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Original article

## Ecological succession evidence in an Upper Jurassic coral reef system (Izwarn section, High Atlas, Morocco)<sup>☆</sup>

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### ABSTRACT

Late Jurassic coral reefs are present in the Western High Atlas of Morocco along the eastern paleomargin of the young Atlantic Ocean. The Izwarn section shows two reef units made of scleractinian corals and microbialites, included in a progradational shallowing-upward succession. Changes in reefal composition and structure observed in a *ca.* 50 cm-thick interval at the base of the reef unit 1 are interpreted to represent the first well-documented ecological succession in Late Jurassic reefs. Bioclastic deposits, sparse and poorly diversified corals (five genera) preserved in life position, and finally a more diversified coral assemblage (11 genera) building a reef framework with stromatolitic crusts reflect pioneer, colonization and diversification stages, respectively. A specific depth window, where light was reduced but sufficient for a catch-up growth mode and below the erosive action of waves, probably at the lower slope of a fore-reef area, has made possible the development and the record of this ecological succession. With a more diversified coral assemblage (16 genera), the reef unit 2 reflects shallower and well-agitated waters of a fore-reef area. Overlaying this second reef unit, the upper part of the section reveals back-reef deposits made of reworked reef elements, whereas a putative reef crest area is not recorded.

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### 1. Introduction

Reefs were particularly abundant, diversified and latitudinally widespread during the Late Jurassic (Webb, 1996; Leinfelder, 2001; Cecca et al., 2005; Martin-Garin et al., 2012). During this epoch, they were globally distributed and assigned to four main realms (i.e., northern Tethys shelf, southern Tethys shelf, North Atlantic, and Pacific), which remain largely unequal in their documentation (Leinfelder et al., 2002). Instead of a great variety of transitional forms, Late Jurassic reefs can be grouped in three main types of builders: coral, siliceous sponge and microbialite reefs (Leinfelder, 1993). According to their composition, they display a peculiar zonation along Upper Jurassic platforms, with coral reefs in shallow settings and sponge and microbialite reefs in deeper settings (Leinfelder et al., 1994; Leinfelder, 2001). Some of these reefs also display

the replacement of one community of reef building by another as the reef grew (Sun and Wright, 1989; Leinfelder, 1992; Leinfelder et al., 1993; Werner et al., 1994; Dupraz, 1999; Matyszkiewicz et al., 2006). However, even if they are assumed to be present in the Late Jurassic (Kiessling, 2002), an example of an ecological succession *sensu* Walker and Alberstadt (1975) with pioneering (stabilization and colonization), diversification and domination stages is still not documented.

In the eastern part of the proto-ocean corresponding to the North Atlantic, only few studies indicate the presence of reefs during the Late Jurassic along the Moroccan margin (Ambroggi, 1963; Adams, 1979; Adams et al., 1980). There are only rare studies that give detailed descriptions of these bioconstructions, which appear to be mainly composed of various builders such as corals, stromatopores and microbialites (Ourribane, 2000; Ourribane et al., 2000; Martin-Garin, 2005; Martin-Garin et al., 2007). Among these studies, Martin-Garin et al. (2007) give the first Jurassic description of a reef tract zonation within a unique facies model, emphasizing the interest and the great potential of these poorly known Morocco reef systems. About 30 km northeast of Agadir

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(High Atlas, Morocco), the section of Izwarn displays a well-preserved coral reef system rich in microbialites (Fig. 1). This reef system provides the opportunity to analyze in detail its composition, its development, and notably its phase of installation. The main objectives of this study are to improve the knowledge of the Late Jurassic Moroccan reefs of the eastern North Atlantic realm, which remain largely undocumented in the literature compared to their Tethyan counterparts, and to illustrate for the first time an ecological succession in Late Jurassic reefs.

## 2. Geological framework

The Izwarn section ( $30^{\circ} 37' 39''$  N,  $9^{\circ} 34' 17''$  W) is located in the Western High Atlas (Morocco), near the Jebel Taznakht, about 15 km southwest of Imouzzer (Fig. 1). This section is situated in the southern part of the El Jadida-Agadir basin, delimited to the north by the Jbilel Massif, to the east by the Paleozoic Massifs of the High Atlas, to the south by the Sous Plain, and to the west by the Atlantic Ocean (Bouaouda et al., 2004). Studied reef interval is attributed to the Lalla Oujja Formation (Adams et al., 1980; Fig. 2). The age of the entire Izwarn section is difficult to establish, notably due to the paucity of ammonites in most of the studied interval. An Oxfordian age was initially attributed to this reef interval (Ambroggi, 1963). Later, based on the presence of the foraminifera *Alveosepta jaccardi* in limestones just above the reef interval, a Kimmeridgian age was assumed for this section (Ourribane, 2000). However, the first appearance data of *A. jaccardi* in the Agadir basin is dated from the Middle Oxfordian (Bouaouda, 2002; Bouaouda et al., 2004). Currently, the reefal Lalla Oujja Formation is mainly placed in the Oxfordian (Bouaouda et al., 2004). Rare ammonites have been sampled along the Izwarn section (Fig. 3). A specimen of *Euspidoceras phoenicium* has been found in the lithological interval 4 of Ambroggi (1963), around 25 m below the base of the studied section. This ammonite is characteristic of the Middle Oxfordian (Transversarium Zone; D'Arpa and Meléndez, 2002). Two other ammonites (*Subdiscosphinctes* sp. and *Orthosphinctes* sp., samples A1 and A2, respectively in Fig. 3) have been found close to the base of the reef unit 1. These ammonites give a Late Oxfordian age (Bimammatum-Planula interval; Cariou et al., 1997) for the studied interval.

During the Late Jurassic, the North Atlantic was a narrow proto-ocean connected to the Tethys. The first major northward extension of the Atlantic occurred during the Late Oxfordian and the Western High Atlas was characterized by high subsidence rates (Zühlke et al., 2004). Late Oxfordian-Early Kimmeridgian paleogeographic reconstructions of Ambroggi (1963) or Adams

et al. (1980) show a general facies belt zonation from proximal settings to the east-northeast to more distal and open sea to the west-southwest (Fig. 1). Close to the recent shoreline, reefs of Cape Ghir are located in a coral sea rich in patch reefs (Adams et al., 1980) and developed on top of an inherited kilometeric paleorelief (Martin-Garin et al., 2007). Reefs of the Izwarn section are located ~30 km to the east of Cape Ghir. They developed close to the eastern limit of the coral reef extension, near a more internal littoral sea (Adams et al., 1980).

