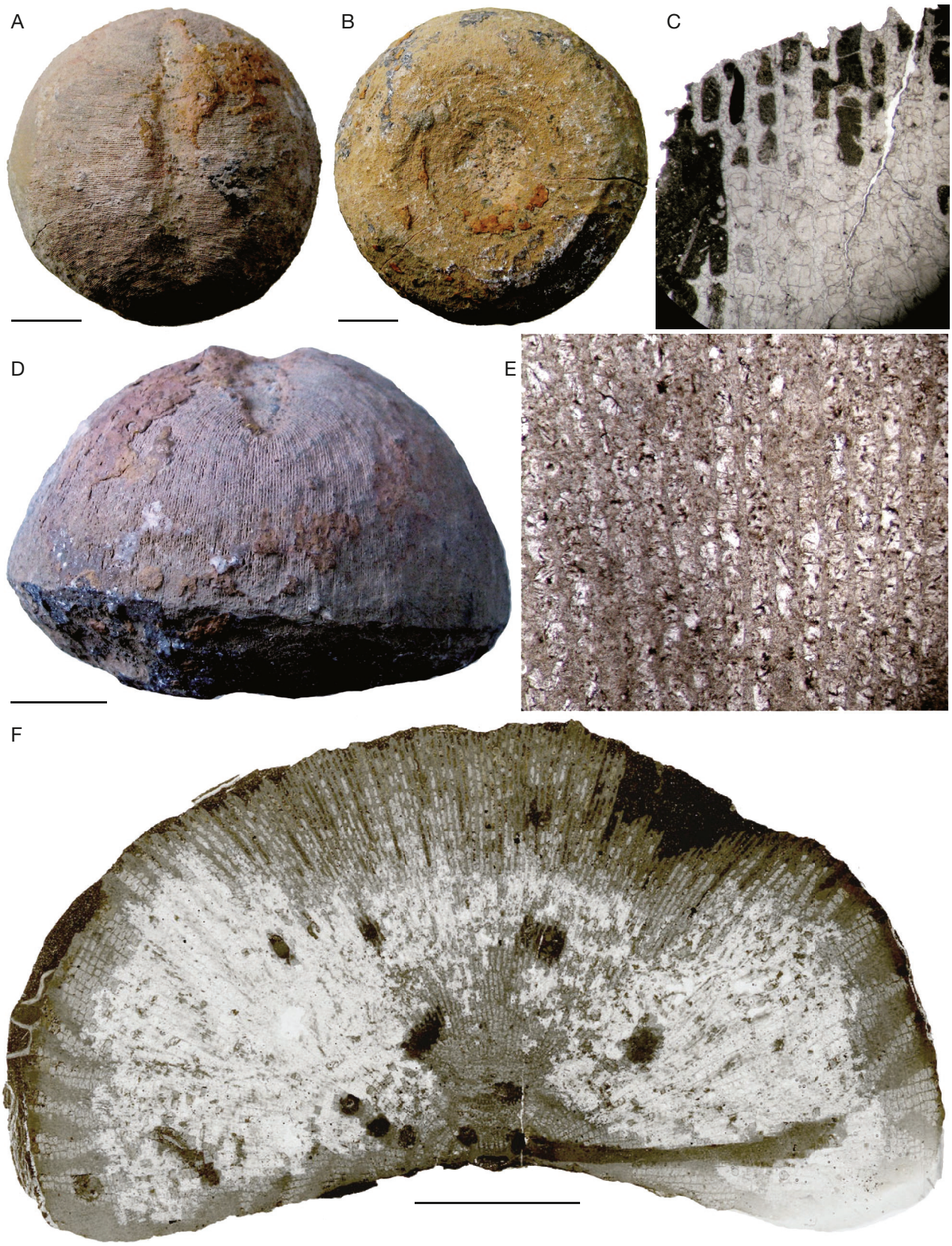

Fig. 18. — *Ellipsoidastraea lucasi* Alloiteau, 1957, Toarcian from Raha Zerga, Algeria: **A**, distal view of the holotype MNHN.F.J08919; **B**, proximal view of the holotype MNHN.F.J08919; **C**, longitudinal thin section of paratype MNHN.F.J17675; **D**, lateral view of the holotype MNHN.F.J08919; **E**, longitudinal thin section of one unidentified MNHN paratype; **F**, longitudinal thin section of paratype MNHN.F.J09576. Scale bars: A, B, D, 2 cm ; F, 1 cm. Photos: MNHN.

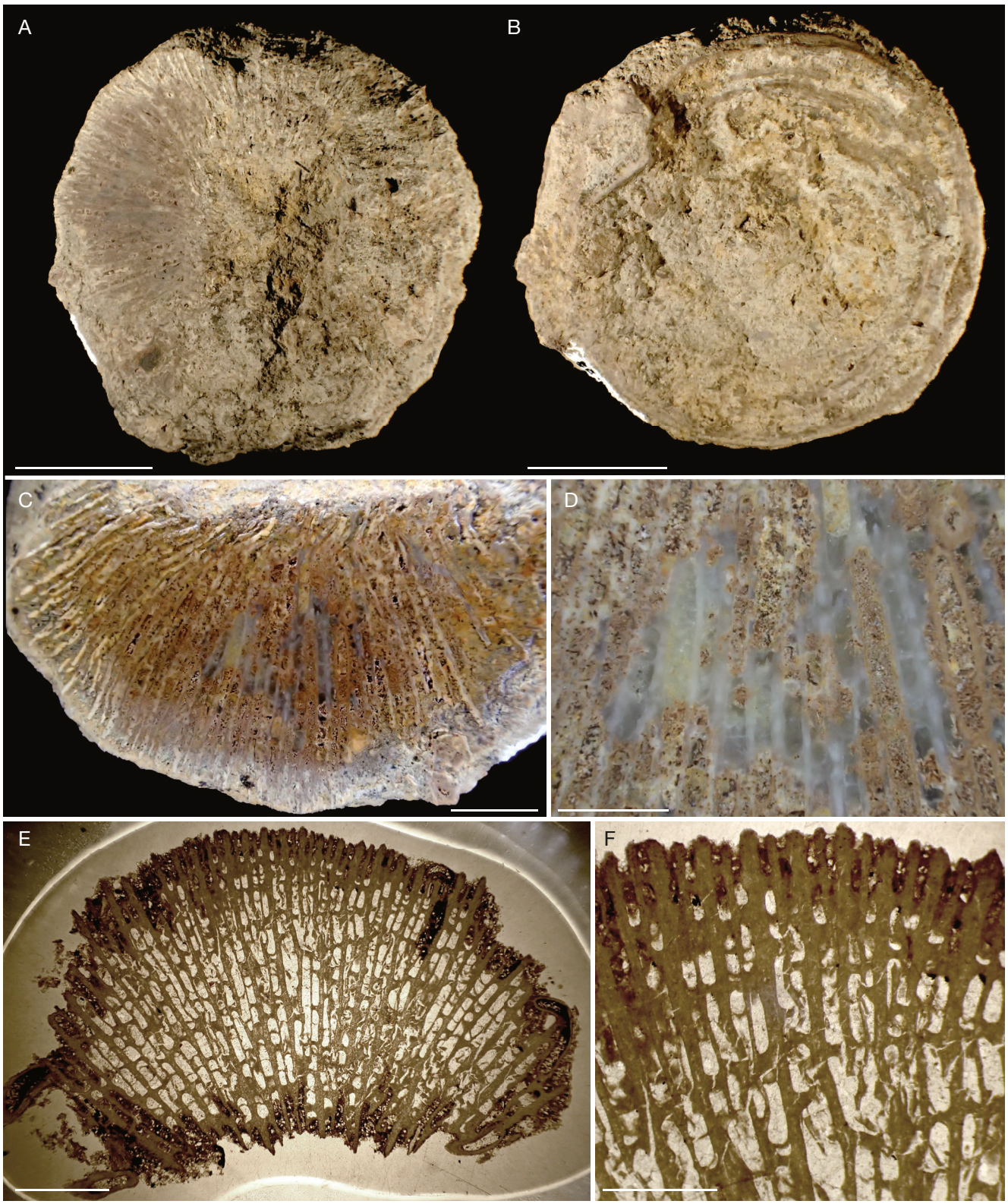

FIG. 19. — *Ellipsoidastraea* sp., Lower Toarcian Jebel Outita, Morocco: **A**, distal view of the specimen MNHN.F.R11625; **B**, proximal view of the specimen MNHN.F.R11625; **C**, distal view of a polished part of the specimen MNHN.F.R11625; **D**, enlargement of the previous picture; **E**, transverse thin section of the specimen MNHN.F.R11624; **F**, enlargement of the previous picture. Scale bars: A, B, 1 cm; C, E, 4 mm; D, F, 2 mm. Photos: R. Vasseur.

Description
Phaceloid corallum with subparallel, subcylindrical corallites. Calices elliptical. Intracalicinal increase. Radial elements are subcompact, straight or curved, mostly free. Septa with a montlivaltid-like structure but the lateral faces of septa hold irregularly arranged granules that can be sharp but also flattened. The inner edge is ornamented with upward trabecular teeth, which create sometimes a papillose axial structure by projection in the elongated axial zone. The regularly arranged trabeculae tend to verticalise at the inner edge of septa. Endotheca abundant, made of tabular and vesiculous dissepiments. Synapticulae probably present but not clearly demonstrated. Epicostal wall, possibly parathecal. The samples offered no external view of the costae.

Dimensions
Calicular diameter: 9 to 13.7 mm – septal density: 6 for 2 mm – number of septa: 72 to 90 – distance between calices centres: 8.2 to 18.2 mm.

Genus *Proleptophyllia* Alloiteau, 1952

Species originally included. — Only the type species.

Type species. — *Montlivaltia granulum* Fromentel & Ferry, 1866 (Fromentel & Ferry 1866: 136, pl. 24, fig. 2), by monotypy.

Proleptophyllia granulum (Fromentel & Ferry, 1866) (Fig. 21)

Montlivaultia granulum Fromentel & Ferry, 1866: 136, pl. 24, fig. 2.

Montlivaultia arenula Fromentel & Ferry, 1866: 134-135, pl. 23, fig. 4, 4a-b.

Proleptophyllia granulum – Alloiteau 1952: 666; 1956: no. 121; 1957: 113, pl. 8, figs 10, 73. — Vasseur 2018: 297-298, fig. 3.78. — Vasseur & Lathuilière 2021: 1222-1223, fig. 22.

Epiphyllum arenula – Alloiteau 1957: 107, pl.5, fig.13.

Cyclophyllopsis cornutiformis Beauvais, 1986b: 34, pl. 7, fig. 1, pl. 8, fig. 1 and text-fig. 23.

Proleptophyllia cf. *granulum* – Lathuilière 2011: 542, pl. 3, fig. 11-12.

Type material. — **Lectotype**. **France •** Designation of a lectotype for stipulation of the existence of a "holotype" (ICZN 1999: Art. 74.6) by Alloiteau (1956); May-sur-Orne, Calvados; Pliensbachian, Lower Jurassic; MNHN.F.M03533.

Studied samples. — 22 specimens: lectotype: MNHN.F.M03533; CPUN MAM16, CPUN CDAm5, CPUN AM16177-2, CPUN AM16182-7, CPUN AM16188-24 and population CPUN MA1004E1-G from Upper Toarcian of Aïn Leuh (Middle Atlas of Morocco).

Description
Turbinate, patellate or subcylindrical solitary coral with calice elliptical to subcircular in outline. Flattened calicular platform, more or less infundibuliform, with a generally deep fossa at the axis. Rejuvenescences are common in the coralla. Radial elements are straight, free or joined, subcompact costosepta with flat granule-like pennulae on lateral faces. Pennulae do not alternate between neighbouring septa and are not arranged in continuous menianae. The distal edge is ornamented of strong teeth. More the teeth are in the axial region, bigger and more detached they are. They produce in the centre the appearance of a papillose axial structure in a pit. Numerous thick dissepiments. Synapticulae present. Wall parathecal. A thin epitheca, sometimes totally eroded wraps the coralla. Probable hexameral symmetry.

Dimensions
Calicular diameter: 13 to 29.5 mm – number of septa: 119 to 182 – septal density: 4 to 6 for 2 mm.

Similarities and differences
Differs from *P. multiradiata* Beauvais, 1986, which shows a convex calicular surface with exert septa and a more discoid morphology.

P. magna Vasseur & Lathuilière, 2021 is bigger and has many more septa.

P. subphaceloida Vasseur & Lathuilière, 2021 closely resembles *P. granulum* but it is distinguished by being the only known colonial form of *Proleptophyllia*. In addition, its calices are slightly bigger and the fossa seems to be less marked.

P. punctulum (Fromentel & Ferry, 1866) is distinct by its very specific shape and the regularity of its septal apparatus.

Genus *Thecactinastraea* Beauvais, 1986

Species originally included. — *Thecactinastraea fasciculata* Beauvais, 1986.

Type species. — *Thecactinastraea fasciculata* Beauvais, 1986 (Beauvais 1986b: 33, pl. 5, fig. 1 et texte-fig. 21) by original designation.

Remarks
Melnikova & Roniewicz (2017), as first revisors, chose to merge *Phacelophyllia* Beauvais, 1986 and *Thecactinastraea* and designated the latter as the senior synonym.

Thecactinastraea fasciculata Beauvais, 1986 (Fig. 22)

Thecactinastraea fasciculata Beauvais, 1986b: 33, pl. 5, fig. 1, txt-fig. 21. — *non* Turnšek *et al.* 2003: 293, pl. 4, fig. 1-5. — Lathuilière *in* Cairns *et al.* 2012 *in* Corallosphere. — Melnikova & Roniewicz 2017: 133, fig. 3C, D. — Stone *et al.* 2022: 643, fig. 9E. — Boivin *et al.* 2025: 20, fig. 12.

Myriophyllum fasciatum Beauvais, 1986b: 37, pl. 9, fig. 1, txt-fig. 25.

Phacelophyllia fasciculata – Vasseur 2018: 279, fig. 3.71. — Boivin 2019: 240, fig. 10.25.

?*Phacelophyllia bacari* Turnšek, Buser & Debeljak, 2003: 298, pl.10, fig. 1-3, pl. 11, fig. 1-5.

Phacelophyllia fasciata – Turnšek *et al.* 2003: 297, pl. 9, fig. 4.

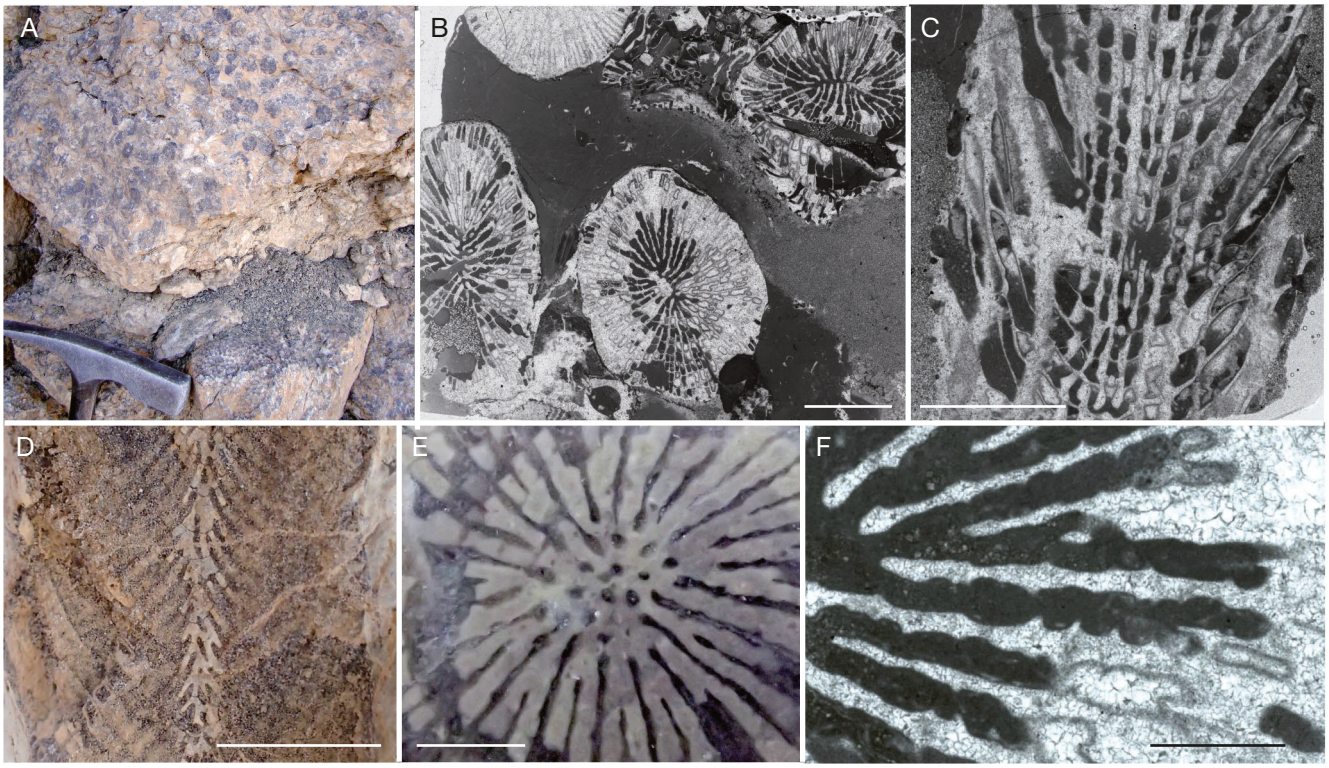

FIG. 20. — *Dermosmilia praecox* n. sp., Upper Toarcian from Amellagou, Morocco: **A**, colony pictured in the Field (Amellagou, Morocco); **B**, transverse thin section in the holotype CPUN AM2603A1-1; **C**, longitudinal thin section in the holotype CPUN AM2603A1-1 showing the endotheca made of vesicular and tabular dissepiments; **D**, longitudinal section observed in the field, revealing the trabecular frame of septa and the projection of trabeculae in the axis of the corallite, which creates the teeth along the inner edge of septa and a papillose axial structure (Amellagou, Morocco); **E**, detail in transverse section of a calix with well-developed papillose axial structure (holotype CPUN AM2603A1-1); **F**, detail in transverse thin section of the mimetic montlivaltid structure of septa (holotype CPUN AM2603A1-1). Scale bars: B, 5 mm; C, 4 mm; D, 6 mm; E, 2 mm; F, 1 mm. Photos: R. Vasseur.

TYPE MATERIAL. — **Holotype**. **Morocco** • 1 specimen in five pieces and two thin sections (longitudinal and transverse); Tarhilest, close to Dayet Ifrah; Lower Jurassic; Du Dresnay Leg.; holotype: MNHN.F.R11611;
Paratypes. **Morocco** • 3 specimens; same data as the holotype; MNHN.F.A30501, MNHN.F.A32010, MNHN.F.C05035.

STUDIED SAMPLES. — 5 specimens: holotype MNHN.F.R11611; paratype MNHN.F.A30501; holotype of *Myriophyllum fasciatum* Beauvais, 1986, MNHN.F.R11629; CPUN MA1004E5-4.

GEOGRAPHIC AND STRATIGRAPHIC RANGES. — Lower Jurassic of Morocco, Tarhilest, close to Dayet Ifrah (Middle Atlas), Toarcian of Aïn Leuh (Middle Atlas), Pliensbachian of Amellagou (High Atlas), Upper Sinemurian or lowermost Pliensbachian of Amellagou, Domerian of Gozd (Slovenia).

DESCRIPTION

Phaceloid corallum with subcircular, subparallel corallites, often deformed by their intracalicinal fissiparous mode of increase. Septa subcompact, straight or curved, free. Lateral faces probably ornamented with straight pennulae (better thin sections are necessary to confirm it), distal edge moniliform. The inner edge of septa is ornamented with trabecular teeth oriented upward. The dissociated trabeculae projections in the axial space of the corallite produce a papillose axial structure. An epitheca *lato sensu* with growth wrinkles encloses the corallites. Synapticulae probably present and endotheca made of numerous dissepiments.

DIMENSIONS

Calicular diameter: 5.5 to 11.4 mm – number of septa: 55 to 80 – septal density: 5 to 6 for 2 mm.

SIMILARITIES AND DIFFERENCES

Differs from *T. termierorum* (Beauvais, 1986) by its free septa. Among rare nominal species classified in the genus *Thecactinastraea*, *T. krimensis* Turnšek, 2000 has poorly ornamented septa, which is not compatible with the genus and family assignation.