## 3. Material and methods

The studied section is part of the Izwarn section type of Ambroggi (1963), and focalizes on its reefal interval (Fig. 3). A 63 m-thick section was directly logged on the field (Figs. 3, 4). Facies types were determined on the basis of a first macroscopic field description, coupled with the determination of textures and relative abundances of skeletal and non-skeletal elements from 19 thin sections.

Due to the important thickness of the reef units 1 and 2 (13.0 and 16.5 m, respectively) and to the outcrop conditions (e.g., gap at the base the reef unit 2), a detailed reef analysis and the coral sampling were deliberately restricted to 4 m-thick intervals at the base of the reef unit 1 and at the top of the reef unit 2 (Fig. 3). This sampling strategy enables the illustration of both phases of reef installation and reef demise, and permits further additional studies on the remaining reef system. For the estimation of the relative abundance of the reef components (microbialites, corals, sediments, and others) a point-counting method using a  $20 \times 20$  cm grid of 100 points was used in the field on randomly scattered surfaces of 2336 cm<sup>2</sup> (reef unit 1) and 2380 cm<sup>2</sup> (reef unit 2). For coral determination, 35 and 44 samples were randomly collected (reef units 1 and 2, respectively). More than 200 polished slabs were prepared for coral determinations and the analysis of microbial carbonates. All coral samples were cut in oriented sections and determined at the generic level, which is presently considered as the most reliable taxonomic rank for Jurassic corals (Lathuilière et al., 2005; Martin-Garin et al., 2010, 2012). Nevertheless, numerous coral genera have unclear taxonomic status and need a thorough revision, which is in progress (<http://www.coralosphere.org/>). Coral determination was completed by the analysis of 26 thin sections. Coral assemblages were deduced from the analysis of 114 and 61 colonial or solitary corals for reef units 1 and 2, respectively. Microbialites and microencrusts were studied from 30 thin sections.

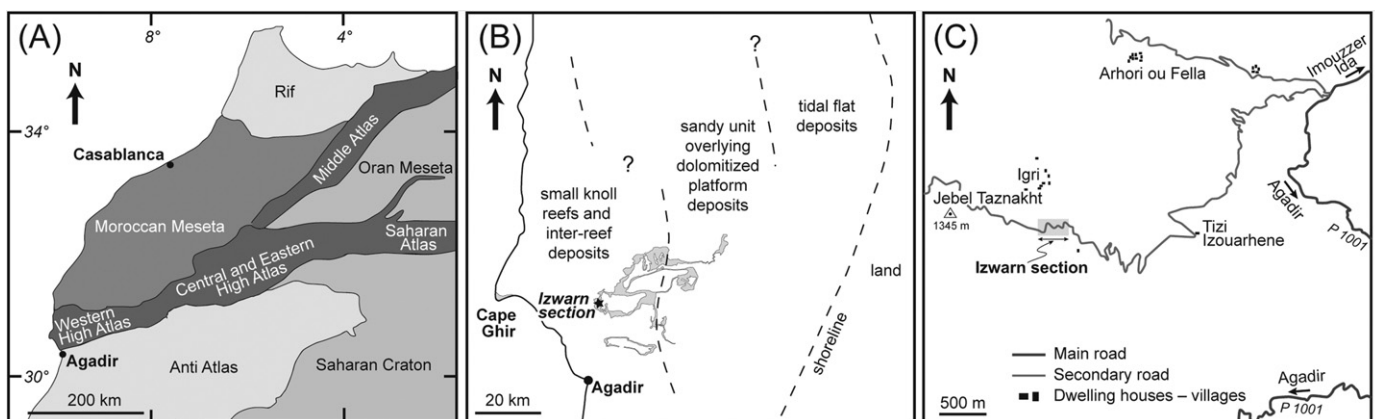


Fig. 1. A. Geological map of the major geological provinces of Morocco (simplified after Warme, 1988). B. Upper Oxfordian palaeogeographic map showing the shoreline position and the main facies belt extensions (Adams, 1979). In grey, Jurassic terrain outcrops (Ambroggi, 1963). C. The Izwarn section is located in the western part of Morocco near Imouzzer (Western High Atlas).

Stage		Formation	Member
Kimmeridgian	Lower	Iggui el Behar	
	Upper	Lalla Oujja	
Oxfordian	Middle		Marl and Shale
	Lower	Ouanamane	Somalirhynchia Limestone
	Upper		
Calloviaian	Middle		
	Lower		Iggui n' Tarhazout Oolite
	Upper	Ameskroud	Transition Dolomite

Fig. 2. Stratigraphy of the Middle and Upper Jurassic of the western High Atlas. From Adams, 1979.

## 4. Results

### 4.1. Section and facies description

The first 6 m of the section display marl-limestone alternations (Figs. 3, 4(A)). It corresponds to the lithological unit 6 of Ambroggi (1963). Centimetre-thick (locally up to 20 cm) marly intervals are thinly laminated and locally include thin bioclastic layers. Mudstone-wackestone (locally packstone) textures characterize the 15–60 cm-thick limestone beds. Some beds are relatively rich in belemnites and one ammonite was found (Fig. 3). Sedimentary structures are rare, represented by sparse parallel laminae associated with thin and discontinuous bioclastic deposits. These limestone beds commonly display an intense bioturbation. The microfacies analysis reveals a relatively diversified biota made of abundant echinoderms and bivalves, associated with some brachiopods, benthic foraminifera, bryozoans, ostracods, gastropods and calcispheres. Peloids are locally abundant and lithoclasts are rare.

From six to 19 m, a grey marly limestone with a mudstone texture corresponds to the lithological unit 7 of Ambroggi (1963). The biota content is poor with some rare echinoderms and ostracods, and different associations of dinoflagellates (Courtinat, 1989).

From 19 to 22 m, the section shows an altered pale grey limestone with a mudstone to wackestone texture (Figs. 4(B), 5(A)). One isolated ammonite (*Subdiscosphinctes* sp., sample A2 in Fig. 3) was found. The fauna is moderately diversified with rare echinoderms, bivalves, serpulids, ostracods, undifferentiated benthic foraminifera and calcareous sponges. Peloids and lithoclasts are rare. The uppermost part (last ca. 50 cm) of this unit displays significant changes in its biota content. This bioclastic interval can be subdivided into three main subunits (Fig. 6(A–D)). The first 10–15 cm-thick subunit shows sparse bioclasts of relative large size (up to 5 cm long), mainly made of echinoderms with abundant sea-urchin spines (Figs. 5(B), 6(A, B)). Brachiopods (terebratulids) and bivalves (pectinids and other undifferentiated thin bivalves) represent the associated fauna. The second 10–15 cm-thick subunit displays more abundant, but smaller (mm-scale) bioclasts (Fig. 6(A, C)). These bioclasts are mainly made of angular fragments of echinoderms (sea-urchins and crinoids), associated with some serpulids and corals. Corals correspond to sparse debris of platy-shape and branching colonies. The uppermost 15–20 cm-thick subunit is characterized by the first in situ platy-shape corals and by less abundant bioclasts (mainly echinoderms and branching coral debris; Fig. 6(D)).

From 22 to 34 m, the section shows a massive bioconstruction (Fig. 3). This reef unit 1 is mainly made of corals and microbialites (Fig. 6(E)) and can be laterally followed over few hundreds of

metres, without any lateral thickness variations (Fig. 4(A, B)). The reef framework appears laterally continuous and inter-reef or lateral-reef sediments were not observed in the investigated area.

From 34 to 40 m, overlaying the reef unit 1, there is a one metre-thick marly unit followed by a pale grey limestone. This limestone has a mudstone to wackestone texture and a poorly to moderately diversified biota with abundant undifferentiated bivalves, common undifferentiated echinoderms and rare benthic foraminifera, sea-urchin spines, ostracods and calcispheres.

From 40 to 56 m, there is a second massive bioconstruction also made of corals and microbialites (Fig. 3). This reef unit 2 is laterally continuous over several hundred of metres and does not seem to display lateral thickness variations (Fig. 4(A, D)). The reef framework appears laterally continuous and neither inter-reef nor lateral-reef sediment areas were observed.

Reef unit 2 is overlain by a massive, peloidal, reef clast grainstone-rudstone (locally packstone) 80 cm-thick (Fig. 5(C)). Grains mainly correspond to peloids and some micritic oncoids. Corals and *Cayeuxia* mainly represent reef clasts. These clasts frequently contain encrusting *Lithocodium* and *Bacinella*. Thin millimetre-scale crusts of dense micrite associated with some nubecularids also constitute these reworked grains.

At 57 m, an oncolitic facies defines two limestone beds (60 and 20 cm-thick, respectively) with a packstone to wackestone texture (Fig. 4(C)). Oncoids are small (mm-scale) and micritic. They are associated with abundant, small micritic lithoclasts and common peloids. Some benthic foraminifera (nubecularids and undifferentiated agglutinated foraminifera), undifferentiated bivalves, and echinoderms represent the fauna. A nodular facies is observed into two small limestone beds (between 58.0 and 58.5 m; Fig. 3). A nodular fabric with abundant lithoclasts, common peloids, and some oncoids characterizes this caliche facies (Fig. 5(D)). Spar-filled wrinkle microcracks tend to surround the nodules. Grains are coated by a thin crust of dense micrite and are connected by micritic bridges. A sparse planar lamination is locally observed. The fauna is rare and is only represented by rare undifferentiated benthic foraminifera and echinoderms.

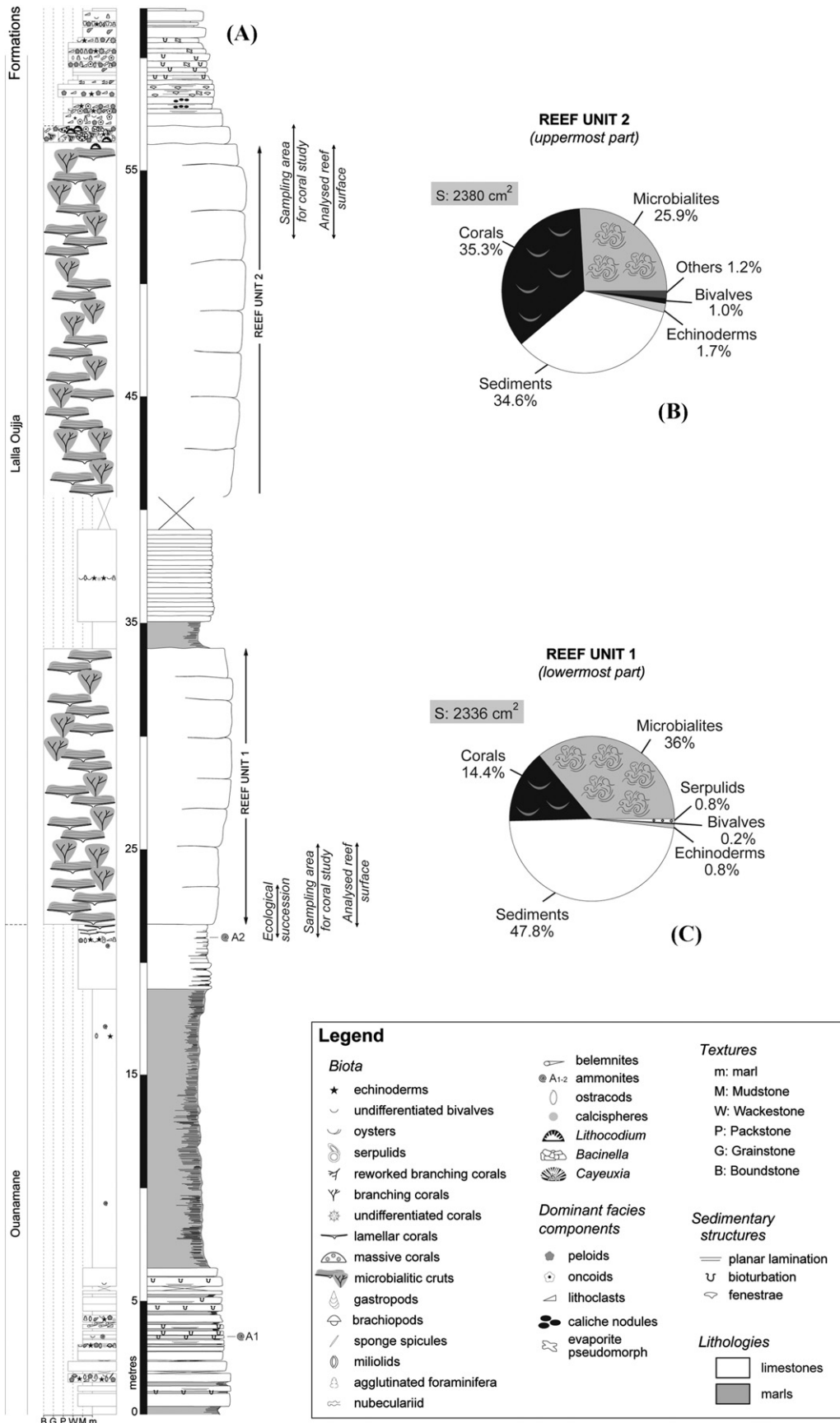
A peloidal facies with a packstone to grainstone texture characterizes two limestone beds (between 58.5 and 59.0 m). This grain-supported facies is made of abundant peloids, common lithoclasts, some aggregates, aligned and laterally elongated *fenestrae*, and a sparse planar lamination. Locally, there are some calcite pseudomorphs of euhedral evaporite crystals. The fauna is rare with only rare echinoderm clasts and putative undifferentiated benthic foraminifera.