Thecactinastraea termierorum (Beauvais, 1986) (Fig. 23)

Phacelophyllia termieri Beauvais, 1986b: 39, pl. 7, fig. 2, txt fig. 27. — ?Turnšek *et al.* 2003: 297, pl. 9, figs 1-3. — Vasseur 2018: 284-285, fig. 3.73. — Boivin 2019: 244, figs 10.26 and 10.27.

Thecactinastraea termierorum – Boivin *et al.* 2025: 20, fig. 13-14.

Phacelophyllia sp. – Brame *et al.* 2019: fig. 7, H, I.

TYPE MATERIAL. — **Holotype**. **Morocco** • 1 specimen; unknown location; Lower Jurassic; G. & H. Termier Leg.; MNHN.F.R11621.

STUDIED SAMPLES. — Holotype MNHN.F.R11621, MNHN.F.R11629, CPUN DA3005E2-1.

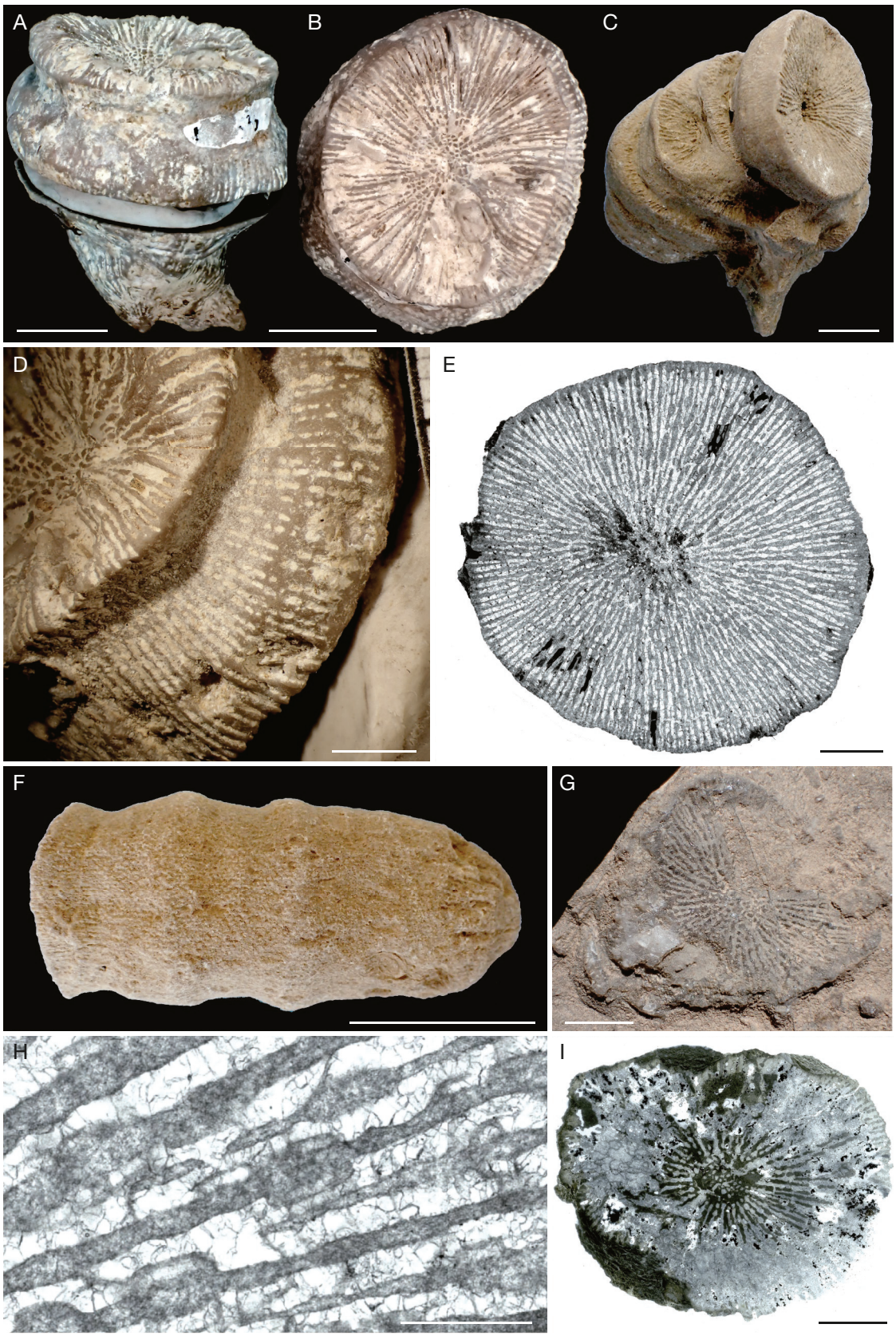

FIG. 21. — *Proleptophyllia granulum* (Fromentel & Ferry, 1866), Pliensbachian of May-sur-Orne, Normandie, France (**A**, **B**, **D**), Middle/Upper Toarcian from Aïn Leuh (**C**, **E**, **F**, **G**, **H**) and Pliensbachian of Amellagou (**I**): **A**, lectotype MNHN.F.M03533; **B**, distal view of the lectotype MNHN.F.M03533; **C**, rejuvenescent specimen from the batch CPUN MA1004E1-G; **D**, detail of costoseptal structure in the lectotype MNHN.F.M03533; **E**, transverse thin section of the specimen CPUN MA1004E1-G (spécimen G'3); **F**, subcylindrical specimen that lost its epitheca, from the batch CPUN MA1004E1-G; **G**, specimen pictured in the field (Dades Valley, Morocco); **H**, detail of the pennular septal ornamentation in the specimen from the batch CPUN MA1004E1-G; **I**, transverse thin section of the specimen CPUN AM16182-7. Scale bars: A, B, C, 1 cm; D, E, 4 mm ; F, 2 mm ; G, I, 5 mm ; H, 1 mm. Photos: R. Vasseur.

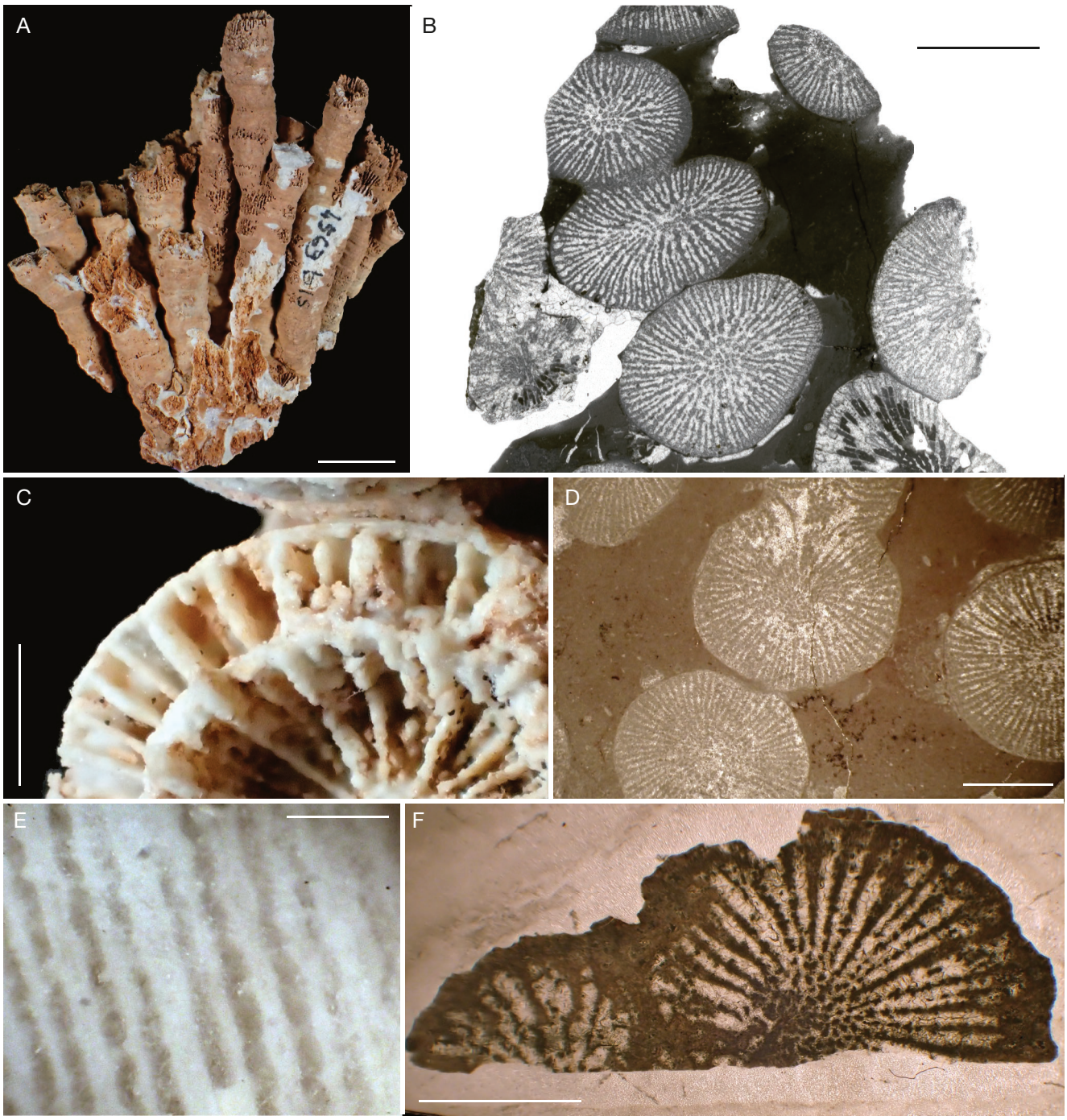

Fig. 22. — *Thecactinastraea fasciculata* Beauvais, 1986, Lower Jurassic of Tarhilest, Morocco (**A**, **C**, **D**, **F**) and Middle/Upper Toarcian of Aïn Leuh (**B**, **E**): **A**, holotype MNHN.F.R11611; **B**, transverse thin section in sample CPUN MA1004E5-4; **C**, detail of the epitheca *l.s.* of a corallite of the specimen MNHN.F.A30501; **D**, transverse thin section of the specimen MNHN.F.R11629; **E**, detail of septal structure in longitudinal section of the specimen CPUN MA1004E5-4; **F**, transverse thin section of holotype MNHN.F.R11611. Scale bars: A, 2 cm; B, 6 mm; C, 2 mm; D, F, 4 mm; E, 0.5 mm. Photos: R. Vasseur.

Geographic and stratigraphic ranges. — Lower Jurassic of Morocco (including Toarcian pre-JE from Dades Valley, High Atlas), possibly Domerian of Gozd (Slovenia), Upper Sinemurian or lowermost Pliensbachian of Amellagou (High Atlas of Morocco).

Description

Phaceloid corallum with subcircular, subparallel corallites, often deformed by their intracalicinal fissiparous mode of increase. Septa subcompact, straight or curved, sometimes contratingent or joined by their inner edge. Lateral faces with straight pennulae, distal edge moniliform. The inner edge of septa is ornamented with trabecular teeth oriented upward. The dissociated trabeculae projections in the axial space of the corallite produce a papillose axial structure typical of the genus. An epitheca *lato sensu* encloses the corallites. Endotheca present, made of dissepiments. Synapticulae probably present.

Dimensions
Calicular diameter: 3 to 10 mm – Number of septa: 60 to 98 – Septal density: 5 to 8 for 2 mm.

Similarities and differences
Distinct from *T. fasciculata* because of its joining septa. Among rare nominal species classified in the genus *Thecactinastraea*, *T. krimensis* Turnšek, 2000 has poorly ornamented septa, which is not compatible with the genus and family assignation.

Family Hispaniastraeidae
Boivin, Vasseur, Lathuilière, Lazăr, Durlet, Martindale, El Hmidi & Martini, 2019

Genus *Hispaniastraea* Turnšek & Geyer, 1975

Species originally included. — *Hispaniastraea murciana* Turnšek & Geyer *in* Turnšek, Seyfried & Geyer, 1975 and *Hispaniastraea ramosa* Turnšek & Geyer *in* Turnšek, Seyfried & Geyer, 1975.

Type species. — *Hispaniastraea murciana* Turnšek & Geyer *in* Turnšek, Seyfried & Geyer, 1975: 22, pl. 20-21, by original designation.

Hispaniastraea murciana Turnšek & Geyer, 1975
(Fig. 24)

Hispaniastraea murciana Turnšek & Geyer *in* Turnšek, Seyfried & Geyer, 1975: 138, pl. 20, figs 1-2, pl. 21, figs 1-2. — Vasseur 2018: 216-217, fig. 3.46. — Boivin *et al.* 2019: 8, fig. 4-5. — Vasseur & Lathuilière 2021: 1231, fig. 29.

Hispaniastraea ramosa Turnšek & Geyer *in* Turnšek, Seyfried & Geyer, 1975: 139, pl. 22, figs 1-3. — ?Prinz 1991: 167, pl. 2, fig. 5. — ?Senowbari-Daryan & Stanley 1994: 52-53, fig. 5, pl. 1, figs 4-8. — ?Turnšek *et al.* 2003: 292-293, pl. 3 figs 1-4.

Chaetetes (*Pseudoseptifer*) *murciana* – Beauvais 1980: 30, pl. 3, fig. 2.

Type material. — **Holotype**. **Spain** • 1 specimen, colony no. 33 (original designation) from collection Seyfried reposited in Departamento de Paleontología of the University of Granada (UG); Zarcilla de Ramos (Province of Murcia); 37°50'44"N, 1°52'28"W (based on nearby landmark); Upper Sinemurian-Lower Pliensbachian, Lower Jurassic; colony no. 33.

Studied samples. — MNHN.F.C05037 (L. Beauvais coll.), CPUN DA0106E2-4, CPUN 2303A1-6, CPUN AM16160-2, CPUN DA2905E1-2, CPUN DA2905E2-2, CPUN DA3105E3-1 from Pliensbachian to Lower Toarcian (pre-JE) of High Atlas and Middle Atlas of Morocco.

Geographic and stratigraphic ranges. — Sinemurian of Murcia (Spain) and Languedoc (France), Pliensbachian of Calabria (Italy) and Pliensbachian to Lower Toarcian (pre-JE) of High Atlas and Middle Atlas of Morocco.

Description
The following description is made in collaboration with S. Boivin on the basis of samples collected both in Pliensbachian and Toarcian strata. Cerioid massive, lamellar or ramose colony. Subcircular to polygonal corallites sometimes strongly distorted, particularly in the middle of the branches. The septal apparatus is characterized by one major septum that dominates in width and thickness. It is straight or curved, compact, ornamented only by periodic auriculae along its inner edge. The auriculae are subcircular in transverse section (they fill up to 3/4 of the lumen surface) and reveal a horizontally elongated rhombic shape or a platelike shape with rims turned upward in longitudinal section perpendicular to the mid-septal plan. The inner edge of the major septum is thus enlarged at each auricula and narrower and rounded between successive auriculae, conferring to the lumen a characteristic horseshoe shape. Minor septa are short, compact, rounded or sharp and generally restricted within the wall that makes them sometimes undistinguishable. The inner edge of septa is covered of granules that alternate with the auriculae of the major septum. In some parts of the colonies where geometrical constraints of construction are weak, all the major septa of the neighbouring corallites are oriented in the same direction. Thin, concave (in distal view) tabulae can sometimes be observed. Microstructure not preserved. Two different modes of budding coexist in the colonies: extracalicular budding and intracalicular septal budding. Many heterogeneously distributed intercalicular canals have been observed. These canals are restricted to some parts of the colonies and their origin is still unknown. The hypothesis of an association between non-corals organisms is considered.

Dimensions
Great diameter of the lumen: 0.46 to 1.95 mm – small diameter of the lumen: 0.14 to 1.44 mm – thickness of the wall: 0.09 to 0.84 mm – distance between calices centres: 0.49 to 2.10 mm – length of major septa: 0.11 to 0.99 mm – thickness of major septa: 0.05 to 0.57 mm – number of apparent septa: 1 to 12.

Similarities and differences
This taxon is morphologically close to a chaetetid sponge group that belongs to the subgenus *Chaetetes* (*Pseudoseptifer*) Fischer, 1970 but differs from the latter by the presence of auriculae on the major septum, intercalicular canals and a serrated aspect of the wall due to abortive septa (see Boivin *et al.* 2019).

H. murciana is easy to distinguish from *H. ousriorum* Boivin *et al.* 2019 by the proportions between the septa, we have not found the latter in the Toarcian in our proper work but an occurrence is mentioned by Stone (2024).

Hispaniastraea ousriorum Boivin, Vasseur, Lathuilière, Lazăr, Durlet, Martindale, El Hmidi & Martini, 2019
(Fig. 25)

Hispaniastraea sp. 1 – Vasseur 2018: 219-220, fig. 3.47.

Hispaniastraea ousriorum Boivin, Vasseur, Lathuilière, Lazăr, Durlet, Martindale, El Hmidi & Martini, 2019: 10, fig. 7, 8 — Stone *et al.* 2026: tab. 3, fig. 11g.

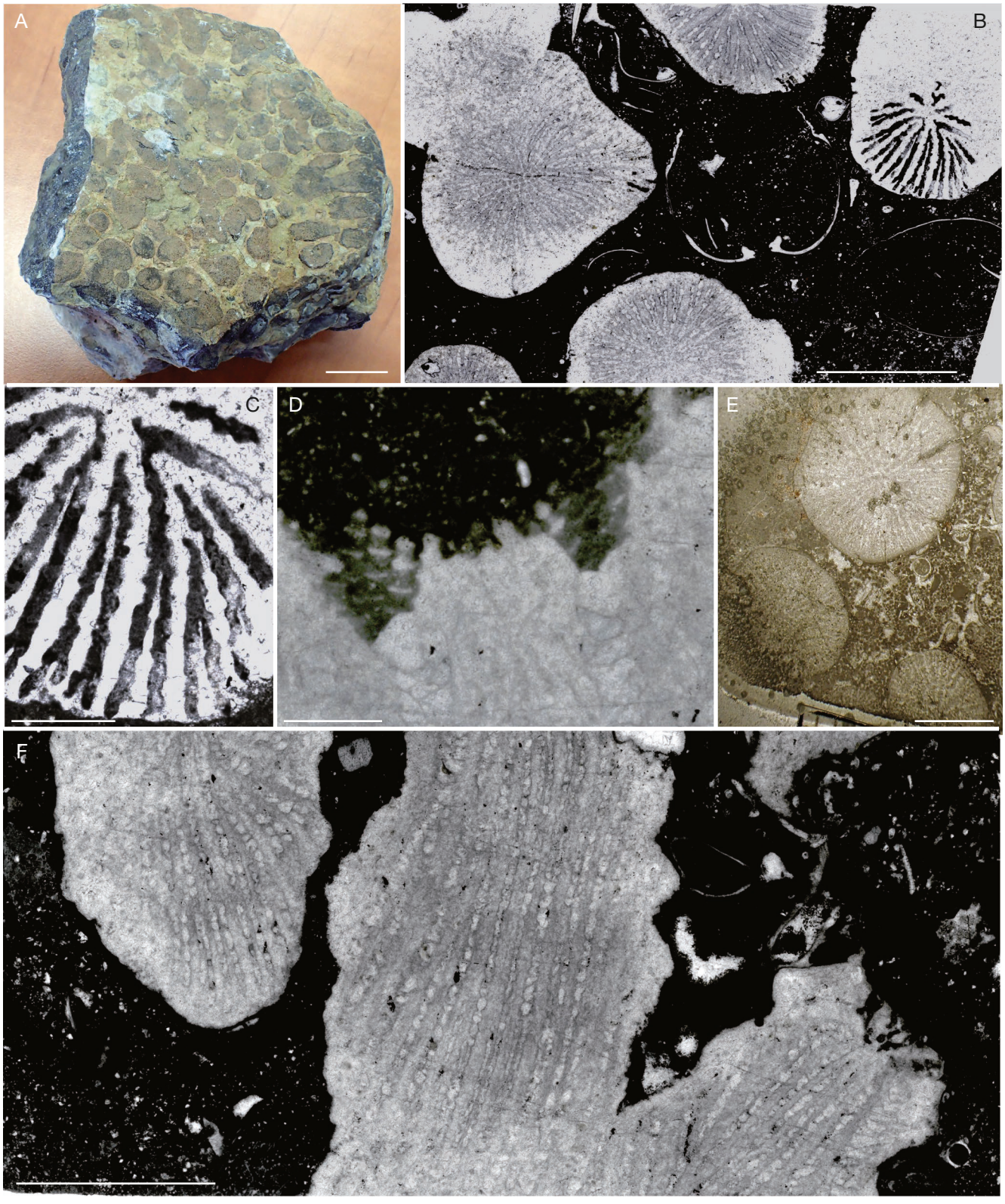

Fig. 23. — *Thecactinastraea termierorum* (Beauvais, 1986), Toarcian (*Polymorphum* Zone), Dades Valley between Tillout and Tidrite, specimen CPUN DA3005E2-1 (**A**-**D**, **F**) and Lower Jurassic, unknown location, holotype MNHN.F.R11621 (**E**): **A**, distal view; **B**, detail in transverse thin section; **C**, detail in transverse thin section of septal ornamentation; **D**, detail in longitudinal distal section of the pennular ornamentation of septa; **E**, transverse thin section of the holotype MNHN.F.R11621; **F**, longitudinal thin section. Scale bars: A, 2 cm; B, 5 mm; C, D, 1 mm; E, F, 4 mm. Photos: R. Vasseur.