Between 59.0 and 61.0 m, there is a bioturbated micritic facies with a wackestone, locally mudstone or packstone textures (Fig. 3). Peloids are common to abundant. Oncoids, lithoclasts, and some calcite pseudomorphs of evaporite crystals are also present. Some coral debris, echinoderms, and undifferentiated bivalves represent the fauna. Undifferentiated benthic foraminifera and ostracods are also present.

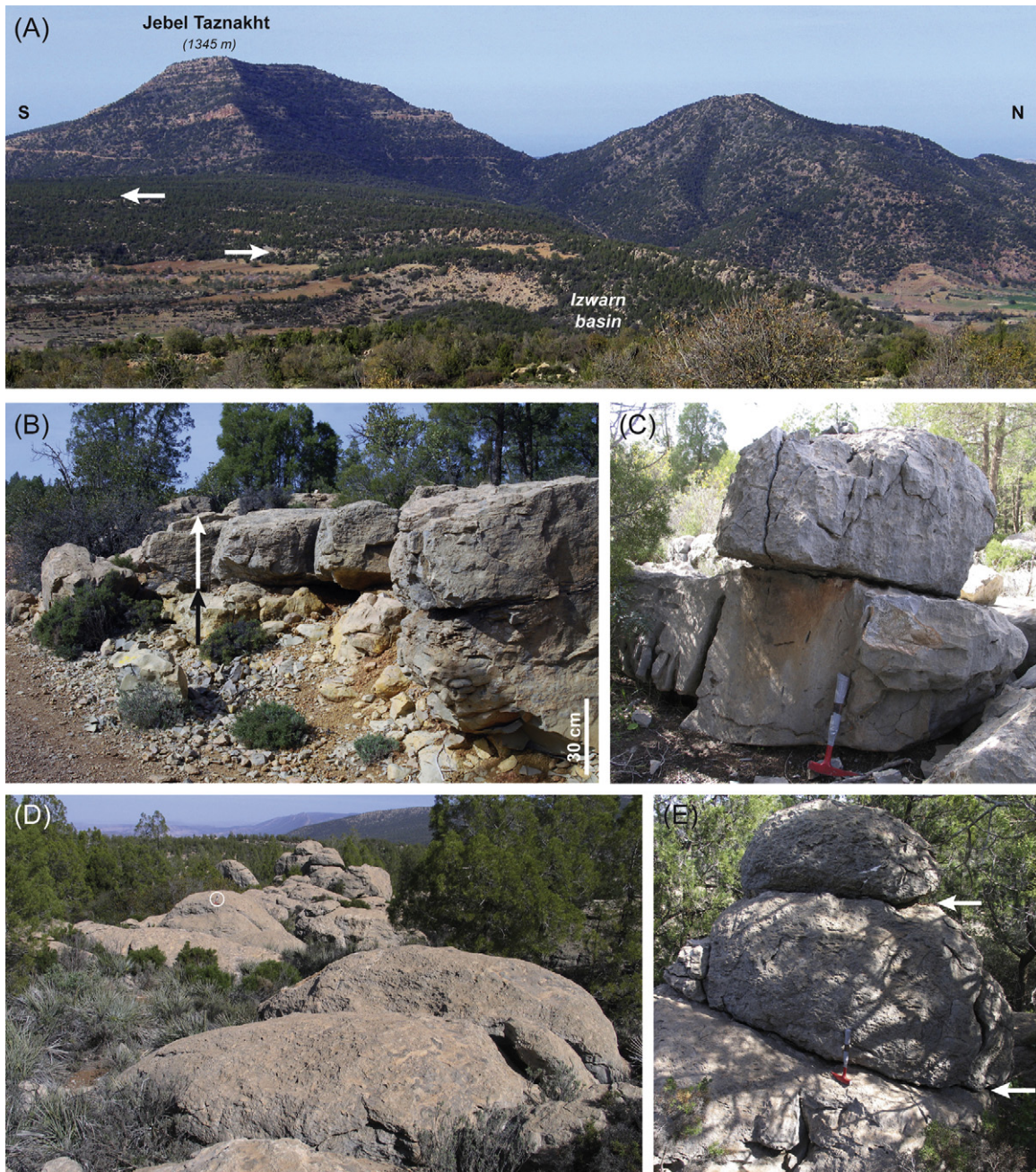
A thin 15 cm-thick limestone bed particularly rich in *Megalodontidae* is observed at 61.5 m. This limestone has a mudstone texture and locally displays an intense bioturbation, which is unfilled by a peloidal packstone. Sparse and rare agglutinated foraminifera, ostracods, and gastropods represent the additional fauna.

### 4.2. Corals

Corals are the main component of the two thick reef units, but are also observed in different limestone beds as sparse isolated colonies or as reworked grains (Fig. 3). In contrast to Ourribane (2000), the participation of stromatoporoids in these reef units was



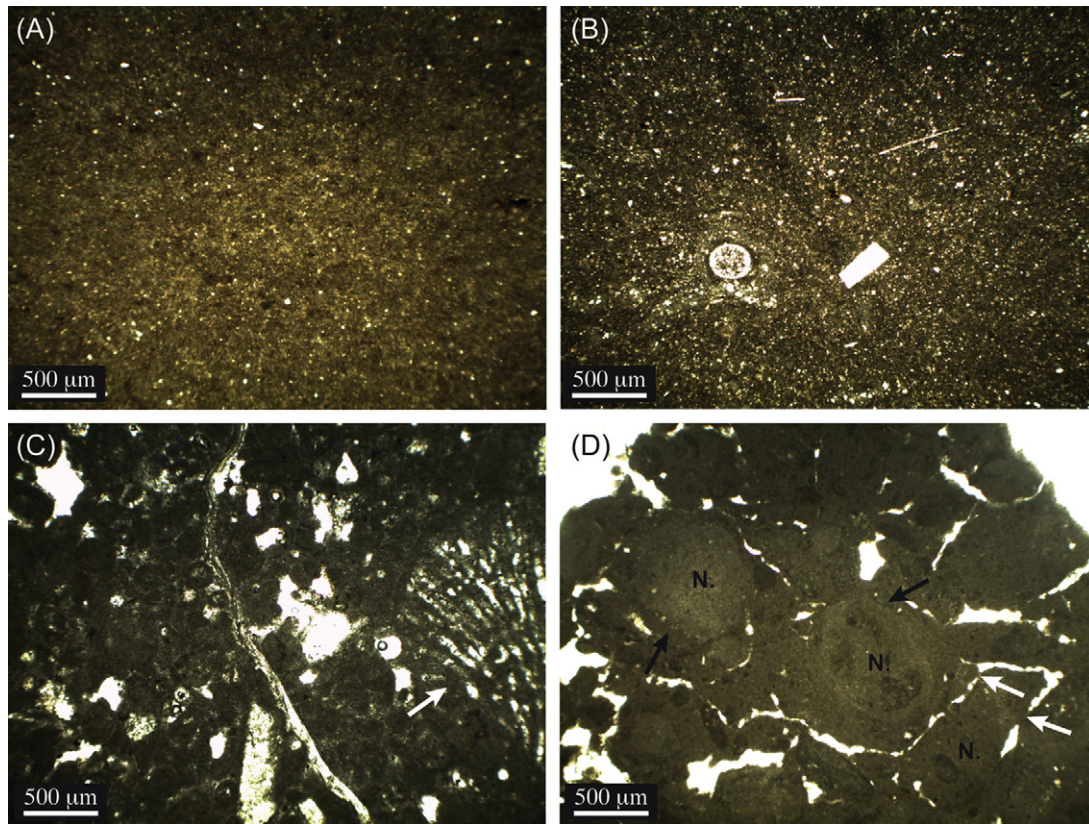
**Fig. 3.** Log of the Izwarn section including lithologies and textures. Sequence interpretations are also indicated along the section. Pic charts show estimates of the reef surface proportions of the main reef components for the two reef units using the point-counting method, expressed in percentage of area.



**Fig. 4.** General field views of the studied area. **A.** Panorama of the Jebel Taznakht near Tizi Izwarn. White arrows mark the base and the top of the studied section on the western flank of the small Izwarn basin. **B.** First bed (or reef-growth phase; white arrow) of the reef unit 1 overlaying the third lithological unit (black arrow). Note the relatively flat upper surface of the first reef-growth phase. **C.** Two limestone beds (bioclastic and oncolitic) at the top of the reef unit 2. **D.** Lateral view of the reef unit 2 within its uppermost part. Note the lateral continuity of the reef framework and the lack of inter- or lateral-reef sediments. An intense diaclose network amplifies the meter scale domal morphology of this reef unit. The hammer (white circle) gives the scale. **E.** Vertical view of the reef unit 2 showing three successive reef-growth phases delimited by surfaces of reef-growth interruptions (white arrows). Note that surfaces of reef-growth interruptions are parallels to subparallels, reflecting a low reef relief.

not observed. Prior to realization of a framework in the reef unit 1, the section reveals three successive 10–20 cm-thick bioclastic subunits, particularly rich in echinoderms (Fig. 6(B, C)). The second subunit displays the first sparse coral debris (Fig. 6(C)). Among the three genera identified, there are three fragments of gracile branching colonies of *Enallhelia*, two platy colony debris (< 4 mm-width and < 3 mm-thick) of *Dimorpharaea*, and one branching colony debris of *Dermoseris* (Fig. 7(A)). The third subunit reveals the first preserved coral colonies in life position with a relatively low coral cover (< 5%; Fig. 6(A, D)). Among the 17 colonies identified, nine correspond to platy colonies of *Dimorpharaea*

dominating a poorly diversified (5 genera) coral assemblage (Fig. 7(B)). These colonies are characterized by their particularly small size, up to 15 cm in diameter for 2–4 mm in thickness (Fig. 6(D)). Other colonies are represented by the genera *Enallhelia* (4), *Thecosmilia* (2), *Cryptocoenia* (1), and *Stylosmilia* (1). The phaceloid corals of the genus *Stylosmilia* are represented by (fragmented?) small, cm-scale colonies where only few calices can be observed. The genus *Enallhelia* is represented by small dendroid colonies that reach up to 10 cm in diameter for 8 cm in height. The plocoid corals of the genus *Cryptocoenia* are represented by small, cm-scale rounded colonies. Above this third subunit, corals