Type material. — **Holotype. Morocco** • 1 specimen; Koudiat Ech Chehem, Guigou Plateau, Middle Atlas Mountains; Upper Pliensbachian; 33°27'9"N, 4°55'41"W; Lower Jurassic; Boivin Leg.; DGR SB367 (Collections of the Direction of Geology, Ministère de l'Énergie, des Mines et du Développement durable – Département de l'Énergie et des Mines, Rabat, Morocco).

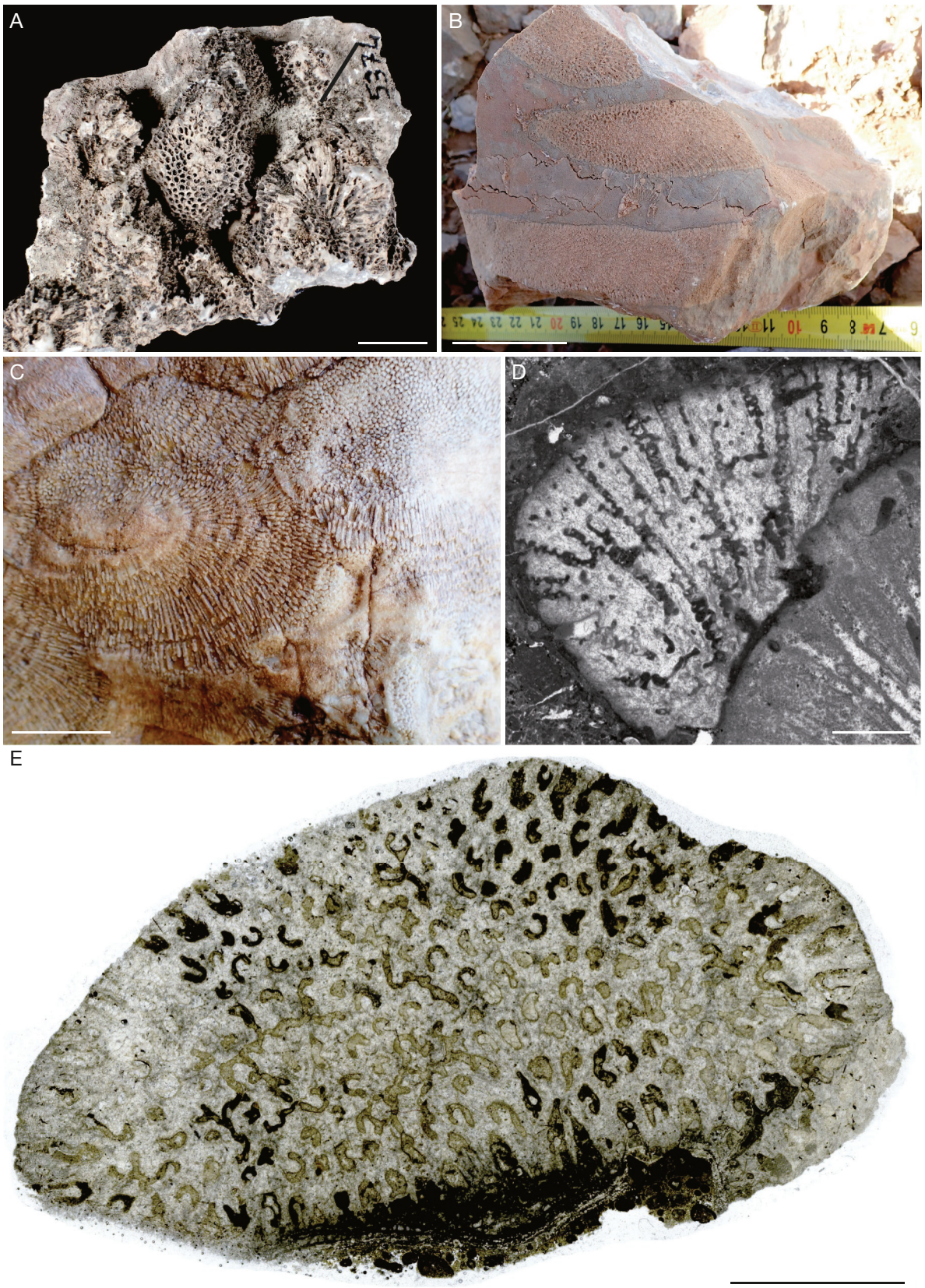

Fig. 24. — *Hispaniastraea murciana* Turnšek & Geyer, 1975: **A**, distal view of the specimen MNHN.F.C05037 (L. Beauvais coll., Pliensbachian of Guigou Plateau, Morocco); **B**, ramose specimen pictured in the field (Dades Valley, Morocco, 31°33'43"N, 5°54'13"W); **C**, massive specimen pictured in the field (Vallone del Gardo, Calabria, Italy, 39°27'51"N, 16°47'26"E); **D**, longitudinal thin section of the specimen CPUN DA2905E1-2 (Pliensbachian of Aït Hammou, Dades Valley, Morocco); **E**, transverse thin section of the specimen CPUN AM16160-2 (Pliensbachian of Amellagou, Morocco). Scale bars: A, 1 cm; B, 4 cm; C, 2 cm; D, 2 mm ; E, 5 mm. Photos: R. Vasseur.

Studied samples. — CPUN AM16160-3, CPUN AM16188-5, CPUN CDAm1 from Pliensbachian of Amellagou, High Atlas of Morocco.

Geographic and stratigraphic ranges. — Upper Pliensbachian of Middle and High Atlas of Morocco, Lower Toarcian of Dades Valley (Jebel Toksine).

Remarks
The same species was found in Pre-JE Toarcian by Stone (2024) in Aguerd Izegzawne, explaining why we include it in this monography.

Description (in collaboration with S. Boivin)
Cerioid massive, lamellar or ramose colony. Subcircular to polygonal corallites. The septal apparatus is composed of a major septum, one to four well-developed septa (S1) and a few minor septa (S2). Major septum is highly dominant in length and thickness, straight, compact, ornamented by auriculae on the inner margin of septum. Ordinary, S1 septa also bear auriculae. Auriculae occur in periodic intervals, and are sub-circular in transverse section. In longitudinal section (perpendicular to the septum plan), auriculae are shaped like a horizontally elongated lozenge or a spoon. Inner margin of S1 is strongly enlarged at the level of the auriculae and rounded between the auriculae. Minor septa very short, compact, rounded, and mostly not discernible in the wall. Inner margins of the minor septa with sharp granules that alternate with auriculae. Thin, concave (in distal view) tabulae can be linked to auriculae. Vestiges of microstructure have been observed: straight axes parallel to the wall or divergent with an angle of 10 to 20° appear in longitudinal section. In transverse section we observed black spots in the middle of the wall surrounding the calices. Many heterogeneously distributed intercalicular canals have been observed. These canals are restricted to some parts of the colonies. One single corallite can be connected to until four canals, and sometimes two corallites can be connected by two different canals. Their origin is still unknown. The hypothesis of an association between non-corals organisms is considered.

Dimensions
Great diameter of the lumen: 0.47 to 0.89 mm – small diameter of the lumen: 0.35 to 0.78 mm – thickness of the wall: 0.09 to 0.72mm – distance between calices centres: 0.27 to 1.18 mm – length of major septa: 0.14 to 0.36 mm – thickness of major septa: 0.03 to 0.21mm – number of apparent septa: 3 to 8.

Similarities and differences
This species differs from *Hispaniastraea murciana* by the presence of 1 to 3 S1 septa (there is always one single major septum in *H. murciana*), and smaller auriculae (the inner space is shared by the auriculae of the different S1 septa).

Family Pleurosmiliidae Fromentel, 1865

Genus *Axosmilia* Edwards, 1848

Species originally included. — *A. extinctorium* Michelin, 1841 only.

Type species. — *Axosmilia extinctorium* Michelin, 1841 (Michelin 1841: 9, pl. 2, fig. 3b), by monotypy.

Remarks
According to Beauvais (1986b), this taxon is distinct from those under the genus *Axosmilia* because this genus includes corals with abundant endotheca and a columella anastomosed with one S1 when *A. outitensis* (Beauvais, 1986) shows free S1 and no endotheca. The study of new *A. outitensis* specimens and different species under the genus *Axosmilia* weaken these arguments: some *Axosmilia* species include specimens with rare endotheca and exclusively free septa. In addition, ghosts structures of endotheca and some S1 joining the columella have been observed in *A. outitensis* specimens. Consequently, discriminant criteria permitting to exclude *A. outitensis* from the genus *Axosmilia* do not exist.

Axosmilia outitensis (Beauvais, 1986) (Fig. 26)

Axotrochus outitensis Beauvais, 1986b: 24, pl. 6, fig. 1, txt-fig. 13, 14.

Parapleurosmilia inflata Beauvais, 1986b: 15, pl. 1, fig. 4, pl. 4, fig. 1.

Axosmilia outitensis – Vasseur 2018: 134, fig. 3. 12.

Type material. — **Holotype**. **Morocco** • 1 specimen by original designation; Jebel Outita; 34°9'44"N, 5°45'49"W (based on nearby landmark); Lower Toarcian, Lower Jurassic; Faugères Leg.; MNHN.F.R11615.
Paratypes. **Morocco** • 12 specimens; Jebel Outita; 34°9'44"N, 5°45'49"W (based on nearby landmark); Lower Toarcian, Lower Jurassic; Faugères Leg.; batch MNHN.F.A30498 (2 specimens), batch MNHN.F.A30499 (10 specimens).

Studied samples. — Six specimens coll. Faugères (holotype and five paratypes), described in Beauvais (1986b: 23, pl. 6, fig. 1 and text-fig. 13, 14), eight specimens coll. Gubler (unpublished original designation: "*Axosmilia* nov. sp." [sic]), MNHN.F.A57323, MNHN.F.C05104, C05105, C05106, C05107, C05108, C05109 and C05110.

Geographic and stratigraphic ranges. — Lower Toarcian of Morocco including Jebel Outita and Moussaoua pass.

Amended description
Solitary coral, trochoid to turbinate (the apical angle is mostly around 50°), straight or slightly curved, with a wrinkled wall covering the external parts of the corallite (the wrinkles correspond to successive growing stages) and reaching the prominent calical edges. This wall is sometimes longitudinally finely striated on its external face. The calix is elliptic in transverse section, following the same lengthening as the axial structure. Radial elements are straight, compact septa with smooth lateral faces, mostly free although some first size-order septa (S1) are linked to the columella in depth. The septal apparatus is made of three or four distinct size-orders of septa (12S1 + 12S2 + 24 S3 (+ 48 S4)) possibly corresponding to four or five ontogenetic cycles, assuming that the twelve S1 septa correspond to the first two septal cycles (6 + 6 septa). Thus, the twelve distinct septal sectors could be paired making six equal septal systems following a very classical scleractinian

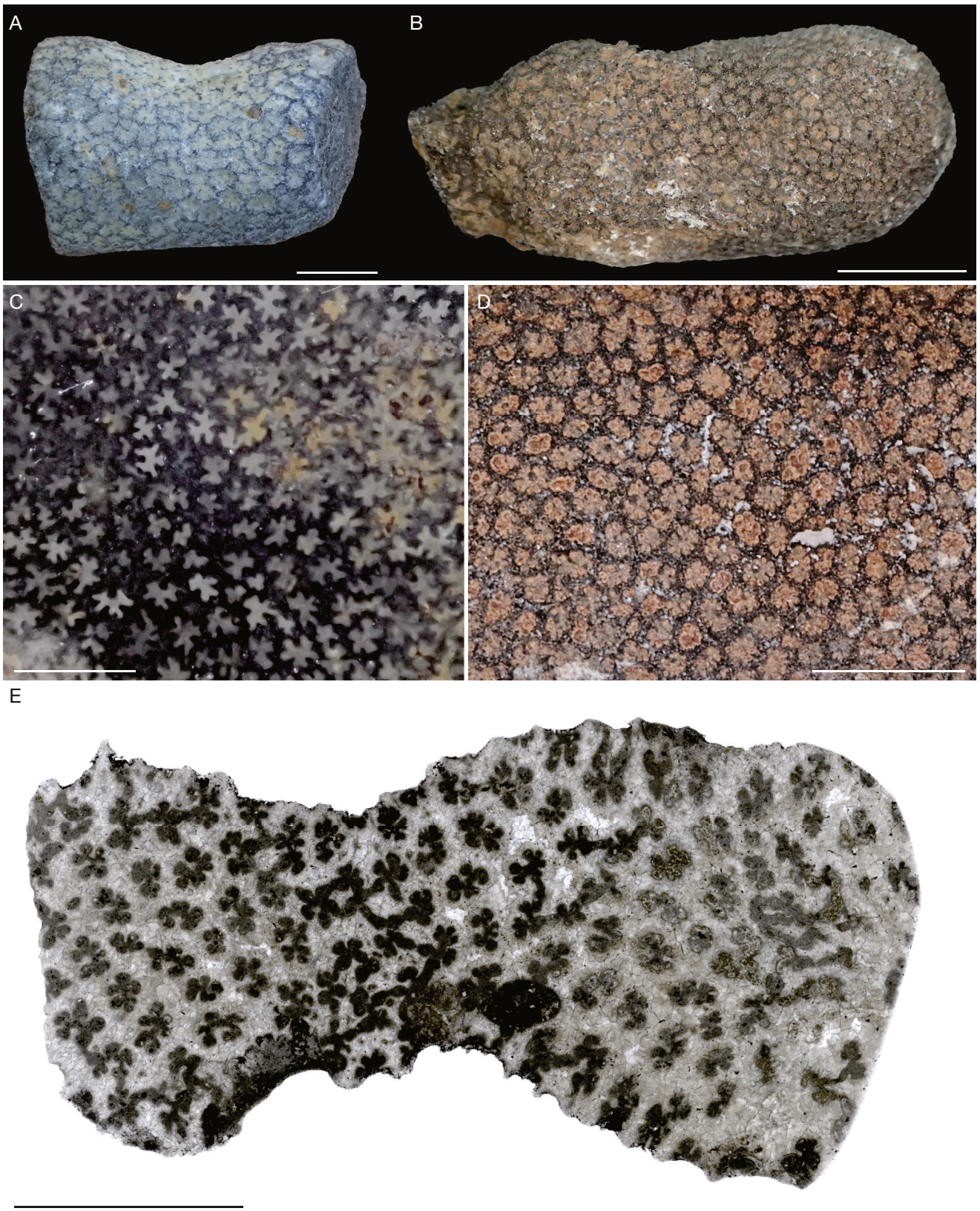

Fig. 25. — *Hispaniastraea ousriorum* Boivin, Vasseur, Lathuilière, Lazăr, Durlet, Martindale, El Hmidi & Martini, 2019 (Pliensbachian of Amellagou, Morocco): **A**, specimen CPUN CDAm1; **B**, specimen CPUN AM16188-5; **C**, transverse polished section of the specimen CPUN AM16160-3; **D**, distal view of the calicular surface of the specimen CPUN AM16188-5; **E**, transverse thin section of the specimen CPUN CDAm1. Scale bars: A, 5 mm; B, 1 cm; C, 2 mm; D, E, 4 mm. Photos: R. Vasseur.

model of development. Septa show sometimes an enlargement or slimming in the inner edge, even if they have generally a constant width lengthwise. Microstructure remains that are present on some specimens reveal a straight or wavy mid-septal line in transverse section and lamellar stereomal deposits enwrapping septa and columella and increasing in depth. Bilateral symmetry is superimposed in addition to the hexameral symmetry featured by the septal apparatus. It is indicated by the elongation of both the calix and the lamellar columella, which shows as the septa a more or less wavy median line. Vestigial endotheca, made of in-depth dissepiments and stereome deposits in the lumen.

Dimensions
Calicular diameter: 11.2 to 27 mm – number of septa: 48 (extrapolated) – septal density: approximately 5 for 5 mm.

Similarities and differences
Differs from the other species under the genus by the scarcity of endothecal structures. Many species have a higher number of septa, less elongated calix and columella and a less pronounced hierarchy in septal thicknesses.

Genus *Placophyllia* Orbigny, 1849

Species originally included. — *Lithodendron dianthus* Goldfuss, 1826.

Type species. — *Lithodendron dianthus* Goldfuss, 1826: 45, by monotypy.

Remark
Based on the observation of type material and topotypes figured in the Corallosphere, *Placophyllia* can be defined as a phaceloid *Pleurosmilia* Fromentel, 1856, with a lamellar columella, a very regular hexameral septal apparatus, bicuneiform costosepta with parathecal internal wall and probably trabeculothecal external wall. For those reasons, we attribute the genus *Placophyllia* to the Pleurosmiliidae.

Placophyllia amnica Melnikova & Roniewicz, 2021 (Fig. 27)

Placophyllia sp. – Melnikova & Roniewicz 2012: 379.

Stylosmilia? sp. 2 – Vasseur 2018: 342, fig. 3.95.

Placophyllia amnica Melnikova & Roniewicz, 2021: 479, Fig. 7A-E.

Type material. — **Syntypes. Tajikistan •** 4 specimens, Zurchiertsek Valley, northern side of the Alichur River valley, South-Eastern Pamir Mountains, Gurumdy Formation, Pliensbachian, Lower Jurassic, ZPAL.H.30/198, 228, 231, 233.

Studied samples. — MNHN.F.A57328; CPUN DA2705E4-1, DA2705E4-8, DA2705E4-18, DA2805E2-1, DA2805E4 from Middle/Upper Toarcian of Aït Athman (Ziz Valley, High Atlas) and Beni Meraz (Moulay Idriss), Morocco.

Geographic and stratigraphic ranges. — Pliensbachian of Tadjikistan and Toarcian of Morocco.

Description
Phaceloid colony whose cylindrical corallites multiply by extracalicular budding. Radial elements are compact, bicuneiform, straight or wavy costosepta free or joined together or to the columella. The thickening of the widest part of septa produce a septothecal inner wall. The septal apparatus shows three distinct size-orders showing a stable hexameral symmetry. The architecture of septa is trabecular with a median wavy mediosepta line, without demonstrative auriculae, and sparse granules on lateral faces. The inner edge is sometimes rhopaloid. A bilateral symmetry appear sometimes by elongation of the fossa. Epicostal epitheca with growth wrinkles wrap the corallites. Styliform or lamellar columella sometimes observed. Endotheca made of vesicular dissepiments. The external wall is either epithecal or trabeculothecal. It is rather distant from the inner wall.

Dimensions
Calicular diameter: 2 to 9 mm – distance between calices centres: 5 to 9 mm – number of septa: approximately 24 to 38 – septal density: 5 for 2 mm.

Similarities and differences
The dimensions of the specimens are very close of those classically described in the Upper Jurassic e.g. *P. dianthus, P. rugosa* Becker, 1875 but we choose the Pliensbachian recently described species *P. amnica* as it represents a closer evolutionary stage and also a wider variability when the younger nominal species have a more stabilized morphology (in particular a lamellar columella always present).

Family Stylinidae Orbigny, 1851

Genus *Diplocoenia* Fromentel, 1857

Species originally included. — *Diplocoenia mirabilis* Fromentel, 1857.

Type species. — *Diplocoenia mirabilis* Fromentel, 1857 by monotypy.