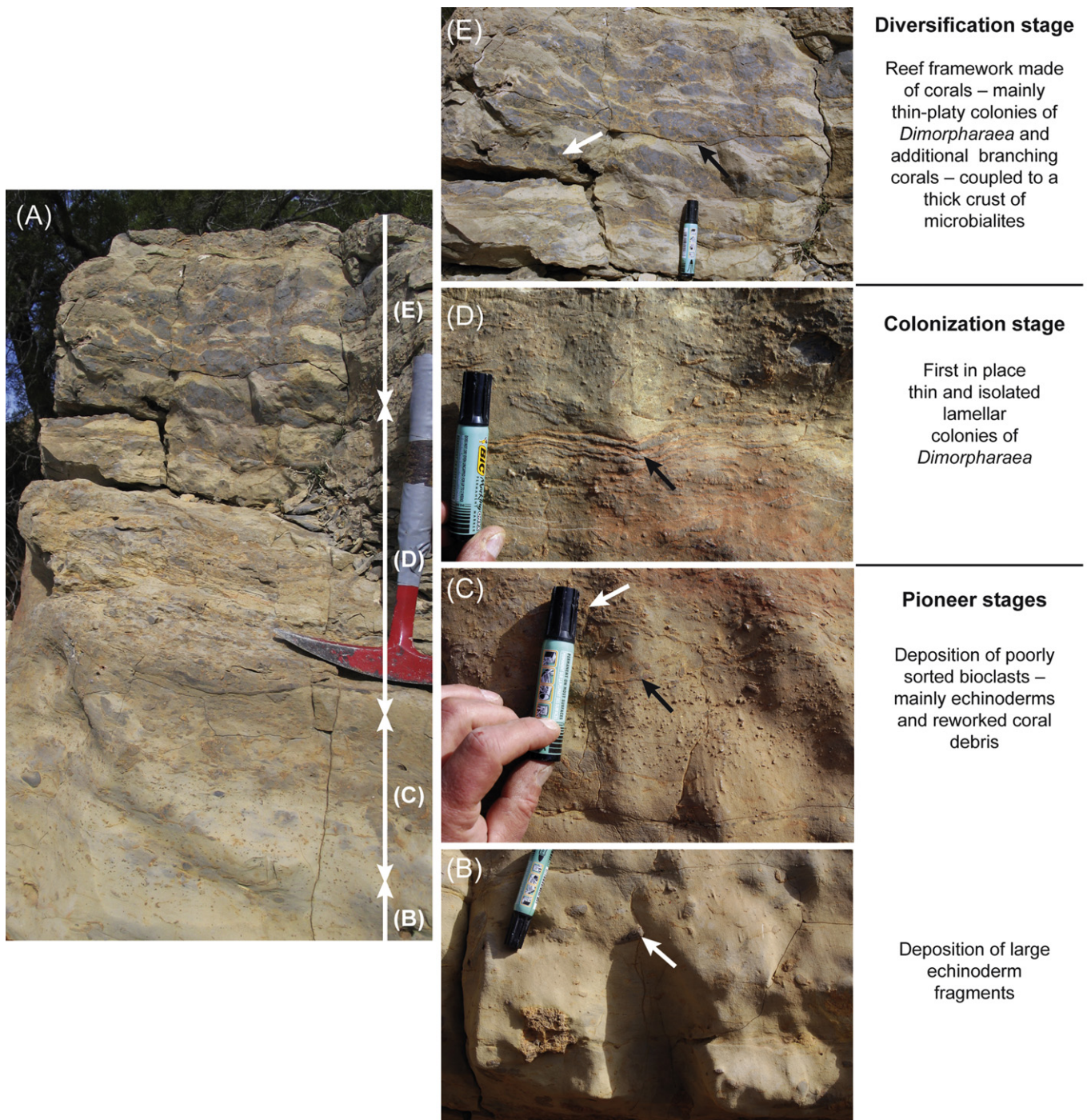
**Fig. 5.** Thin sections of some facies types (natural light photographs). **A.** Mudstone with rare fragments of undifferentiated small bioclasts and quartz grains; thin section IZ5. **B.** Wackestone with subangular echinoderm fragments, serpulids and thin undifferentiated bivalves and quartz; thin section MTC40. **C.** Packstone to grainstone with peloids, undifferentiated bivalves, and *Cayeuxia* (arrow); thin section IZ7. **D.** Caliche nodules. Subspherical to subangular nodules (N) coated by a thin crust of dense micrite (black arrows) and connected by micritic bridges (white arrows); thin section IZ10.

become more abundant and diversified; they contribute to the formation of a framework (Figs. 6(E), 8(A)). The lower part of this reef unit 1 (basal four metres) displays a relatively low coral cover close to 15% (Fig. 3). With 11 genera identified, the coral diversity is moderate (Fig. 7(C)). Corallite arrangements are frequently thamnasterioid, and commonly dendroid and phaceloid; cerioid and plocoid arrangements are rare. These platy-shape colonies reach 25 cm in diameter (mean ca. 15–16 cm) and generally do not exceed 5–6 mm in thickness (Figs. 8(A, C, D), 9(B)). Among the 78 colonies identified, *Dimorpharaea* remains the most abundant genus (40% of the coral assemblage; Fig. 10(A)). Other massive colonies are rare and correspond to the genera *Cryptocoenia* (4% of the coral assemblage), *Microsolena* (3%) and *Isastrea* (1%; Fig. 10(H)). *Cryptocoenia* are represented by small cm-scale rounded colonies. Largest colonies of *Isastrea* exceed 30 cm in width and 9 cm in height. Branching colonies are more abundant and are mainly represented by dendroid colonies of *Enallhelia* (19% of the coral assemblage; Fig. 10(B)) associated with some phaceloid forms (*Stylosmilia*, 9%; *Calamophylliopsis*, 8%; *Dermoseris*, 6%; *Thecosmilia*, 5%). These branching colonies are generally reduced in size. Largest colonies of *Calamophylliopsis* reach 60 cm in diameter and 40 cm in height (Fig. 8(B)). Colonies of *Enallhelia* do not exceed 15 cm in diameter and 7 cm in height. The largest colonies of *Thecosmilia* probably exceed 25 cm in diameter.

The coral assemblage of the reef unit 2 was only studied in its uppermost part (i.e., last four metres). In this interval, the coral cover reaches more than 35% of the reef surface (Fig. 3). With 16 genera identified the coral diversity is relatively important, with common thamnasterioid and phaceloid corallite arrangements (Fig. 7(D)). Plocoid, cerioid, flabello-meandroid, and meandroid corallite arrangements are also present. Platy-shape colonies of

*Dimorpharaea* are still present, but less abundant (16% of the coral assemblage). These colonies reach larger sizes (> 1 m in diameter and > 2 cm in thickness; Fig. 8(G)). *Dimorpharaea* is also represented by more massive and rounded colonies (> 11 cm in diameter and 7 cm in height). Colonies of the genera *Actinaraea* (10%) and *Fungiastraea* (8%) represent other dominant massive forms. Colonies of *Actinaraea* can display a massive rounded form that exceeds 35 cm in diameter. The genera *Microsolena* (6%), *Stylinia* (4%), *Comoseris* (2%), *Etallonasteria* (2%), *Thamnasteria* (2%), *Isastrea* (2%) and *Cryptocoenia* (2%) represent additional massive colonies. Colonies of *Stylinia* occasionally present a branching morphology (> 10 cm in diameter and > 15 cm in height; Fig. 10(G)). The largest colonies of *Isastrea* exceed 30 cm in width and 11 cm in height. Branching phaceloid colonies are relatively abundant (42% of the coral assemblage), with *Thecosmilia* (16%; Fig. 10(E, F)), *Stylosmilia* (10%; Fig. 10(C)), *Calamophylliopsis* (10%), and *Dermoseris* (6%; Fig. 10(D)). Robust colonies of *Rhipidogyra* (2%) and dendroid colonies of *Cladophyllia* (2%) represent additional branching corals. *Stylosmilia* are represented by colonies of relatively large sizes (> 4 m in diameter; Fig. 8(H)). Largest colonies of *Thecosmilia* reach 60 cm in diameter and 20 cm in height (Fig. 8(G)).

In the massive bed at the top of the reef unit 2, corals are still common, but they are preserved as reworked colonies or as debris. Corals are strongly dissolved and recrystallized, making their determination difficult. Seven genera have been determined among 11 specimens (Fig. 7(E)). Phaceloid and plocoid corallite arrangements are common. Dendroid and thamnasterioid corallite arrangements are also present. *Actinaraea*, *Cladophyllia* and *Stylosmilia* appear more common and *Calamophylliopsis*, *Stylinia*, *Enallhelia*, *Dimorpharaea* are present. The coral colonies do not



**Fig. 6.** Installation stages of the first reef unit. **A.** General view of the reef installation. **B.** Bioclasts of large size (mainly echinoderms; white arrow) in a limestone with a mudstone fabric. **C.** Abundant small bioclasts in a limestone with a wackestone texture. Echinoderm and coral debris mainly represent bioclasts. Thin lamellar colonies of *Dimorpharaea* and gracile branching colonies of *Enallhelia* represent coral debris (black and white arrows, respectively). **D.** Thin platy *Dimorpharaea* colony in life position (black arrow). **E.** Reef framework made of platy *Dimorpharaea* colonies (black arrow) and some branching colonies (white arrow), encrusted by dark-grey microbialites.

reach large sizes (e.g., up to 10 cm in width and 8 cm in height for phaceloid colonies of *Stylosmilia*).

#### 4.3. Microbialites and microencrusters

At the base of the reef unit 1, no traces of biofilms were observed facilitating the installation of first corals. These corals are generally devoid of microbialitic crusts. Only locally, some rare mm-scale crusts of leiolites (i.e., structureless microbia-

lites) are observed on upper surfaces of platy colonies of *Dimorpharaea* and between branching colonies of *Enallhelia* (Fig. 9(A)). Once a reef framework was realized, microbialites constitute more than the third (36%) of the reef cover (Figs. 3, 6(A, E)). They form stromatolitic crusts up to 8 cm-thick on the upper surface of lamellar corals such as *Dimorpharaea* (Fig. 9(B)) and columns on the upper side of some robust branches of phaceloid corals such as *Thecosmilia* (Fig. 9(C)). Relatively thin mm to cm-thick crusts of leiolites encrust gracile branching

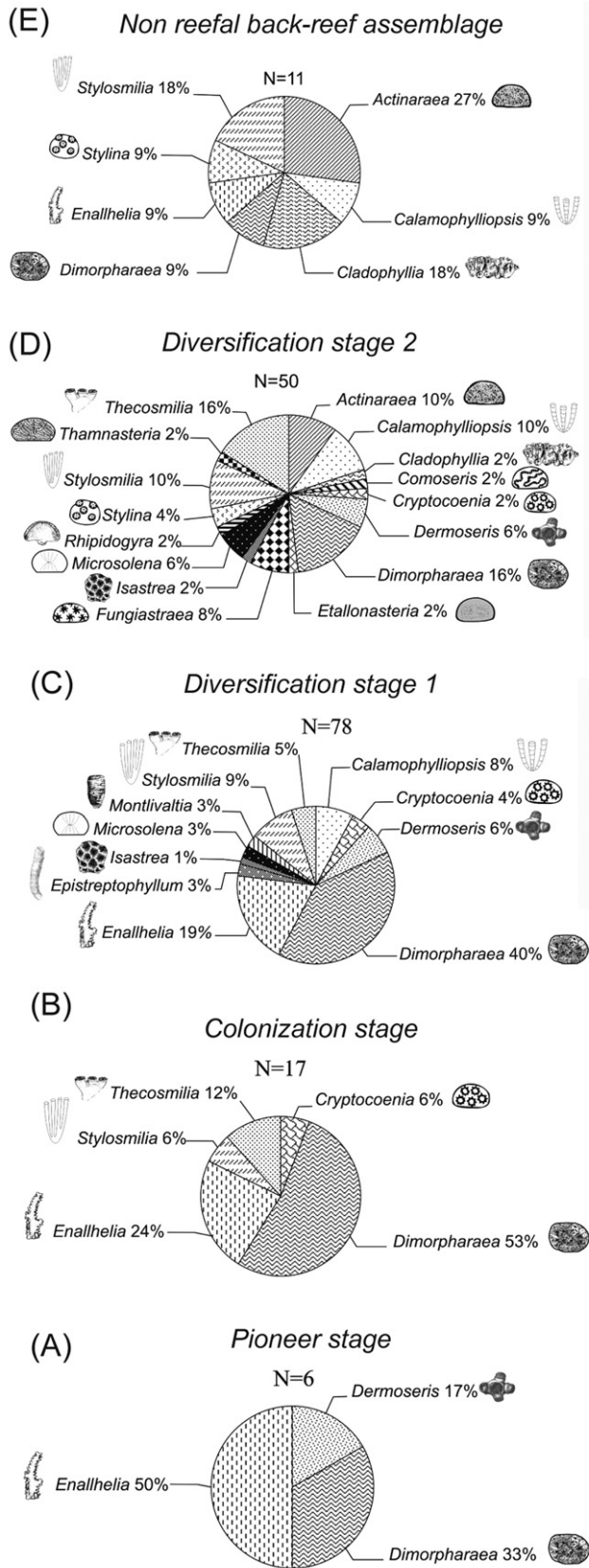


Fig. 7. Relative abundance of the coral taxa in the first (A–C) and second (D, E) reef units.