Remarks
The syntype of *D. mirabilis* was claimed to be lost by Löser (2009) but it was recovered (see Löser 2016). The syntype is available in the collections of the MNHN: MNHN.F.A37411.

Diplocoenia elmii n. sp. (Fig. 28)

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Diplocoenia? sp. – Lathuilière 2011: 532, pl. 2, fig. 3-4.

Diplocoenia sp. 1 – Vasseur 2018: 173, fig. 3. 28.

Type material. — **Holotype. Morocco •** 1 specimen; Aïn Leuh (Middle Atlas), Al Yabes levels; 33°11'32"N, 5°21'8"W; Middle/Upper Toarcian, interval Gradata zone, Gemma subzone up to basal Meneghini zone according to Elmi *et al.* (2002), Lower Jurassic; Vasseur Leg.; CPUN MA1004E4-8.

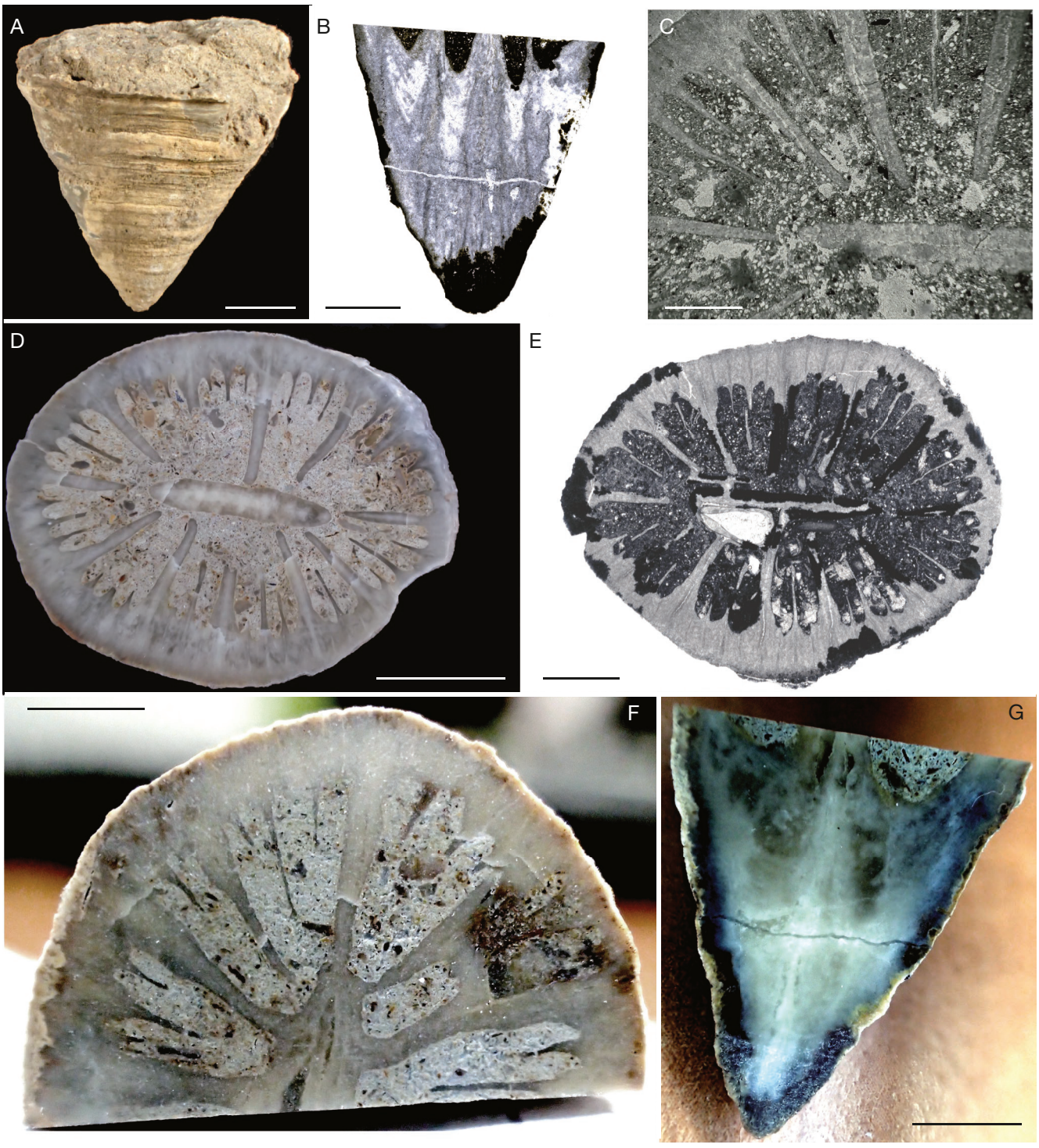

Fig. 26. — *Axosmilia outitensis* (Beauvais, 1986): **A**, specimen MNHN.F.C05107 (Toarcian of Jebel Outita, Morocco); **B**, longitudinal thin section of the specimen MNHN.F.C05105; **C**, septa and columella microstructure detail in thin section, holotype MNHN.F.R11615 (Lower Toarcian of Jebel Outita, Morocco); **D**, transverse section of the holotype MNHN.F.R11615; **E**, transverse thin section of the specimen MNHN.F.A57323; **F**: transverse section of the specimen MNHN.F.C05105 showing endothecal structures; **G**, longitudinal section of the specimen MNHN.F.C05105 showing endothecal structures. Scale bars: A, D, 5 mm; B, E, G, 4 mm; C, 1 mm; F, 2 mm. Photos: R. Vasseur.

Studied samples. — CPUN MAM10; CPUN MA0804E2-MA0804E2-13, MA0804E2-14; CPUN MA1004E4-8, MA1004E4-19, MA1004E4-20, MA1004E4-21, MA1004E4-22, MA1004E4-23, MA1004E4-24, MA1004E4-25, MA1004E4-26; CPUN MA1004E5-8.

Type locality and age. — Morocco, Aïn Leuh (Middle Atlas), Al Yabes levels; Middle/Upper Toarcian, interval Gradata zone, Gemma subzone up to basal Meneghini zone according to Elmi *et al.* (2002), Lower Jurassic.



FIG. 27. — *Placophyllia amnica* Melnikova & Roniewicz, 2021 (Middle Toarcian of Ziz Valley, Morocco): **A**, lateral view of specimen CPUN DA2705E4-8; **B**, thin section in specimen CPUN DA2805E2-1 showing two corallites in oblique section; **C**, transverse thin section in specimen CPUN DA2805E2-1; **D**, lateral view of a corallum in specimen CPUN DA2705E4-8 partially out of the matrix. Scale bars: A, 1 cm; B, C, D, 5 mm. Photos: R. Vasseur.

DIFFERENTIAL DIAGNOSIS. — We compared our specimens to the Jurassic nominal species that have been assigned to the genera *Diplocoenia*, *Diplocoeniastraea* Achiardi, 1880 and *Pseudodiplocoenia* Alloiteau, 1958 (see Lathuilière 1989 for a list) and came to the conclusion that no existing nominal species fits the dimensions of *D. elmii*. However, three species with comparable dimensions have kept our attention. *Diplocoenia tazerdunetensis* Beauvais, 1966a lacks the plocoid appearance, *Diplocoenia varia* Alloiteau, 1958 has no external wall (astreoid colonial structure) and *Pseudodiplocoenia soltanensis* Beauvais, 1966a shows a mural sulcus and an absence of "inner wall" which seems incompatible at least with our samples and possibly with the whole genus *Diplocoenia*.

ETYMOLOGY. — The species is dedicated to Serge Elmi who has collected the first specimen and precised the stratigraphy of the type locality (Elmi *et al.* 2002).

GEOGRAPHIC AND STRATIGRAPHIC RANGES. — Middle/Upper Toarcian of Aïn Leuh, Middle Atlas of Morocco.

DESCRIPTION

Cerioid colony of plocoid appearance, massive or lamellar, encrusting. Extracalicular mode of budding. Radial elements are straight, compact, free septa except the major septa that sometimes reach the columella. The septal apparatus tends to be octameral but this character seems to be labile. Lateral faces are smooth or sparsely granulated and the inner edge of first size-orders septa is ornamented with periodic hastiform auriculae. Columella generally present, varying in aspect: it looks sometimes parietal and linked to the septa or sometimes free and styliform. Wavy discontinuous wall of unknown nature often considered by authors as the external wall. Endotheca made of vesicular dissepiments that creates the appearance of a second internal wall. Growth bands of 0.5 to 0.9 mm in vertical extension can be observed in longitudinal section.

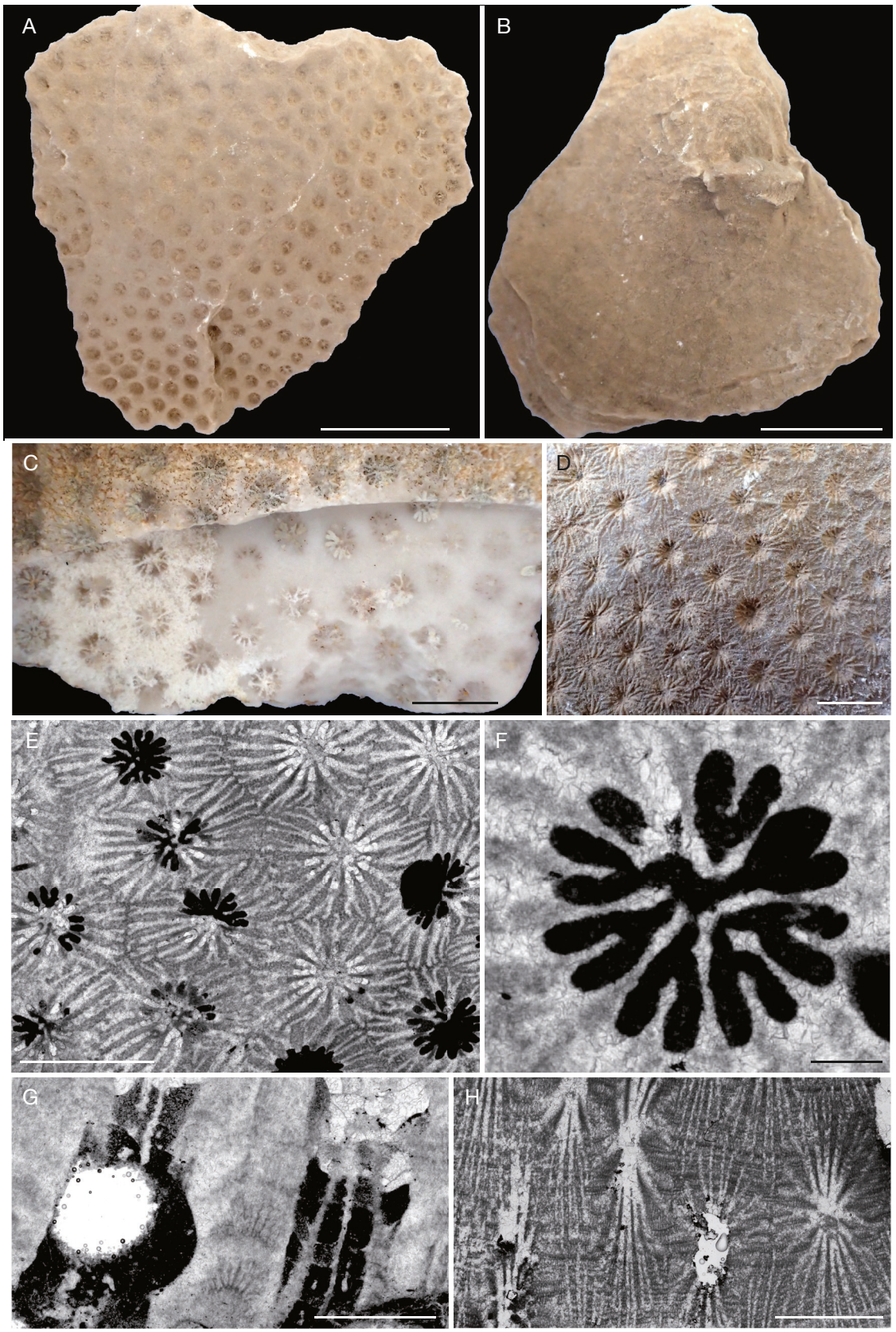

Fig. 28. — *Diplocoenia elmii* n. sp. (Middle/Upper Toarcian of Aïn Leuh, Morocco): **A**, distal view of specimen CPUN MA1004E4-22; **B**, proximal view of specimen CPUN MA1004E4-22; **C**, transverse section in specimen CPUN MA1004E4-19; **D**, distal view of specimen CPUN MA1004E4-24; **E**, transverse thin section in the holotype CPUN MA1004E4-8; **F**, detail in transverse thin section of one calix with hastiform auriculae in the holotype CPUN MA1004E4-8; **G**, longitudinal thin section in the holotype CPUN MA1004E4-8; **H**, oblique thin section in the specimen CPUN MA0804E1-14. Scale bars: A, B, 2 cm ; C, 5 mm; D, E, H, 4 mm; F, 0.5 mm ; G, 2 mm. Photos: R. Vasseur.

Dimensions
Calicular diameter: 2.1 to 3.5 mm – distance between calices: 2 to 5 mm – number of septa: 26 to 34 – septal density: 4 to 5 for 1 mm.

Genus *Stylosmilia* Edwards & Haime, 1848

Species originally included. — *Stylosmilia michelini* Edwards & Haime, 1848.

Type species. — *Stylosmilia michelini* Edwards & Haime, 1848 by monotypy.

Remarks
The species described below seem a little marginal within the genus *Stylosmilia* because they do not combine all the typical characters of the type species, especially a well expressed styliform columella and regular auriculae.

Stylosmilia sp.
(Fig. 29)

Stylosmilia sp. 1 – Vasseur 2018: 340, fig. 3.94.

Studied samples. — CPUN DA0206E1-6, CPUN 1603A8-14, CPUN 1603NR from Upper Toarcian of Amellagou and Aguerd Izegzawne (High Atlas of Morocco).

Description
Phaceloid corallum with a wide angle of extracalicular budding and cylindrical calices. Radial elements are bicuneiform costosepta straight or wavy, free or joined, with small heterogeneously distributed granules on lateral faces. Inner edge is sometimes thickened (rhopaloid or podoid), which suggests the presence of auriculae not confirmed in longitudinal section. Some first order septa reach the styliform (lamellar in one single calice) columella with their inner edge or join each other in the axial zone when the columella is absent. Endotheca present, made of tabular dissepiments. No synapticulae. Septothecal wall. An epitheca wraps the costae all around the corallite.

Dimensions
Calicular diameter: 2 to 5.5 mm – number of septa: 20 to 35 – septal density: 4 to 8 for 2 mm.

Similarities and differences
Differs from the Liassic species *Stylosmilia dresnayi* Beauvais, 1986 by the presence of an epicostal epitheca and lower septal densities. This species is characterized by a weak expression of auriculae and columella and a high and variable number of septa in comparison to many nominal species e.g. the classical *S. michelini*, *S. corallina* Koby, 1881 and *S. tenuis* (Koby, 1889). Comparing with Chinese nominal species: 1) the Upper Cretaceous *S. kangpaensis* Wu, 1975 and the Middle/Upper Jurassic *S. catenula* Liao & Li, 1980 are the closest in terms of dimensions. It is difficult to merge the present species with *S. kangpaensis* without filling the huge temporal gap between them, in the case of *S. catenula*, its columella seems more constant and the presence of auriculae is not documented; and 2) *S. tanggulaensis* Liao & Li, 1980 seems more related to *Placophyllia* according to the rather constant lamellar columellae visible in the figuration, a secondary wall quite distant to the external one, wavy septa (also suggested in the figuration) and a marginal mode of budding. The Tithonian *S. flexuosa* Koby, 1905 has quite small corallites (2 mm in diameter).

Family Stylophyllidae Frech, 1890

Genus *Haimeicyclus* Alloiteau, 1957

Species originally included. — Only *H. haimei* (Chapuis & Dewalque, 1853)

Type species. — *Montlivaltia haimei* Chapuis & Dewalque, 1853, by monotypy.

Remarks
Beauvais published also *Haimeicyclus* as a new genus (Beauvais 1986b: 54) with the same type species but, despite the name was proposed conditionally, the authorship should be returned to Alloiteau (1957) according to ICZN (art 11.5.1). In addition, a confusion is made between the type species and the type specimen. The type material is probably in Liège (collection Chapuis & Dewalque) and not in Paris (collection Fromentel).

Haimeicyclus haimei (Chapuis & Dewalque, 1853)
(Fig. 30)

Montlivaltia haimei Chapuis & Dewalque, 1853: 263, pl. 38, fig. 5. — Terquem & Piette 1865: 126. — Duncan 1867: 35, pl. 10, fig. 24-32; 1868: 68, text fig. 7. — ? Quenstedt 1879: 576, pl. 164, fig. 32. — ? Tomes 1901: 76. — Lejeune 1935: pl. 1, fig. 3, 9, 17; pl. 2, fig. 4; pl. 3, fig. 1, 4; pl. 7, fig. 1. — Joly 1936: 166, pl. 3, fig. 1-7. — Beauvais 1976: 72, pl. 16, fig. 5. — Negus 1991: 254, tab. 1.

Cyclolites granulatus – ?Quenstedt 1852: 658, pl. 59, fig. 21.

Montlivaultia haimei – Edwards & Haime 1857: 324. — Fromentel 1861: 109. — Fromentel & Ferry 1866: 116, pl. 18, fig. 4. — ?Dareste de la Chavanne 1912: 596, pl. 17, fig. 12.

Montlivaultia tenui-septa – Fromentel & Ferry 1866: 112, pl. 18, fig. 2.

Stylophyllopsis cf. *haimei* – ?Jaworski 1926: 141.

Montlivaultia tenui-septa-granigera haimei – ?Zuffardi-Comerci 1932: 60.

Montlivaltia haimei var. *alta* Joly, 1936: 166, pl. 3, fig. 8-10.

Haimeicyclus haimei – Alloiteau 1957: 105. — Beauvais 1986b: 54. — Stolarski & Russo 2002a: 183 ; 2002b: 653. — Vasseur 2018: 214, fig. 3.45. — Lathuilière *et al.* 2021: 111-112.

Haimeicyclus tenuisepta – Beauvais 1986a: 211, pl. 25, fig. 3. — Fontaine *et al.* 1989: 1087, 1090. — Beauvais 1989: 292.

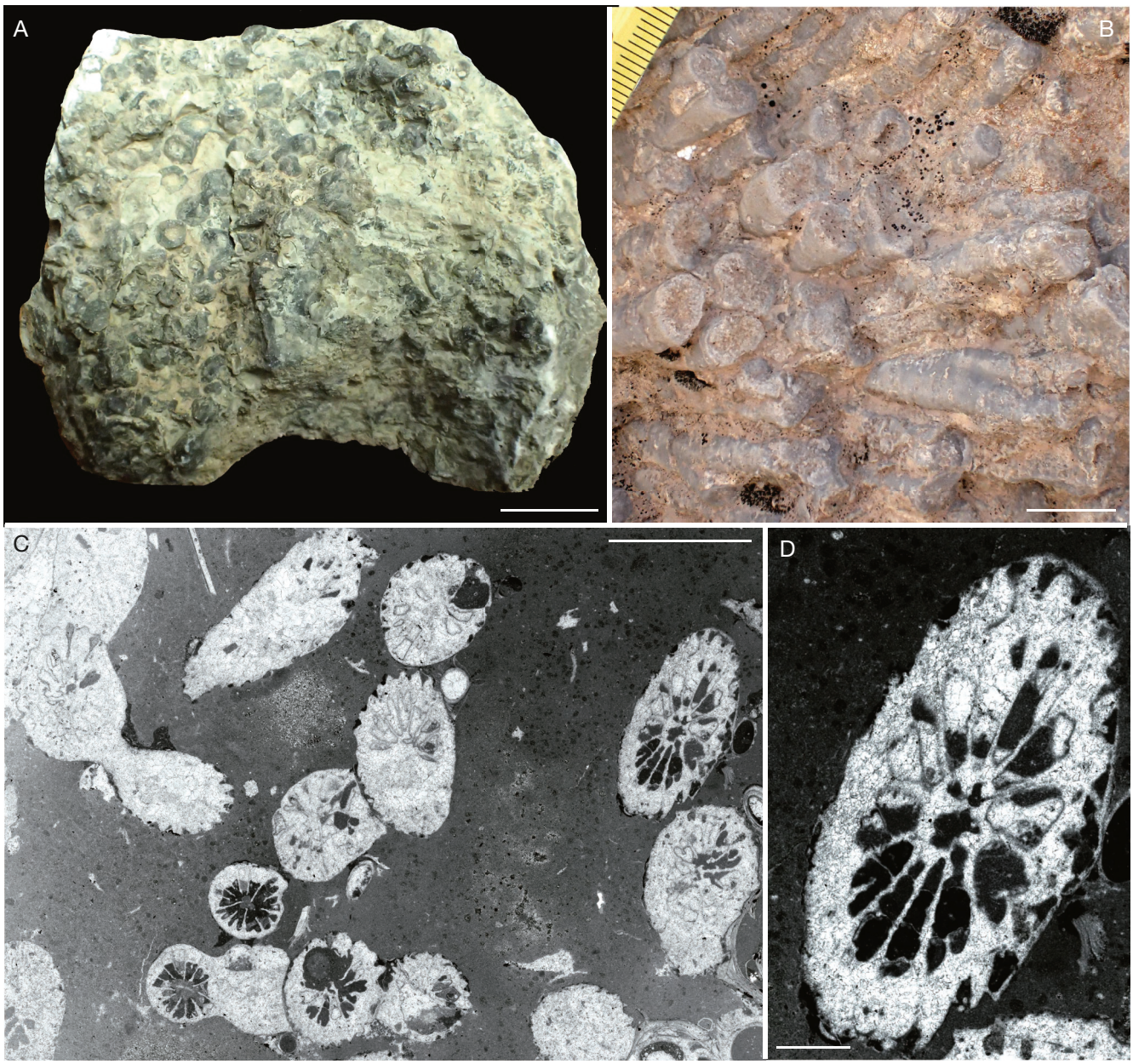

Fig. 29. — *Stylosmilia* sp. (Upper Toarcian of Amellagou, Morocco): **A**, distal view of the specimen CPUN 1603NR; **B**, *Stylosmilia* sp. 1 pictured in the field (31°43'34"N, 5°44'50"W); **C**, transverse thin section of the specimen CPUN 1603A8-14; **D**, enlarged view on one calice in transverse thin section (specimen CPUN 1603A8-14). Scale bars: A, 2 cm; B, 1 cm; C, 5 mm; D, 1 mm. Photos: R. Vasseur.

Stylophyllopsis framei – ?Beauvais 1989: 292.

Type material. — **Syntypes**. **Belgium** • Unknown number of specimens, probably in Liège; from Jamoigne, Termes; Lower Liassic, Early Jurassic; Chapuis & Dewalque Leg.

Studied samples. — CPUN DA3005E2-2, CPUN DA0106E3-3, CPUN DA0306SB from Lower/Middle Toarcian of Dades Valley (High Atlas of Morocco).

Geographic and stratigraphic ranges. — Sinemurian of Sicilia, Lower Jurassic (Hettangian-Sinemurian) of Belgian, France, Germany, Luxembourg, England, Lower/Middle Toarcian of Dades Valley (High Atlas of Morocco), Lias of Argentina and Indonesia (Sumatra).

Description

Solitary coral, discoid, circular in outline, which lower face is coated by an epitheca with concentric bulges and attachment scars. Costosepta exsert, subcompact with a stylophyllid structure, made of septal spines, with a distal edge ornamented by small, regular, round teeth due to the projection of the septal spines. The septal apparatus is made of six equal systems, each of them including generally four distinct size-orders of septa (a fifth order of abortive septa appears sometimes in thin section). These geometrical size-orders can be interpreted as successive ontogenic cycles corresponding to a six-folded symmetry following the very classical scleractinian Edward's

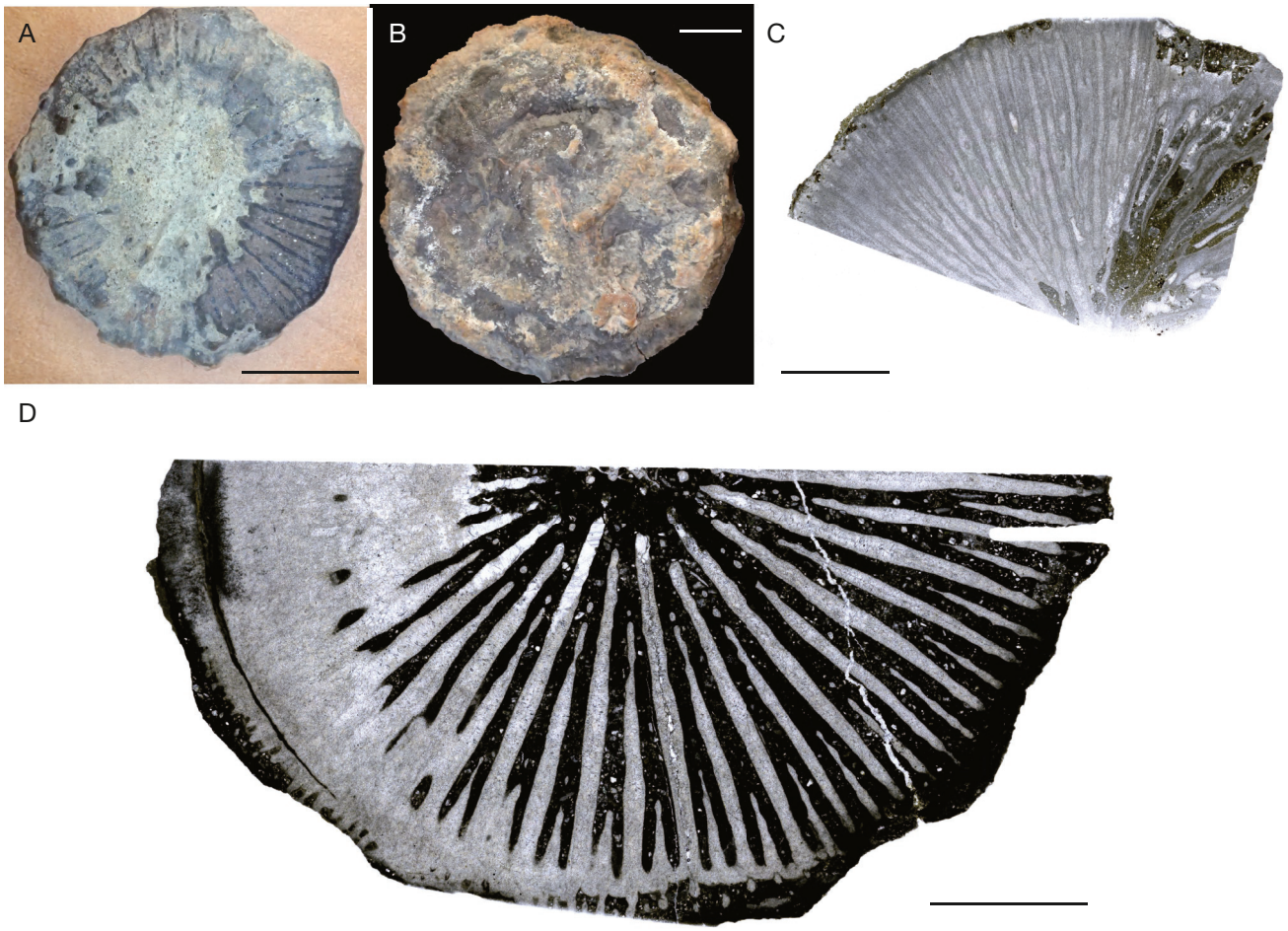

Fig. 30. — *Haimeicyclus haimei* (Chapuis & Dewalque, 1853), Lower/Middle Toarcian of Dades Valley, Morocco: **A**, distal view of the specimen CPUN DA0306SB; **B**, proximal view of the specimen CPUN DA0306SB; **C**, transverse thin section of the specimen CPUN DA3005E2-2; **D**, transverse thin section of the specimen CPUN DA0306SB. Scale bars: A, 1 cm; B, 5 mm; C, D, 4 mm. Photos: R. Vasseur.

model of development, assuming that the first size-order (S1) of septa corresponds to the first two septal ontogenetic cycles (6 + 6 septa) of the theoretical model. Septal spines can separate each other at the inner edge of septa and, by projecting in the axial cavity, form a parietal papillose axial structure. Endotheca present, made of peripheric dissepiments. Parathecal wall in depth.

Dimensions

Calicular diameter: 25.1 to 26.8 mm – corallite high: 5.9 to 7.1 mm – number of septa: 90 to 96 (96 by extrapolation) – septal density: 3 for 2 mm – septal spines density: 5 to 8 for 5 mm.

Similarities and differences

We have mostly limited our synonymic list to the nominal species *haimei* although it appears that several species usually referred to *Montlivaltia* in Lower Liassic are potential synonyms but the state of the illustrations in the literature does not allow a reliable comparison. We noticed that the syntypes of *Montlivaltia granigera* Fromentel & Ferry, 1866 are heterogeneous in terms of generic assignation.

Family Synastreidae Alloiteau, 1952

Remarks

On the basis of the observation of the type material, we did not notice significant differences between the families Synastreidae and Latomeandridae Alloiteau, 1952. As first revisers, we choose to merge them into Synastreidae because the type material *Synastrea agaricites* is much better preserved.

Genus *Axophyllia* Orbigny, 1849

Species originally included. — Only the type species *A. nantuacensis* Orbigny, 1849.

Type species. — *Axophyllia nantuacensis*, Orbigny, 1849 (Orbigny 1849: 8), by monotypy.

Remarks

Previously, the genus was only known by a single specimen from Landeyron (Ain, France), probably Kimmeridgian. The family attribution is proposed pending a firm comfirmation of the pennular character of septa.

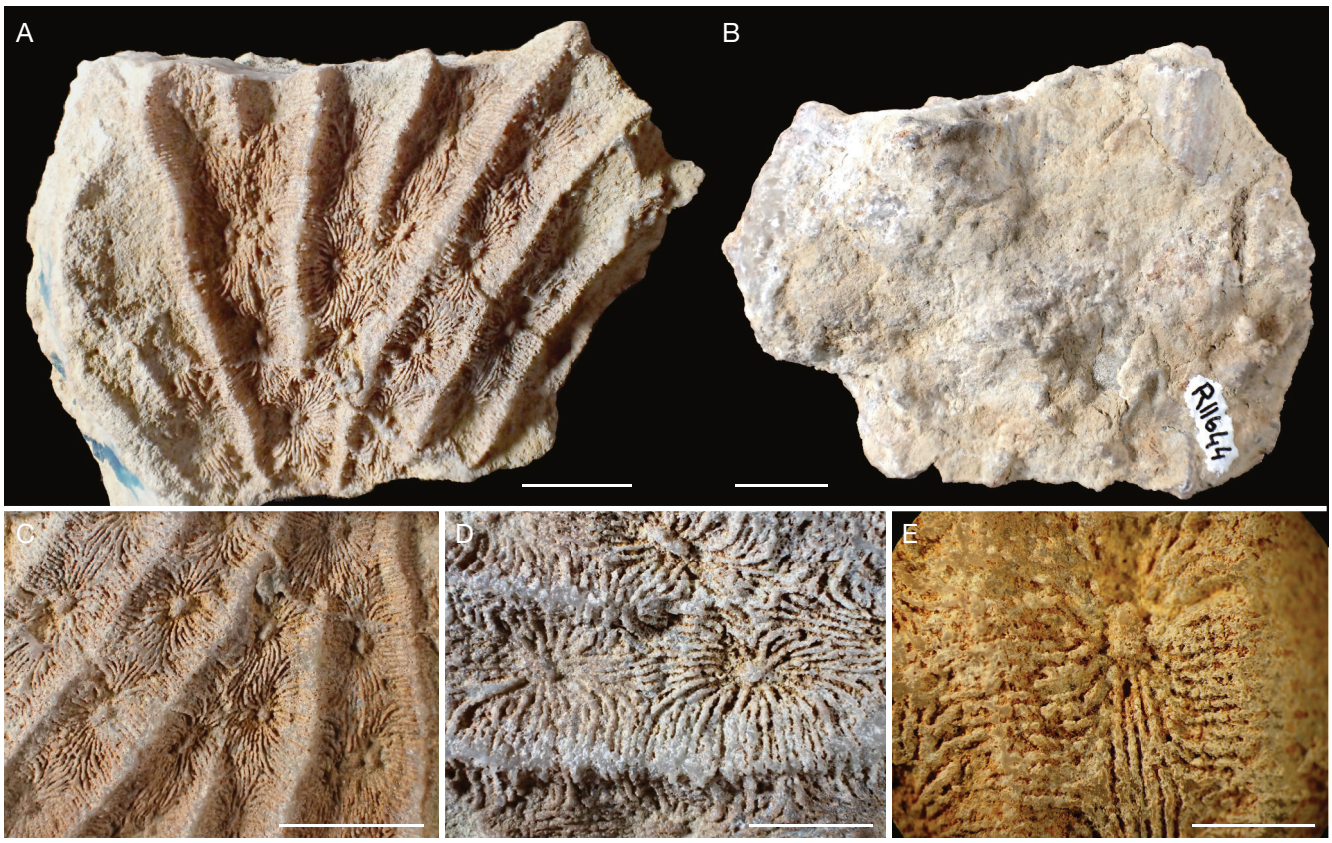

Fig. 31. — *Axophyllia convergens* (Beauvais, 1986), n. comb., holotype MNHN.F.R11644, Toarcian of Moulay Idriss, Morocco: **A**, distal view; **B**, lower side; **C**-**E**, details of upper side. Scale bars: A, B, C, 1 cm; D, 5 mm; E, 2 mm. Photos: R. Vasseur.

Axophyllia convergens (Beauvais, 1986), n. comb.
(Fig. 31)

Microphyllia convergens Beauvais, 1986b: 58, pl. 15, fig. 1.

Microphyllia ? *convergens* – Vasseur 2018: 239, fig. 3.55.

Type material. — **Holotype**. **Morocco** • 1 specimen, piece of colony; Moulay Idriss; 34°6'0"N, 5°30'0"W, coordinate based on nearby landmark; locality 33613 (Paleobiodb); Upper Toarcian (180.1-175.6 Ma), Lower Jurassic; Faugères leg.; MNHN.F.R11644 (coll. L. Beauvais via coll. Faugères no. 237).

Studied sample. — Holotype MNHN.F.R11644.

Amended description
Lamellar meandroid colony without holotheca with straight subparallel, radial series (3 to 5 calices for one series in the observed fragment but obviously more in the original entire colony) regularly forked. Valleys are separated by tectiform collines with no ambulacrum. Intracalicular budding. Valleys septa connect the different calices in one series. Radial elements are straight or curved septa or biseptal sheets, subcompact, sometimes joined, usually confluent from one colline side to the other. Lateral ornamentation of septa present, of unknown nature. Distal edge of septa is moniliform, made of trabeculae regular in diameter and spacing. Trabeculae are externally subvertical and tend to lie down in the internal part of septa, projecting in the space between septa and the protruding parietal spongious or styliform axial structure. Endotheca made of vesicular dissepiments and maybe synapticulae. Wall of unknown nature present.

Dimensions
Calicular diameter: 4.1 to 8 mm – distance between calices centres: 5.6 to 8.5 mm – septal density: 6 for 2 mm –trabecular density: 6 to 8 for 2 mm – diameter of trabeculae: 140 to 230 microns.

Remarks
The generic attribution is changed due to the regular axial structure which is more compatible with the poorly known genus *Axophyllia*. Presently the genus is documented by only two specimens, one from Kimmeridgian (*A. nantuacensis*) and the other from Toarcian (*A. convergens* n. comb.). More material would be necessary, in particular from the interval between these two stages to determine: 1) if there is a phyletic link between these two species; or 2) if these specimens are only extreme variants of *Microphyllia.* The pennular character still needs to be comfirmed on both species.

Genus *Latiastrea* Beauvais, 1964

Species originally included. — *Latiastrea foulassensis* Beauvais, 1964, *L. valfinensis* (Koby, 1885), *L. minima* (Koby, 1885), *L. variabilis* (Etallon, 1859).

Type species. — *Latiastrea foulassensis* Beauvais, 1964 (Beauvais 1964: 255, pl. 37 fig. 1 et text-fig. 52), by original designation, here considered as a junior synonym of *L. minima*.

Remarks

This taxon has a septal morphology similar to *Microphyllia* but differs by its mostly cerioid colonial morphology, shorter and non-radiating rows and a tendency of higher trabecular densities and smaller calices. It also differs from the genus *Latomeandra* that is more phacelo-meandroid and *Guembelastraea* Cuif, 1976 because of its subcompact septa, a trend to submeandroid morphologies for some calices and the presence of axial structures. To finish, it seems to diverge from *Mixastrea* Roniewicz, 1976 and *Comophyllia* Orbigny, 1849 by the lack of lamellar linkages between calices during the intracalicular budding. The genus differs from *Brachyseris* Alloiteau, 1948 (non 1947) that shows strictly confluent septa.

Latiastrea cf. ***minima*** (Koby, 1885) (Fig. 32)

Latimæandra minima Koby, 1885: 242, pl. 63, fig. 4.

Isastrea minima – Ogilvie 1897: 192.

Isastraea cf. *minima* – Felix 1903: 174.

Latimaeandra minima – Koby 1905: 106, pl. 16, fig. 1. — Mirshink 1937: 73.

Isastraea aff. *minima* – Bendukidze 1948: 286; 1949: 85, pl. 8, fig. 5 + txt fig. 8; 1982: 63.

Microphyllia minima – Geyer 1955a: 346; 1955b: 205; 1965: 232. — Frajová 1956: 57. — Lyuleva & Permyakov 1980: 96, pl. 22, fig. 4. — Rosendahl 1985: 60. — Fezer 1988: 88. — Lauxmann & Kapitzke 1991: 3, pl. 2, fig. 1, pl. 3, fig. 1-2. — Nose 1995: 108. — Laternser 2001: 161.

Isastraea minima – Alloiteau 1957: 163. — Zuffardi-Comerci 1959: 227, pl. 2, fig. 7-8. — Bendukidze 1961: 55.

Latiastrea foulassensis Beauvais, 1964: 255, pl. 37, fig. 1, txt-fig 52. — Caratini & Beauvais 1969: 28, pl. 4, fig. 1. — Liao & Xia 1985: 142, pl. 7, fig. 2, 3. — Errenst 1991: 18, pl. 17, fig. 4ab.

Latiastrea minima – Beauvais 1964: 256. — Roniewicz 1966: 244, pl. 20, fig. 1.

Latomeandra minima – Krasnov 1964: 87.

Latiastraea foulassensis [sic] – Beauvais 1975: 114, fig. 25. — Liao & Xia 1994: 103, pl. 19, fig. 1, 2. — Liao & Deng 2013: 119, pl. 51, fig. 3-4.

Latiastraea minima – Eliášová 1990: 126; 2008: 154. — Errenst 1991: 19, pl. 17, fig. 6 a, b.

Latiastrea sp. 1 – Vasseur 2018: 229, fig. 3. 51.

Type material. — **Holotype**. **France** • 1 specimen; Valfin-lès-Saint-Claude (Franche-Comté); 46°26'18"N, 5°51'26"E (based on nearby landmark); Kimmeridgian, Upper Jurassic; Beauvais leg., MNHN.F.R10749.

Studied samples. — CPUN 1603A3E3, 1603A3E4; CPUN 1603A5E3; CPUN 1603A8-1, 1603A8-3, 1603A8-6, 1603A8-7, 1603A8-10, 1603A8-11; CPUN 2603A1-6, 2603A1-7, 2603A1-8, 2603A1-11; CPUN 1603A9-2; CPUN A110; CPUN A113; CPUN A115; CPUN A123; CPUN A125; CPUN A126; CPUN A127; CPUN A128; CPUN A131; CPUN A132; CPUN A133; CPUN A134; CPUN A138; CPUN A139; CPUN A140; CPUN A141; CPUN A142; CPUN ToA1; CPUN DA0206E1-2; CPUN MA1004E4-7; CPUN MA1004E5-12 (35 specimens from Upper Toarcian of Amellagou and Middle/Upper Toarcian of Aïn Leuh).

Description

Cerioid to submeandroid massive colony with polygonal calices multiplying by intracalicular budding. Radial elements are subcompact, straight or slightly curved, free or joined, subconfluent septa. Lateral faces are ornamented with pennulae with edges curved inward and the distal edge hold irregular teeth. Trabeculae at inner edges of septa sometimes project in the axial cavity, forming a papillose to spongy axial structure. A true essential styliform columella has been observed in the calices of one single specimen (CPUN 2603A1-11). However, some other specimens seem to show variable essential axial structures joined by first order septa in depth. The obvious important intraspecific variability in this taxon led us to include the specimen with styliform columella. Endotheca made of vesicular dissepiments. Synapticulae present. Wall of unknown nature, no epitheca.

Dimensions

Calicular diameter: 2 to 10 mm – septal density: 8 to 15 for 2 mm – trabecular density: 6 to 16 per 2 mm.

Similarities and differences

We do not see any morphological difference between our samples and the type material of the species. However, we introduce the cf. to draw the attention on the large gap between our Toarcian specimens and the Kimmeridgian ones.

L. bendukidzeae Lebanidze, 1991and *L. pakongensis* Liao & Xia, 1985 are similar in morphometric values but further investigations are necessary to establish a firm synonymy (as junior synonyms).

L. variabilis (Etallon, 1859) is anterior but shows a lower septal density as well as *L. greppini* (Koby, 1885), *L. goldfussi* (Koby, 1885), *L. somaensis* (Eguchi, 1951) and *L. tosaensis* (Eguchi, 1951).

The Cretaceous *L. mucronata* Sikharulidze, 1979 was discarded because of its non pennular septal structure.

The variabilities of *L. foulassensis* the type species and *L. minima* overlap, this is the reason why we place the latter as a senior synonym.

Genus *Latomeandra* Orbigny *in* Edwards & Haime, 1849

Latomeandra Orbigny *in* Edwards & Haime, 1849: 271.

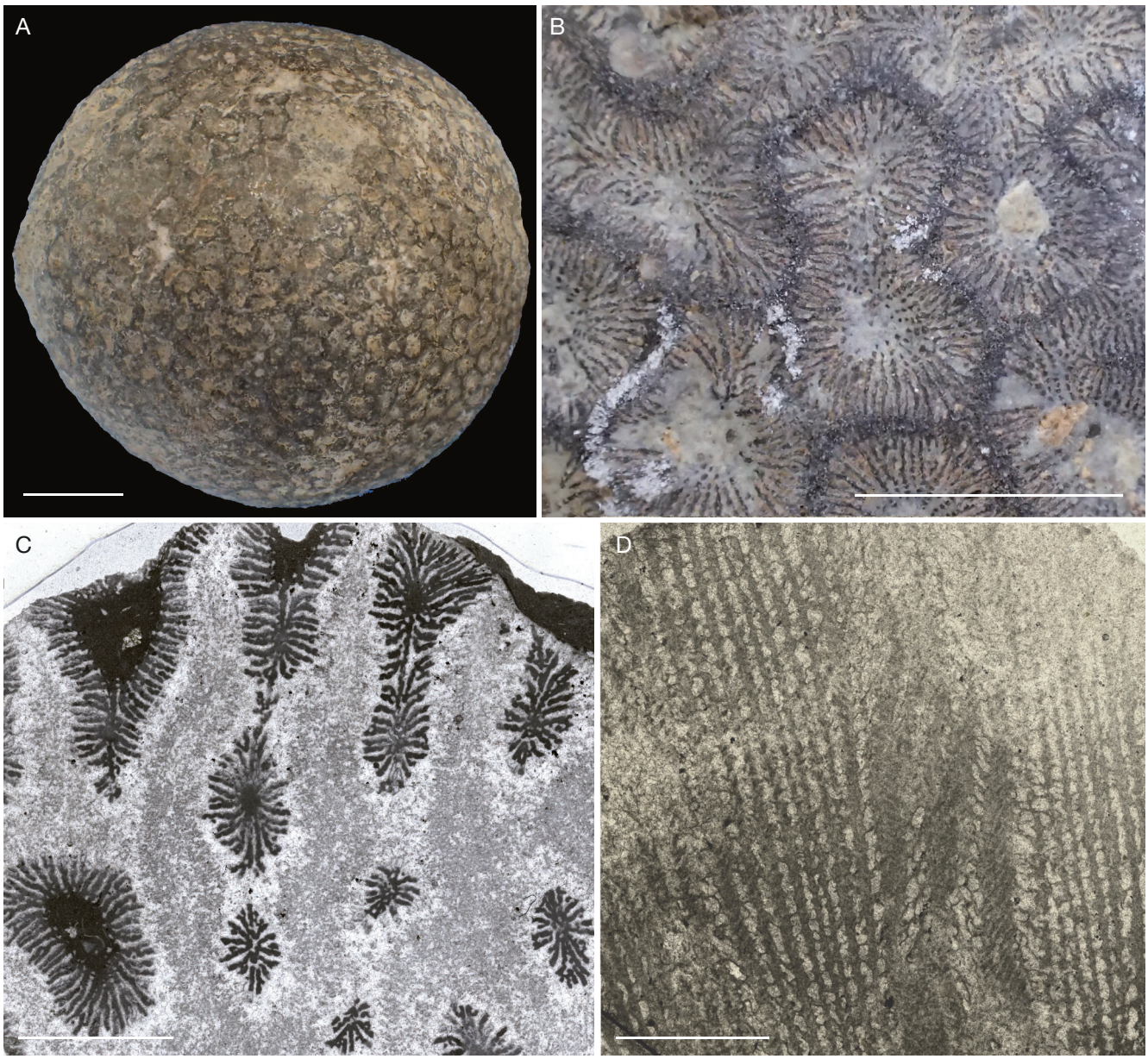

Fig. 32. — *Latiastrea* cf. *minima* (Koby, 1885), Upper Toarcian of Amellagou, Morocco: **A**, distal view of the specimen CPUN 1603A8-1; **B**, detail in distal view of the specimen CPUN 1603A8-1; **C**, detail in transverse thin section of the specimen CPUN 1603A8-3; **D**, detail in longitudinal thin section of the specimen CPUN 1603A8-11. Scale bars: A, 2 cm; B, C, 5 mm; D, 3 mm.

Species originally included. — *Lithodendron plicatum* Goldfuss, 1826, *L.* ?*ataciana* (Michelin, 1847), *L.* ?*corrugata* (Michelin, 1843), *L.* ?*raulini* (Michelin, 1843), *L.* ?*edwardsii* (Michelin, 1843), *L.* ?*soemmeringii* (Goldfuss, 1829).

Type species. — *Lithodendron plicatum* Goldfuss, 1826 (Goldfuss 1826: 45, pl. 13, fig. 5), by monotypy (ICZN art 68.3).

Remarks

We choose to keep *Latomeandra* as a morphogenus separate from *Microphyllia* and *Latiastrea. Microphyllia* is used for massive meandroid forms with elongated valleys, *Latiastrea* corresponds to cerioid morphologies with incipient, short valleys. In the literature, nominal species (nearly 100 species of *Latomeandra*) are still often wrongly classified as many authors have followed Koby's concept in which *Latomeandra* (current usage) is named *Chorisastraea* Fromentel, 1861 and *Microphyllia* (current usage) is named *Latomeandra.* We use *Latomeandra* here for phacelo-meandroid colonial morphologies never forming long valleys nor massive colonial structures. In this respect, we also see a difference with *Stibastrea* Etallon, 1859, a poorly known genus in which long valleys are separated from each other by elongated grooves without any isolated calices. The distinction between *Latomeandra* and *Microphyllia* seems stable enough to be used however we do not discard the possible occurrence of transient forms such as *L. mayeri* Koby, 1885. We could not formally reattribute all the nominal species because the documentation of fine structures is generally insufficient to back reliable generic attributions.

Latomeandra cf. ***plicata*** (Goldfuss, 1826)
(Fig. 33)

Lithodendron plicatum Goldfuss, 1826: 45, pl. 13, fig. 5 — *pars* Quenstedt 1856: 711, pl. 87, fig. 2 *non* 1.

Caryophyllia plicata – Blainville 1830: 312. — Lamarck 1836: 358.

Cladocora plicata – Geinitz 1846: 570.

Astrea goldfussana – Bronn 1848: 126.

Latomeandra plicata – Edwards & Haime 1849: 271; 1851b: 85. — *pars* Vaughan & Wells 1943: 119, *non* pl. 10, fig. 14. — Alloiteau 1952: 672, pl. 6, fig. 4; 1957: 238, 315. — Geyer 1954: 147, pl. 10, fig. 13; 1955a: 346. — Wells 1956: 380, fig. 269-6. — Beauvais 1964: 246, pl. 34, fig. 7. — Lambelet 1968: 166. — Meyer 1983: 6, fig. 35-37. — Rosendahl 1985: 58. — Fezer 1988: 88. — Bertling 1993: 99, pl. 4, fig. 11-13. — Nose 1995: 108. — Laternser 2001: 161, pl. 12, fig. 14. — Helm *et al.* 2003: 82. — *non* Pandey & Fürsich 2003: 82, pl. 24, fig. 4. — Helm 2005: 104, pl. 31, fig. 2.

Latimeandra plicata – *pars* Edwards & Haime 1857: 544. — Etallon 1859: 511/111. — Bölsche 1866: 449, pl. 7, fig. 3.

Chorisastrea plicata – Fromentel 1861: 163; 1865: 18. — Speyer 1926: 266.

Cladophyllia grandis – ?Bölsche 1866: 448.

Latimaeandra plicata – Brauns 1874: 23. — Struckmann 1878: 26.

Chorisastrea dubia pars Becker, 1875: 161, pl. 39, fig. 7, 8.

Rhabdophyllia disputabilis Becker, 1875: 151.

Thecosmilia irregularis – Struckmann 1878: 26. — *pars* Speyer 1926: 262.

Chorisastraea caquerellensis Koby, 1885: 218, pl. 64, fig. 1-9; 1905: 102, pl. 24, fig. 7.

Chorisastrea crassa Koby, 1885: 219, pl. 64, fig. 10-18.

Chorisastraea cf. *caquerellensis* – Speyer 1926: 267.

Lithodendron plicatum – Klopfer 1974: 74.

Latomeandra sp. – Lathuilière 2011: 539, pl. 11, fig. 10-11. — Vasseur 2018: 231, fig. 3.52.

Type material. — **Lectotype**. **Germany •** 1 specimen; Gingen; 48°39'35"N, 9°46'57"E (based on nearby landmark); Kimmeridgian, Upper Jurassic; Goldfuss Leg.; BIOB-PB-Goldfuss-157.

Studied samples. — CPUN DA2705E4-1, DA2705E4-3, DA2705E4-11, DA2705E4-13, DA2705E4-14, DA2705E4-15, CPUN DA2805E3, CPUN MA0804E2-2, batch CPUN MA1004E3-3, CPUN MA1004E4-4 (13 specimens from Toarcian of Dades Valley and Aïn Leuh, Morocco).

Geographic and stratigraphic ranges. — Toarcian of Morocco and Upper Jurassic of Germany, Switzerland, Portugal and France.

Description
Phacelo-meandroid colony with calices of variable rounded shapes multiplying by intracalicular budding. Radial elements are subcompact, straight or curved, free or joined, subconfluent septa. Septa of valley present. Lateral faces of septa hold pennulae with inward curved edges and the distal edge shows irregular teeth decreasing in diameter from the periphery to the axis of the calix. Trabeculae of septa sometimes project in the axial cavity forming a papillose to spongy parietal axial structure. However, some specimens show in depth essential axial structures of variable shape joined with some first-order septa. Endotheca made of vesicular dissepiments. Synapticulae present. The coral exhibits neither an epitheca sensu stricto nor a pennular envelope as defined by Gill (1967), since the trabeculae are never oriented outward, regardless of their proximity to the periphery. However, a common primary wall encloses the colony constituted by the thickening of outer edges of septa. Macroscopically in external view, very thin radial elements can be distinguished by contrast locally, but they do not appear as a relief in transverse thin section. Regular growth bands appear on some samples, allowing the measure of presumed annual vertical growth rates (see below).

Dimensions
Calicular diameter: 4 to 13 mm – septal density: 6 to 8 for 2 mm – trabecular density: 5 to 7 for 2 mm – vertical growth rate: 2.5 mm per year.

Similarities and differences
Dimensions are compatible with the Kimmeridgian species *L. plicata* , the type species of the genus, and many other nominal species from Upper Jurassic including nominal species that are still in the junior synonym genus *Chorisastraea* (*C. crassa* Koby, 1885 and *C. elegans* Koby, 1885). However there is no documented *Latomeandra* with these shape and dimensions between Toarcian and Oxfordian. *Stibastrea structa* Gregory, 1900, *S. paeninsula* Gregory, 1900 and *S. felixi* Hoppe, 1922 are possible synonyms but these Bathonian taxa are poorly described especially in their septal structure and show singular morphological characters with independent valleys forming lobes without isolated calices. In addition we did not detect any form of strict *Latomeandra* colonial morphologies during the Bathonian – Callovian interval (the generic attribution of *L. plicata* in Pandey & Fürsich (2003) is much more probably a *Rhabdophyllia* Edwards & Haime, 1851, strictly phaceloid with distinct costae and wavy septa). *L. richei* (Koby in Riche, 1893) has no pennular structure and is not a *Latomeandra* according to Lathuilière (2000b) (maybe *Paraphyllogyra* Beauvais, 1970c ?). For all these reasons, we attribute these specimens to *L. plicata*, with a cf. considering the time gap between our Liassic specimens and the Late Jurassic ones and a slightly higher trabecular density in the type species *L. plicata.*

Genus *Microphyllia* Orbigny, 1849

Species originally included. — Only the type species.

Type species. — *Meandrina soemmeringii* Münster *in* Goldfuss, 1829 (Goldfuss 1829: 109, pl. 38, fig. 1), by monotypy (Orbigny 1849: 8).

Remarks
We have tried to give a stable and appropriate name for the pennular meandroid Toarcian corals under study. In this perspec-

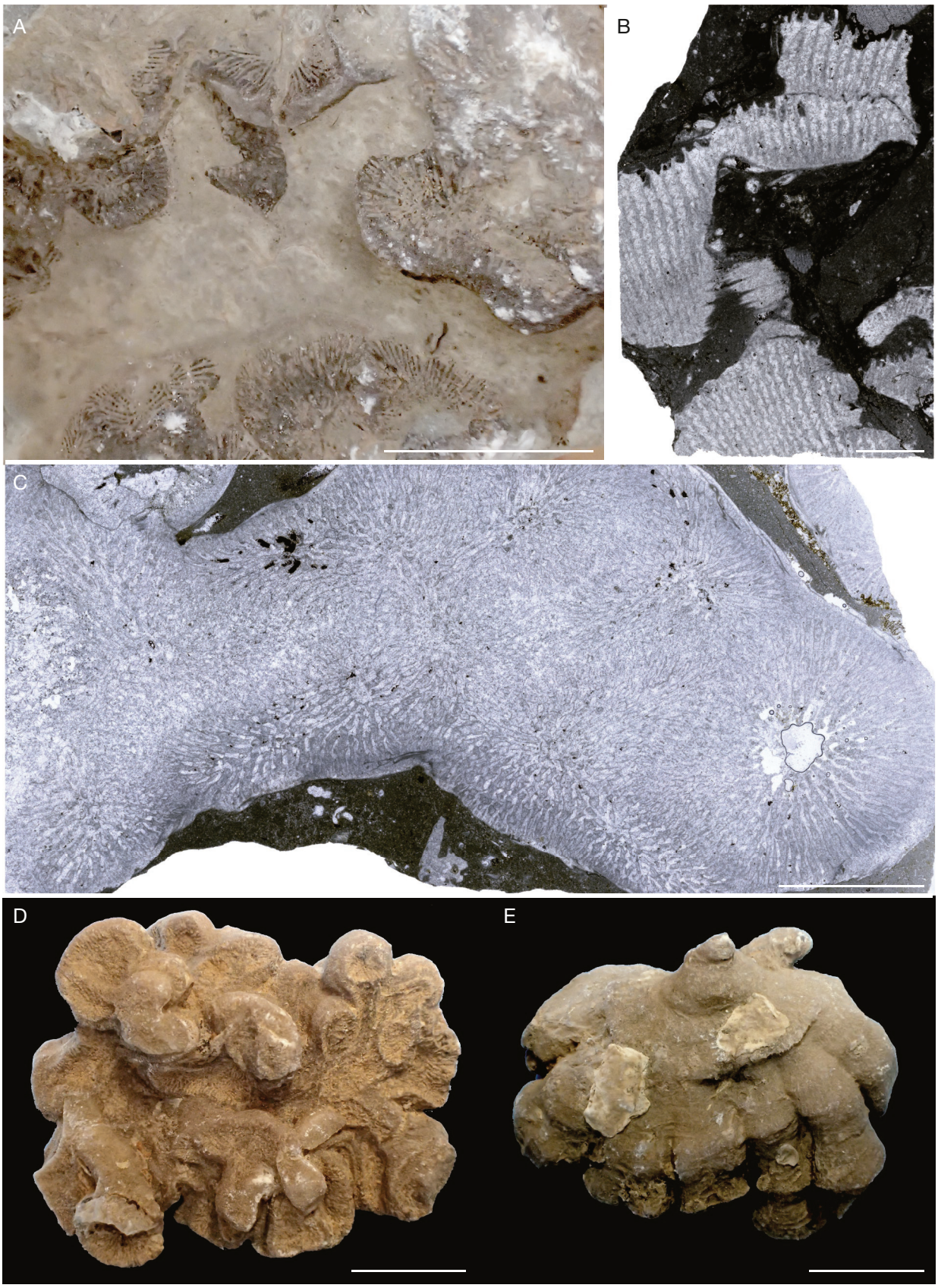

Fig. 33. — *Latomeandra* cf. *plicata* (Goldfuss, 1826), Toarcian of Dades Valley, Morocco (**A**, **B**, **C**) and Middle/Upper Toarcian of Aïn Leuh, Morocco (**D**, **E**): **A**, distal view of the specimen CPUN DA2705E4; **B**, detail in longitudinal thin section of pennular septal structure of the specimen CPUN DA2705E4-15; **C**, transverse thin section in the specimen CPUN DA2705E4-11; **D**, distal view of one of the specimens from the batch CPUN MA1004E3-3; **E**, proximal view of one of the specimens from the batch CPUN MA1004E3-3. Scale bars: A, D, E, 1 cm; B, 2 mm; C, 5 mm. Photos: R. Vasseur.

tive, we analysed a significant set of citations belonging to 104 nominal Jurassic species. The back and forth of species between various genera led us to analyse more closely the characters and their variation that allowed (rightly or wrongly) the definition of species and genera. Under our scope the following genera and their belonging species have been considered: *Latomeandra*, *Latiastrea*, *Microphyllia*, *Comophyllia*, *Collignonastraea* Alloiteau, 1958, *Kobymeandra* Alloiteau, 1953, *Axophyllia* and *Brachyseris*.

Considered characters and their stability

Valleys short (few corallites) vs long (more than three corallites). This character shows sometimes transitional character state, especially between the centre of colonies and their periphery. However, the transition is exceptional enough to maintain the distinction between *Latiastrea* and *Brachyseris* which never have long valleys and *Microphyllia* and other considered genera having both short and long valleys.

Valleys detaching as branches vs remaining contiguous. This character shows exceptionally transient characters but seems stable enough to justify the distinction of *Latomeandra* among other genera. The case of *Stibastrea*, a genus based on *Stibastrea edwardsi* Etallon, 1859, known only by the plaster cast of its holotype by monotypy (MNHN.F.A32303) is precisely a transient morphology. It shows detached corallites in the centre of the colony and detached valleys at the periphery. Another transient genus is *Gyrodendron* Quenstedt, 1880. The type material consists of a small colony with valleys choked and non-contiguous at the periphery but still attached to the mother corallite. We consider both situations as extreme variations for *Latomeandra*. In the ancient literature, the genus *Latomeandra* included many massive species that have been or still need to be reclassified.

Valleys radial vs concentric. This character seems to be solid. All the considered genera seem to have radiating collines and valleys open at the periphery of the colony at least at young stages. We found no evidence of concentric series in the genera under study here.

Valleys radial vs complex and meandering. This character was put forward to distinguish *Collignonastraea* and *Comophyllia* (not initially but subsequently) from other genera. The topotypes of *Collignonastraea jumarensis* Gregory, 1900, the type species of the genus, reveal that all the intermediates exist between colonies clearly arranged in radiating valleys and more complex meandering valleys that occupy in priority the centre of the colony. It seems that this character is highly dependent of the astogenic stage. As a consequence, in Bathonian species, which are often small and limited in size (and probably in age ?), the paedomorphic radiating pattern is well expressed, and the genus *Collignonastraea* has been widely used in this stage for this reason. However, even in the Bathonian which is well documented in Kachchh, the transitional character is obvious for various authors (Gregory 1900; Pandey & Fürsich 1993; Pandey *in* Corallosphere, observations of the present authors on collected samples from Kachchh). The recent *Mycetophyllia lamarckiana* Edwards & Haime, 1848 figured by Zlatarski & Martinez Estalella (1982) displays a very similar and even wider variation of patterns in one single species.

Valleys monoserial vs multiserial. In the width of a valley, either a single corallite or several corallites arranged in a thamnasterioid pattern are observed. The character varies up to situations in which valleys are extremely wide and large portions of the colony appears to be thamnasterioid. A transitional character was observed in places where radiating valleys are dividing. It seems that some species have various constructional rules in this respect, some admit no exception to the monoserial rule, and some others admit exceptions restricted to this special place. In *Microphyllia soemmeringii* as well as in *Collignonastraea jumarensis* we observed two corallites within the enlarged valley at this place. The regular multiserial character state is considered significant to characterize the genus *Comophyllia*. It was proposed as a significant distinctive character in the short initial diagnosis of Orbigny (1849: 9).

Collines with confluent vs non-confluent (or at random) radial elements. Among the genera under consideration, the random organisation of confluence is the rule and this character state is a solid way to distinguish them from *Brachyseris* in which radial elements are confluent.

Axial structure absent (fossa) vs. parietal vs. styliform. Some rare species have a regular presence of fossa, e.g. *Comophyllia polymorpha* (Koby, 1907). Some other rare species have a stable styliform columella, e.g. *Axophyllia nantuacensis*. Most other forms of pennular meandroid corals show an axial cavity in which the detachment of the inner edges of septa creates a non-discrete structure, which shows significant variations among the corallites of a single colony.

Lamellar linkage (or valley septum) present vs absent. This character probably deserves the attention of taxonomists because it has a functional significance in terms of polyp integration. We would like to draw the readers' attention to the fact that the continuity of the valley interseptum is more important than that of the valley septum, as it facilitates the sharing of metabolites between the polyps. This valley interseptum (sometimes there are two) is preserved from junctions with septa that are attached to the collines. It seems that the lamellar linkage is present in *Comophyllia*. In *Collignonastraea* the lamellar linkage is the rule but this rule finds a limit when a valley is closing upstream by the growth of a new wall. The lamellar linkage is present in *Microphyllia* at least in the small piece of colony of its type specimen. Its distribution in the type species and the species of the genus is not well documented.

Trabecular density low vs high. Among the specimens under study, the trabecular density contributes to their specific distinction in association with other characters. The measure of this value is absent in most available descriptions in the literature.

Generic frame resulting from these considerations

Axophyllia is kept apart for its styliform columella.

Brachyseris has short valleys and confluent septa on collines.

Collignonastraea was created by Alloiteau (1958) based on *C. jumarensis*, with the following characters to differentiate the new genus from *Microphyllia*: 1) open valleys; 2) discontinuous collines; and 3) circumoral budding at the beginning of *Collignonastraea* when the first stages are not observed in *Microphyllia*. The type specimen of *Microphyllia soemmeringii*

(the type species) is a fragment of colony with radiating valleys and collines and nothing allows us to think that the general organisation of valleys is different from *Collignonastraea*. Concerning the first stages, in the population of *Collignonastraea* of Kachchh, which shows a wide variability, the initial stage of circumoral budding is not always observed. *Collignonastraea* has generally uniserial valleys and admits two corallites in a valley width only at the confluence of valleys. For this reason we consider here *Collignonastraea* as a junior synonym of *Microphyllia* that can be differentiated from *Comophyllia* by its ordinary uniserial valleys.

Comophyllia was based on *Comophyllia elegans* Orbigny, 1849 as an independent genus characterised by wide valleys with several corallites in the width of a valley, having a thamnasterioid organisation. The lectotype MNHN.F.A09634 is not excellently preserved.

Latiastrea is distinguished from *Microphyllia* by the rapid growth of collines producing very short valleys. Pending a population study, we keep these two genera separate.

Latomeandra is distinguished from *Microphyllia* by its mode of growth producing mono or polycentric phaceloid branches or isolated valleys. *Gyrodendron* is considered a young astogenic stage of *Latomeandra* in which only separated valleys are present. *Jugodendron* Quenstedt, 1880, *Illinodendron* Quenstedt, 1880 and *Stibastrea* are considered junior synonyms.

Microphyllia is distinguished from *Latomeandra* by its massive structure, from *Latiastrea* by its capacity to produce long valleys (more than three corallites). It is distinguished from *Comophyllia* by the general rule of uniserial valleys that find exceptions only at the confluence of valleys. It is distinguished from *Axophyllia* by its axial structure which is variable and parietal in nature. It differs from *Brachyseris* by its non-confluent radial elements and longer valleys.

Collignonastraea is considered here as a junior synonym of *Microphyllia*.

Edwardsoseris Alloiteau, 1948 is considered a junior synonym of *Microphyllia* (Lathuilière *in* Cairns *et al.* 2012).

Kobymeandra is considered a junior synonym of *Microphyllia*.

Microphyllastraea Alloiteau, 1955 based on *Microphyllastraea karrenbergi* Alloiteau, 1955 in Basse *et al.*: 676, pl. 28, fig. 2, 5; is poorly known (holotype by monotypy lost) and possibly a synonym of *Microphyllia*.

The Triassic genus *Stuoresia* Cuif, 1976 and the Liassic *Eomicrophyllia* Melnikova & Roniewicz, 2021 belong to Tropiastraeidae Cuif, 1977, a family initially characterised by continuous menianae in the sense of Gill (1967). However, there is no evidence of continuous menianae in *Eomicrophyllia* published images. In addition, Melnikova & Roniewicz (2021) created the genus *Eomicrophyllia* within the Tropiastreidae on the basis of pennular edges directed upward in contrast to *Microphyllia* which is considered a Latomeandridae by Morycowa & Roniewicz (1995), a family merged with Synastreidae in the present work. Our appreciation of the variability of the character of pennular edges directions in *Microphyllia* (even in the type species *Microphyllia soemmeringii*) leads us to consider it a weak character to discriminate *Microphyllia* from *Eomicrophyllia*. For those reasons, *Stuoresia* and *Eomicrophyllia* are left apart in the present discussion.

Highly porous genera such as *Comoseris* Orbigny, 1949 (and its junior synonyms *Meandraraea* Etallon, 1859 and *Latimaeandraraea* Fromentel, 1861) and *Microphyllopsis* Beauvais, 1966 are also not considered in the present discussion.

Microphyllia cf. ***soemmeringii*** (Münster *in* Goldfuss, 1829) (Fig. 34)

Meandrina soemmeringii Münster *in* Goldfuss, 1829: 109, pl. 38, fig. 1.

Microphyllia soemmeringi – Beauvais 1964: 248, pl. 34, fig. 6.

cf. *Microphyllia soemmeringi* – Errenst 1991: 16, pl. 17, fig. 1 a, b.

Microphyllia irregularis – Beauvais 1986b: 57, text fig. 32 — Vasseur 2018: 242, fig. 3.56.

Microphyllia sp. 2 – Lathuilière 2011: 542, pl. 3, fig. 5-9.

TYPE MATERIAL. — **Syntype. Germany •** Syntype erroneously designated as a neotype in Beauvais (1964) IPB 291(Goldfuss collection); Nattheim; 48°42'0"N, 10°11'59"E (based on nearby landmark); Upper Kimmeridgian, 154.8-149.2 Ma, Upper Jurassic; number of specimens in the initial type series unknown; the localities mentioned by Goldfuss are Nattheim, Heidenheim, and Basel; Münster Leg.

STUDIED SAMPLES. — MNHN.F.C05036 (coll. L.Beauvais via coll. Du Dresnay), CPUN MAM15 (coll. S.Elmi), CPUN MA0804E2-1, CPUN MA0804E2-5, CPUN MA1004E4-3, CPUN MA1004E4-16, CPUN 2603A1-6, CPUN 1603A8-12, 1603A8-13, 1603A8-15 from Middle and High Atlas of Morocco.

DESCRIPTION

Massive, decimetric meandroid colony without holotheca, with calicular series of variable shape and length (2 to 10 calices for one series), regularly dichotomous. Valleys are separated by tectiform collines with no ambulacrum. Valleys septa connect the different calices in one series. Radial elements are straight or curved septa or biseptal sheets, subcompact, sometimes joined, and subconfluent from one colline side to the other. Lateral faces show pennulae with pennular rims oriented inward. Trabeculae irregular in diameter and spacing, providing a coarse and irregular beaded aspect to the distal edge. Astonishingly high variations of the septal densities have been measured in one single specimen (MNHN.F.C05036), preventing to split our specimens into several species. Trabeculae are externally subvertical and tend to lie down in the internal part of the septa, forming a parietal columella variable in shape according to the corallite centres in the colony, sometimes papillose, sometimes styliform. Endotheca made of vesicular dissepiments. Synapticulae present. A wall is present but its nature cannot be defined clearly.

DIMENSIONS

Calicular diameter: 3.2 to 8.2 mm – distance between calices centres: 3.7 to 6.5 mm – septal density: 10 to 25 for 5 mm – trabecular density: 3 to 6 for 2 mm – diameter of trabeculae: 170 to 570 micrometers.

Similarities and differences

We observed in one single specimen (MNHN.F.C05036) from Beauvais' collections an amazingly high heterogeneity in septal densities (10 to 25 per 5 mm) among the different valleys. We first hypothesized a potential control of somatic mutations or the case of a pseudocolony made by several planulae but then measured such septal density discrepancies within a single valley. Consequently, we consider now that this is a normal variability of the species at least for its Toarcian representatives. This high variability is in agreement with measurements provided by Beauvais (1986b: 57). The values vary in a range of ± three septa per 2 mm within a valley for Du Dresnay and Faugères specimens. Koby's original material seems more stable with a range of variation of only ± one septum per 2 mm according to the dimensions measured by Beauvais (1986b).

Remarks

These specimens were attributed to the Oxfordian species *M. irregularis* Koby, 1885 in Vasseur (2018) following Beauvais (1986b) who already attributed her Toarcian specimens to this species. Further investigations reveal that many other nominal species could correspond, including the Kimmeridgian type species of *Microphyllia.* We found no Liassic equivalent in the reviewed nominal species (including *Eomicrophyllia nalivkini* Melnikova & Roniewicz, 2021, smaller in size and with higher septal densities). A more detailed study of the variability of the group during the Jurassic times is necessary. Attributing a stable name depends on our capacity to describe the variability of taxa in the successive stages. For now, the literature does not allow us to document precisely enough the variability during the Dogger. For these reasons, we use a cf. before the specific attribution and keep a short list of synonyms.

Microphyllia sp.
(Fig. 35)

Microphyllia sp. 1 – Lathuilière 2011: 542, pl. 3, fig. 10. — Vasseur 2018: 245, fig. 3.57.

Studied samples. — **Morocco •** 2 specimens; Aïn Leuh (Middle Atlas), Couches d'Al Yabès; 33°11'32"N, 5°21'8"W; PaleoDB collection 233562; Middle/Upper Toarcian, interval Gradata zone, Gemma subzone up to Meneghini zone, Lower Jurassic; Elmi Leg.; CPUN MAM13, MAM14.

Description

Massive meandroid colony without holotheca, with straight subparallel, radial series (3 to 5 calices for one series in the observed fragment) opened and dichotomous. Valleys are separated by tectiform collines without ambulacrum. Intracalicular budding. In one single series, the different calices are connected by valley septa. Radial elements are straight or curved, subcompact, sometimes joining septa or bisepta. Confluence is difficult to establish from one side to the other of one single colline. Lateral faces of septa are pennular. Trabeculae are externally subvertical and tend to lie down in the internal part of the septa. Consequently, pennular rims point toward the axis of the corallite in transverse section. Parietal axial structure of undefined nature, made of joining septa. Endotheca made of vesicular dissepiments. Synapticulae present. The nature of the wall is unknown.

Dimensions

Calicular diameter: 4 to 9 mm – distance between calices centres: 3.5 to 9.9 mm – septal density: 7 for 2 mm – trabecular density: 7 to 10 for 2 mm.

Similarities and differences

Differs from other Liassic species by its lower average septal densities and its higher trabecular densities.

Genus *Periseris* Ferry, 1870

Species originally included. — *Agaricia elegantula* Orbigny, 1850, *Thamnastraea cistela* Edwards et Haime, 1849.

Type species. — *Agaricia elegantula* Orbigny, 1850 (Orbigny 1850: 293), by original designation (Orbigny 1850: 199).

Remarks

A possible synonymy with the Triassic genera *Thamnasteriamorpha* Melnikova, 1971 and *Thamnotropis* Cuif, 1975 is still to be investigated.

Periseris elegantula (Orbigny, 1850)
(Fig. 36)

Agaricia elegantula Orbigny, 1850: 293.

Periseris elegantula – Lathuilière 1990: 38, pl. 1-5, *cum syn*. (50 references); 2000b: 157, fig. 13.1-13.2. — Pandey & Fürsich 1993: 37, pl. 11, fig. 2, text-fig. 22; 2003: 94, pl. 28, fig. 1-6; ?2006: 65, pl. 5, fig. 4-7. — Morycowa & Mišík 2005: 430, fig. 8.1-4. — Vasseur 2018: 277, fig. 3.70.

Periseris sp. – Lathuilière 2011: 540, pl. II, fig. 5-9.

Type material. — **Lectotype**. **France •** 1 specimen; Langres, Haute Marne; 47°52'0.59"N, 5°20'3.47"E (based on nearby landmark); Bajocian (Middle Jurassic); MNHN.F.A26574.

Studied samples. — CPUN DA0106E1-1; CPUN DA0106E3-1; CPUN DA0106E3-3 from Lower Toarcian (*Polymorphum* zone) of Dades Valley (High Atlas, Morocco).

Description

Flattened subhemispheric thamnasterioid corallum (14 to 38 mm in size). Radial elements are subcompact (upward) to compact (in-depth), pennular septa or biseptal sheets sometimes joined and often sinuous. Distal edge with regular small teeth, which diameter decrease from the periphery to the centre of the calix. Pennular rims turned upward and alternating from a septum to the neighbouring one. Styliform columella in depth. Endotheca present, made of numerous dissepiments. Synapticulae present. Epitheca present on the lower side of the colony.

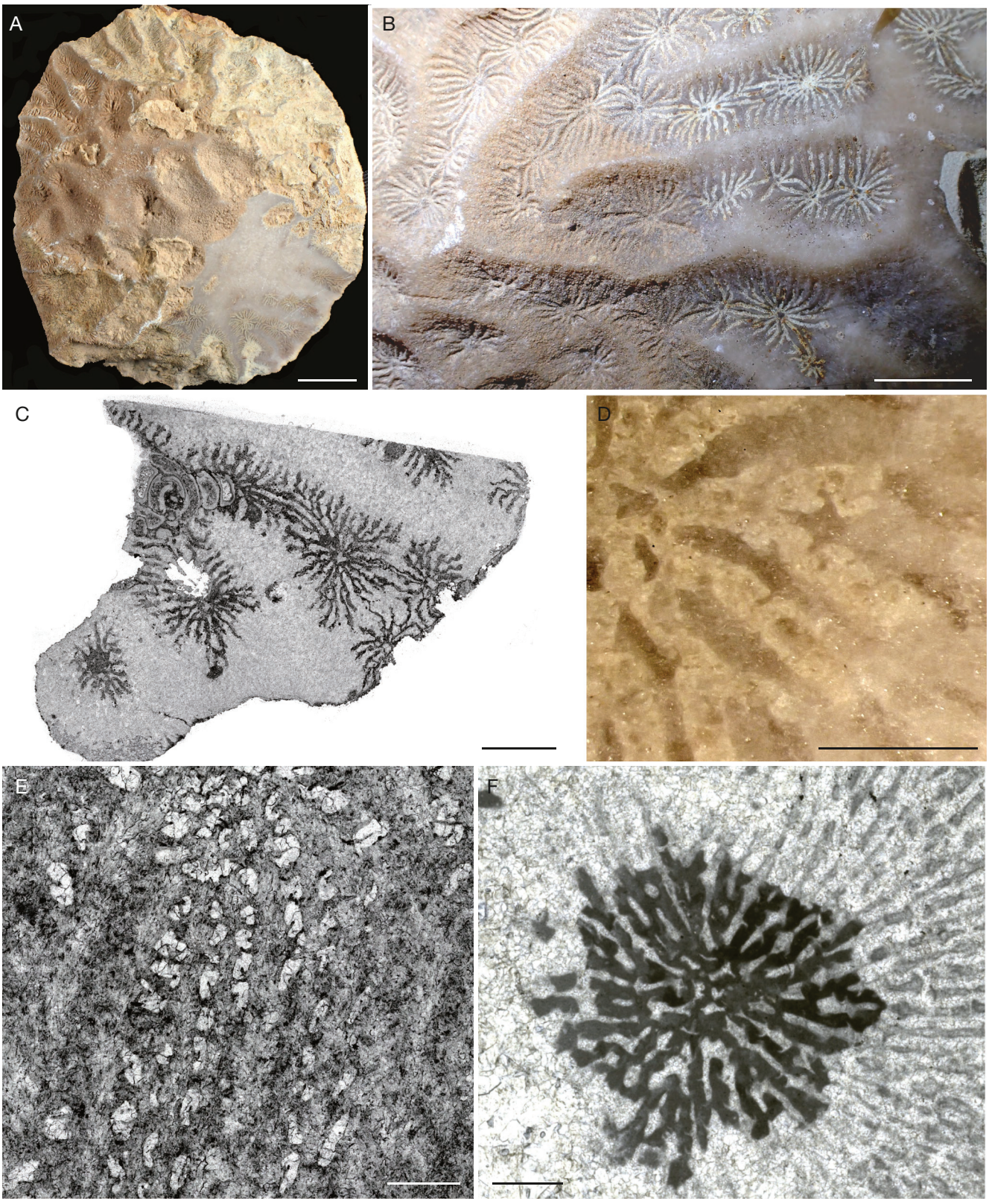

Fig. 34. — *Microphyllia* cf. *soemmeringii* Münster *in* Goldfuss, 1829, Upper Lias of Oued Ifar, Morocco (**A**, **D**, **E**), Middle/Upper Toarcian of Aïn Leuh, Morocco (**B**, **C**) and Upper Toarcian of Amellagou, Morocco (**F**): **A**, distal view of the specimen MNHN.F.C05036; **B**, distal view of the specimen CPUN MA1004E4-3; **C**, transverse thin section of the specimen CPUN MAM15; **D**, detail of pennular septal structure in transverse section of the specimen MNHN.F.C05036; **E**, detail in longitudinal thin section of pennular septal structure in the specimen MNHN.F.C05036; **F**, detail in transverse thin section of one calice of the specimen CPUN 2603A1-6. Scale bars: A, 1 cm; B, 5 mm; C, 4 mm; D, E, F, 1 mm. Photos: R. Vasseur.

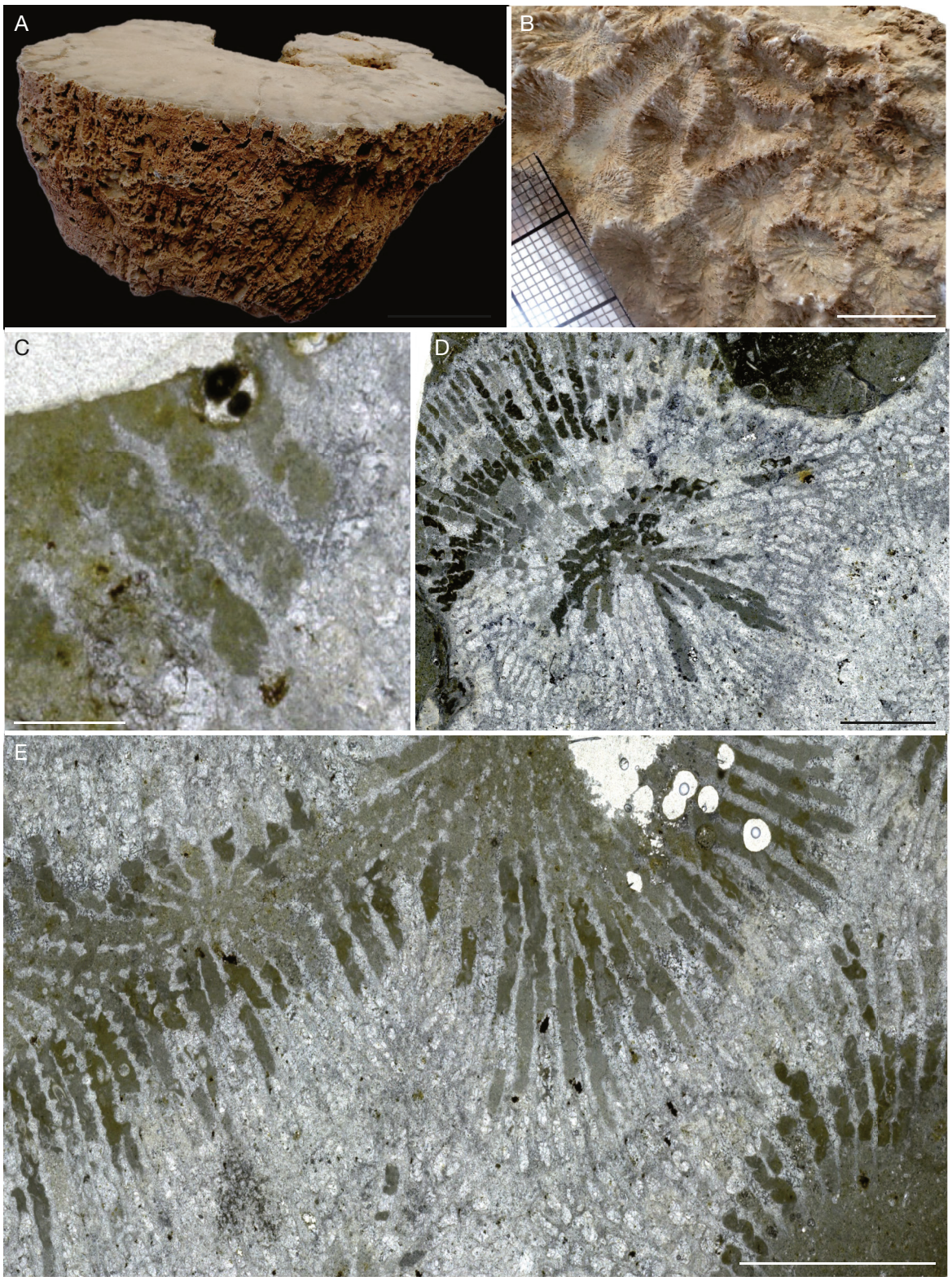

Fig. 35. — *Microphyllia* sp. 1, Middle/Upper Toarcian of Aïn Leuh, Morocco: **A**, specimen CPUN MAM 14. General view; **B**, detail in distal view of the specimen CPUN MAM 13; **C**, detail in longitudinal thin section of pennular septal structure of the specimen CPUN MAM 13; **D**, detail in transverse thin section of the specimen CPUN MAM 14; **E**, detail in transverse thin section of the specimen CPUN MAM 14. Scale bars: A, 3 cm; B, 2 cm; C, 0.5 mm; D, 2 mm; E, 3 mm. Photos: R. Vasseur.

Dimensions

Calicular diameter: 2.5 to 4 mm – distance between calices centres: 2.5 to 4 mm – number of septa: approximately 20 – septal density: 6 to 7 for 2 mm.

Similarities and differences

The specimen named *Periseris* sp. in Lathuilière (2011) differs a little by its smaller and closer calices, higher values of septal densities and by the presence of holotheca. Considering

the intraspecific variability described by Lathuilière (1990), only the last character appears significant to distinguish the two Toarcian taxons. Given that the specimen without holotheca is relatively badly preserved, we cannot exclude the possibility of a post-mortem loss of holotheca by erosional processes. Then, we choose here to describe all the samples together under the same single species pending a more significant sampling.

Genus *Synastrea* Edwards & Haime, 1848

SPECIES ORIGINALLY INCLUDED. — *Astrea agaricites* Goldfuss, 1826.

TYPE SPECIES. — *Astrea agaricites* Goldfuss, 1826, by monotypy.

REMARKS

The traditional distinction between the genera *Synastrea* and *Dimorphastrea* Orbigny, 1850 is based on the circumoral gemmation which appears to us as a labile character regarding the studies on microsolenid genera *Dimorpharaea* and *Microsolena* (Pandey & Fürsich 2003) or between the different forms (isotropic or stretched) within the genus *Thamnasteria* according to Lathuilière (2000b).

Dimorphoseris Duncan, 1872 based on *D. oolitica* Duncan, 1872 presents the same characteristics as *Dimorphastrea* with the exception of the columella that we could not see clearly on the type material and that could be less developed in favor of a small fossa.

Protoseris Edwards & Haime, 1851 based on *P. waltoni* Edwards & Haime, 1851 is also impossible to distinguish from *Synastrea.*

The comparison with similar Cretaceous genera such as *Astraeofungia* Alloiteau, 1952 and *Fungiastraea* Alloiteau, 1952 would deserve to be done.

Synastrea agaricites (Goldfuss, 1826) (Fig. 37)

Astrea agaricites Goldfuss, 1826: 66, fig. 9 a, b, c.

Synastrea agaricites – Löser 2002 *cum syn.*: 641-642; 2016: 651, fig. S55a, b, c, d. — Baron-Szabo 2001: 266, fig. 3B; 2002: 140, pl. 100, fig. 1, 2, 4; ?2008: 162, pl. 14, fig. 4; 2014: 68, pl. 74, fig. 4-5.

Synastraea arduennensis Orbigny, 1850: 386. — Fromentel 1861: 220; 1865: 24. — Pillet & Fromentel 1875: 102, pl. 12, fig. 2. — Cottreau 1928: 78, pl. 50, fig. 6-7.

Thamnastraea ? *arduennensis* – Edwards & Haime 1851b: 113.

Thamnastraea arduennensis – Edwards & Haime 1857: 566.

Dimorphastrea sp. 1 – Vasseur 2018: 170, fig. 3.27.

TYPE MATERIAL. — **Lectotype** (**here designated**). **Austria** • 1 specimen: two syntypes have been observed in collections in Bonn (n°IPB223), we select the best preserved one as the lectotype (**here designated**). This lectotype was figured by Goldfuss (1826: pl. 22, fig. 9) and also by Baron-Szabo (2002: pl. 100, fig. 1,2) who considered it as a holotype and Löser (2016: fig. S55a,b,c) who considered it as a syntype; Nufsbach in Abtenau, Salzbourg; Santonian, Upper Cretaceous.

STUDIED SAMPLES. — CPUN MA1004E3-2, CPUN MA1004E4-9, CPUN MA1004E4-32, CPUN MA1004E4-33 from Middle/Upper Toarcian of Aïn Leuh, Middle Atlas of Morocco.

GEOGRAPHIC AND STRATIGRAPHIC RANGES. — The species is widely documented in Löser (2002: 642) for the Cretaceous occurrences referred to the nominal species *Synastrea agaricites*. The possible extension of the synonymy to numerous Jurassic species and the present study make the range much more extended, at least down to the Upper Toarcian of Aïn Leuh (Middle Atlas of Morocco).

DESCRIPTION

Thamnasterioid colony. Radial elements are straight or flexuous (sometimes petaloid), subcompact biseptal blades with lateral faces ornamented with pennulae. A papillose axial structure made of the projection of septal trabeculae sometimes appears in depth. Endotheca made of thin vesicular dissepiments. Synapticulae present. No wall between the calices. A concentrically wrinkled holotheca covers the base of the colony.

DIMENSIONS

Calicular diameter: 4 to 10 mm – distance between calices centres: 3.2 to 6.8 mm – number of septa: 23 to 44 – septal density: 5 per 2 mm.

SIMILARITIES AND DIFFERENCES

We compared these specimens with the different Jurassic species within the genera *Synastrea*, *Protoseris*, *Dimorphastrea* and *Dimorphoseris* and identified possible synonymies with *Synastrea perroni* (Fromentel, 1856), *Synastrea oceani* Orbigny, 1850, *Synastrea patina* (Becker, 1875), *Synastrea confusa* Orbigny, 1850, *Synastrea constricta* (Etallon, 1859), *Synastrea dubia* Fromentel, 1861, *Dimorphastrea choffati* (Koby, 1904), *Protoseris jaccardi* (Koby, 1886), *Protoseris robusta* Becker, 1875, *Protoseris suevica* Becker, 1875, *Dimorphastrea concentrica* Milaschevitsch, 1876, *Dimorphastrea langii* (Quenstedt, 1880), *Dimorphastrea vasiformis* Koby, 1886, *Dimorphastrea corallina* Fromentel, 1861, *Dimorphastrea cossmanni* (Koby, 1907), *Dimorphastrea cupuliformis* (Fromentel, 1861), *Dimorphastrea delaunayi* Koby, 1907, *Dimorphastrea dubia* Fromentel, 1861, *Dimorphastrea fallax* Becker, 1875, *Dimorphastrea platyphylla* Koby, 1904, *Dimorphastrea heteromorpha* Quenstedt, 1857, *Dimorphastrea stipitata* Reuss, 1867, *Dimorphoseris oolitica* Duncan, 1872. However, a substantial revision of the synonymies of these species is necessary and we did not considered the post-Jurassic for which species included within the genera *Astraeofungia*, *Fungiastraea* and *Leptoseris* Edwards & Haime, 1849 should be examined. We want to draw attention to the long temporal distribution of this morphology and the generally low number of specimens in fossil communities. The shape appears to be very constant at least from the Toarcian (for the species) or the Pliensbachian (for the genus) to the Upper Cretaceous and perhaps much more (considering some *Leptoseris*?).

The distinction between *S. agaricites* and *D. fungiformis* also described in the present work is made only on the septal structure, microsolenid (i.e. regularly porous) in *D. fungiformis* and subcompact in *S. agaricites*.

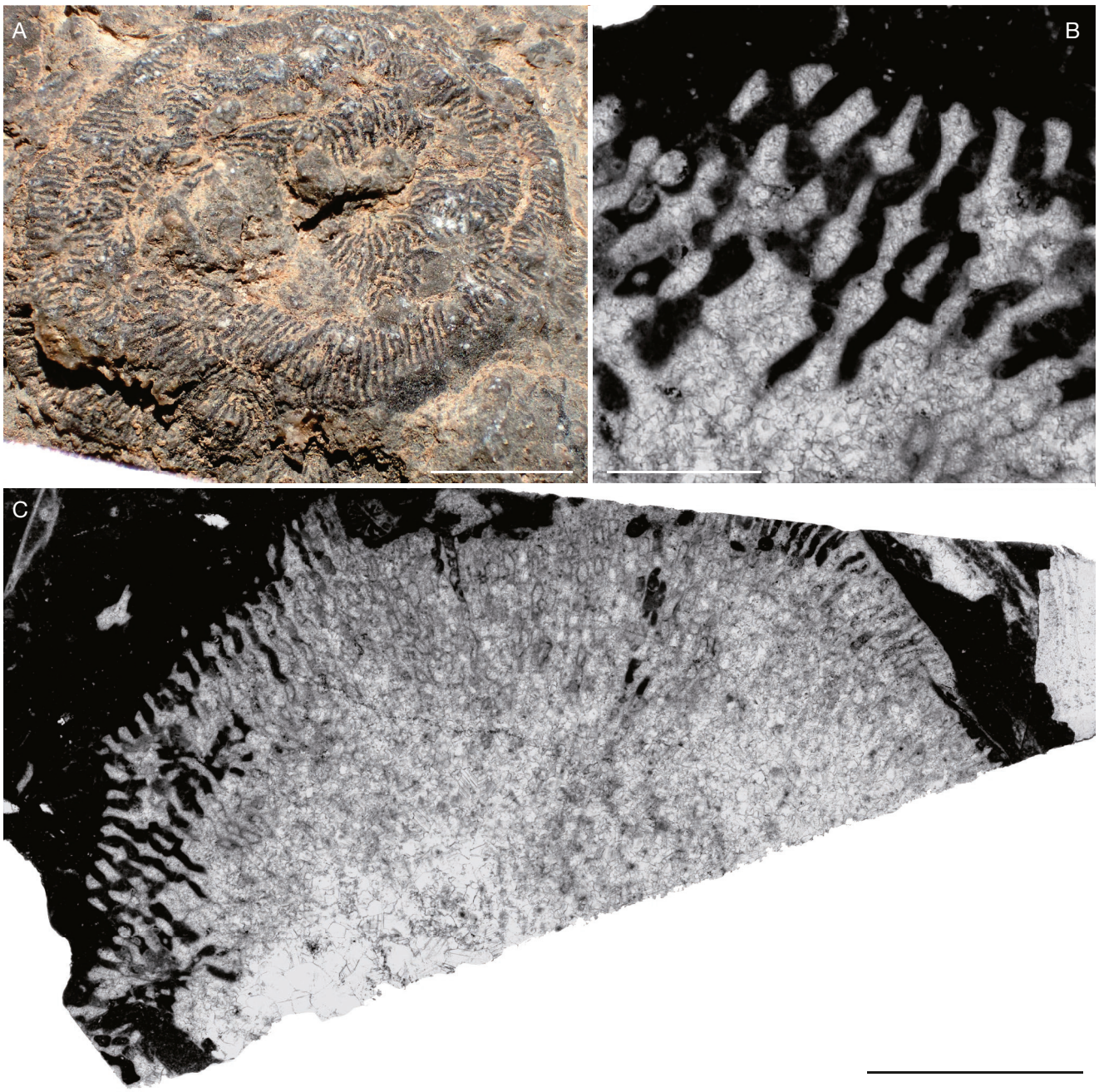

FIG. 36. — *Periseris elegantula* (Orbigny, 1850), Lower Toarcian (*Polymorphum* zone) of Dades Valley, Morocco: **A**, distal view of the specimen CPUN DA0106E3-1; **B**, detail of pennular septal structure in longitudinal section of the specimen CPUN DA0106E3-1; **C**, longitudinal thin section of the specimen CPUN DA0106E3-1. Scale bars: A, 5 mm; B, 1 mm; C, 4 mm. Photos: R. Vasseur.

CONCLUSIONS

The description of non-Thecosmiliidae Toarcian coral faunas provide a strong evidence for the multi-phased nature of the Pli-Toa crisis with a first event corresponding to the Pli-To boundary and a second event that took place during the Jenkyns event. In fact, Pre-JE Toarcian faunas are very different to solitary and phaceloid-rich Pliensbachian faunas that contain an important proportion of Triassic-inherited taxa, many solitary exclusive to this stage and a very few taxa that maintain beyond the stage.

Pre-JE Toarcian coral faunas appear as a transition state with the appearance of new taxa unknown up-until pre-JE Toarcian and with a continuity in the Middle-Upper Jurassic, a few taxa inherited from the Lower Jurassic and no taxa with Triassic roots, suggesting a situation of both extinctions and recovery for scleractinians. Coral-dominated reefs are rare in the field and lithiotid bivalves still compete with corals for the ecological resources. Those communities could presumably be constituted by both azooxantellate and zooxantellate forms in proportions that cannot be estimated without further investigations.

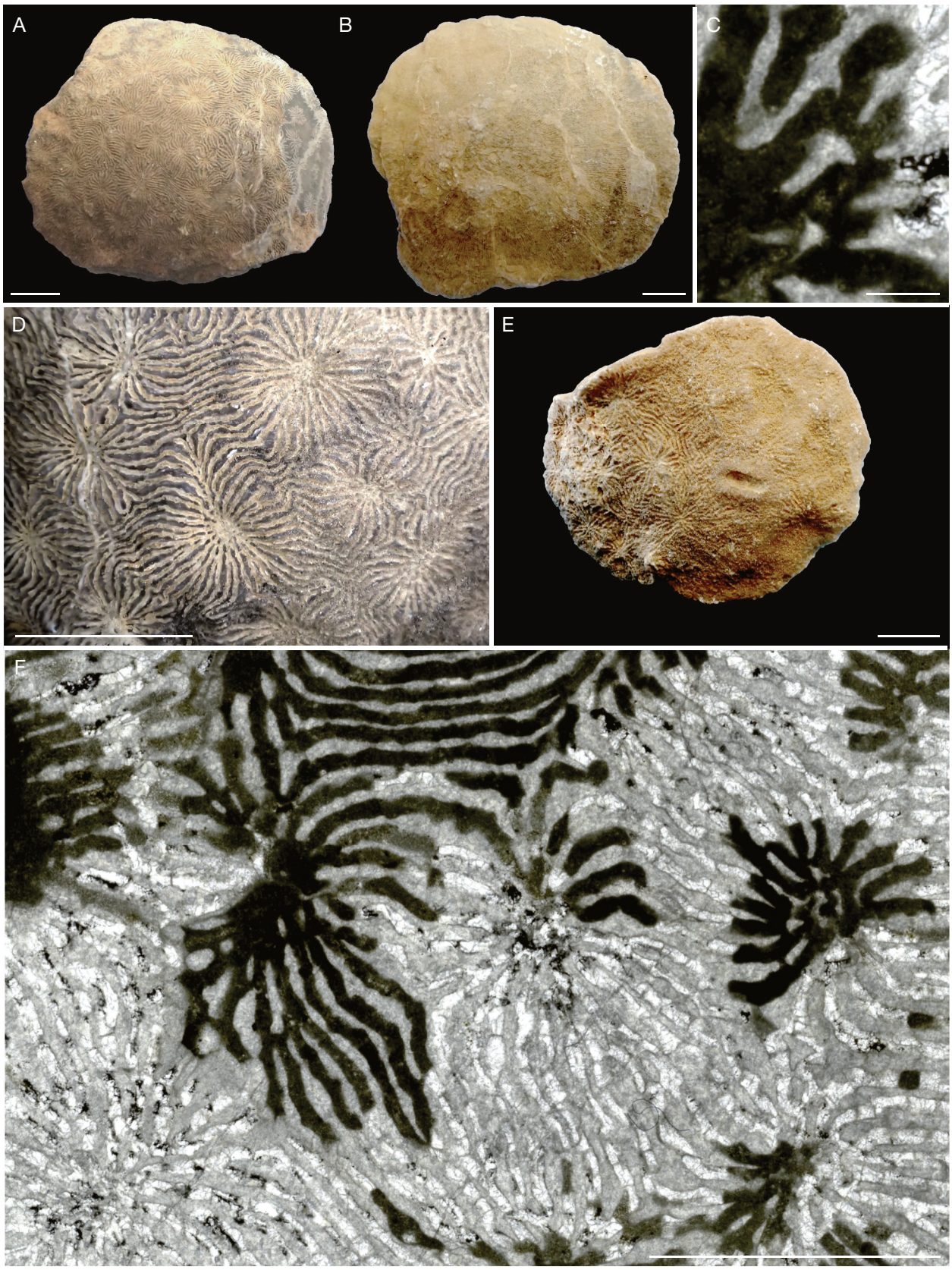

Fig. 37. — *Synastrea agaricites* (Goldfuss, 1826), Middle/Upper Toarcian of Aïn Leuh, Morocco: **A**, distal view of the specimen CPUN MA1004E3-2; **B**, proximal view of the specimen CPUN MA1004E3-2; **C**, detail in transverse thin section of the pennular septal structure of the specimen CPUN MA1004E4-9; **D**, detail in distal view of the specimen CPUN MA1004E3-2; **E**, distal view of the specimen CPUN MA1004E4-32; **F**, transverse thin section of the specimen CPUN MA1004E4-9. Scale bars: A, B, D, 1 cm; C, 0.5 mm; E, 8 mm; F, 5 mm. Photos: R. Vasseur.

The Post-JE Toarcian is characterized by large reefs, where high-integrated forms significantly outcompete phaceloid forms in both biomass and diversity. The majority of the genera that make up the diversity of these assemblages persist and diversify throughout the Middle and Upper Jurassic. Photosymbiosis is probably well established in those reefs considering the size and importance of high-integrated forms (particularly meandroid forms) and bioconstructions, along with their paleo-bathymetric positioning.

A few number of new taxa (one new genus and four new species) have been described, because Toarcian assemblages present clear affinities with both Liassic that have been described by the authors previously and Middle-Upper Jurassic faunas already well described in the literature. The publication about Toarcian Thecosmiliid corals will also probably include a few new species.

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