corals such as *Stylosmilia*, *Enallhelia* or *Calamophylliopsis* (Fig. 9(D)). These branching corals display coalescent leiolitic crusts inside the colony, whereas the external surface displays a laminated crust. Stromatolitic crusts on lamellar coral colonies frequently display planar upper surfaces along which successive laminae are truncated (Fig. 8(C, D)). Abundant mm-scale and angular fragments of these stromatolitic crusts are observed reworked in the overlaying sediments. Microscopically, the stromatolitic lamination is more or less wavy and corresponds to the alternation of thin layers of dense micrite with thicker layers of clotted micrite (Fig. 11(A, C)). The stromatolitic lamination can also correspond to the alternation of thin 50–100  $\mu\text{m}$ -thick layers of dense micrite with 0.5–2 mm-thick layers of peloids filled with sparitic cement (Fig. 11(B)). Leiolites and rare thrombolites are made of a dense to clotted micrite. Most of microbialitic crusts display a first and thin mm-scale layer of dense micrite directly observed on the coral surface (Fig. 11(A)). Microencrusts associated with microbialites are relatively poorly diversified: *Tubiphytes*, *Terebella*, nubecularids, some serpulids and rare bryozoans, *Bullopore* and calcareous sponges represent them.

In the upper part of the reef unit 2, the participation of microbialites is more moderate with only 26% of the reef cover (Fig. 3). The distribution of microbialites appears more heterogeneous; some coral colonies are devoid of microbialitic crusts (Fig. 8(E)). When present, microbialites encrust the upper surface of some lamellar corals such as *Dimorpharaea* and *Fungiastraea* (Figs. 8(F), 9(F)) or some branching colonies such as *Calamophylliopsis* and *Stylosmilia* (Fig. 9(E)). Microbialitic crusts do not exceed 3–4 cm in thickness and tend to develop small mm-scale columns in their upper part (Fig. 9(F)). Microbialites generally correspond to thrombolites and leiolites. Locally, a laminated fabric is outlined by the presence of *fenestræ* (Fig. 11(F)). Microscopically, microbialites are made of clotted to dense, locally peloidal micrites (Fig. 11(D, E)). Frequent *Tubiphytes*, *Terebella*, and nubecularids represent the microencrusts, associated with some *Lithocodium* and *Bacinella* (Fig. 11(H)), as well as *Tolypammina*, *Bullopore*, bryozoans, and calcareous sponges. Directly above the reef unit 2, reworked reef elements display frequent *Lithocodium* and *Bacinella* fragments (Fig. 11(G)). *Troglotella* is also frequently observed perforating some branching coral debris (Fig. 11(D, G)).

## 5. Discussion

### 5.1. Shallowing-upward sequence

Sedimentological and palaeontological investigations point to a general shallowing-upward trend along the section. The facies encountered at the base of the section (0–22 m) reflects an open sea depositional setting, allowing the presence of pelagic fauna with ammonites and belemnites. The absence of wave-induced sedimentary structures suggests a position below the storm wave base. Truncated and reworked stromatolitic crusts in the reef unit lower part are interpreted to reflect the first indication of a significant wave action. Considering rapid lithification of stromatolites (Dromart et al., 1994; Macintyre et al., 2000), angular shapes of stromatolitic clasts suggest storm events. A more continuous wave action, indicated by a grain-supported texture, is only recorded in the uppermost part of the reef unit 2. The deposits overlaying the reef unit 2 still indicate a shallowing-upward trend with the deposition of a set of facies of shallow back-reef environments (e.g., rudstones, oncolites and megalodont-rich beds), and then tidal flat settings (e.g., pseudomorphs of evaporites, *fenestræ* and caliche nodules).



## 5.2. Ecological succession evidence

Shallowing-upward sequences are frequently observed in the fossil record of coral reefs (Frost and Weiss, 1979; Neumann and Macintyre, 1985; Vennin et al., 2004; Palma et al., 2009). In these sequences, corals colonize the substratum and grow to sea-level with predictable changes in coral assemblages. As the reef grows upwards, the physical environment changes (e.g., increase of light intensity and water energy) and shallower-dwelling corals may replace deeper-dwelling ones. Such an evolution in ancient reefs has been considered to reflect an ecological succession if the corals themselves were able to modify the environments during their growth (Walker and Alberstadt, 1975; Copper, 1988; Reinhold, 1995). However, biotic changes can also be controlled by extrinsic physical (e.g., sea-level fluctuations) and chemical parameters. In that case, the faunal shift should be considered as a community replacement rather than an ecological succession (Aronson et al., 1998). Shallowing-upward sequences may also reflect a combination of intrinsic and extrinsic influences, making difficult to clearly identify the factors that triggered coral assemblage changes (Budd et al., 1988; Riegl and Piller, 2000).

In the Late Jurassic, the Moroccan passive margin recorded a general subsidence (Ellouz et al., 2003; Zühlke et al., 2004). The shoreline of the Agadir basin also progressively migrated to the east from the Lias to the Early Kimmeridgian (Bouaouda, 2004). Along the Izwarn section, the only indication of a putative tectonic activity is the rapid transition from the reef unit 1 to overlying marls and limestones (Fig. 3). The biota content and the mud-supported texture of these limestones are consistent with a depositional setting below the fair-weather wave base in an open marine environment and thus may reflect a sudden deepening. The rest of the section reflects a relatively continuous sedimentation and progressive sediment infilling of the available space. The transgressive trend observed in the Agadir basin associated with the progradational shallowing-upward succession of the Izwarn section is only consistent with an accumulation rate higher than the accommodation rate. In that context, sediment production and reef-growth could catch-up with the relative sea-level rise. Thus, phases of coral installation and reef formation observed at the base of the reef unit 1 are assumed to be an intrinsically-driven, successional, shallowing-upward sequence.

Another difficulty to clearly identify ecological successions in ancient reef sequences is their duration. Walker and Alberstadt (1975) recognized four vertical zones in reef successions, corresponding to stabilization, colonization, diversification, and domination stages. According to these authors, these stages have occurred over a considerable length of time that is not successional in the ecological sense. For Miller (1991), only faunal shifts over short periods of time from decades to centuries may be reasonably considered as ecological successions. Other authors consider that a temporal scale up to millennia is relevant to observe successional changes in reefs (Copper, 1988; Aronson et al., 1998). At Izwarn, the stratigraphic reef interval exceeds 25 m in thickness and the two reef units are 13.0 and 16.5 m-thick, respectively. Considering few mm-year growth rates for Late Jurassic corals and coral-microbialite reefs (Nose and Leinfelder, 1997; Schmid et al., 2001; Olivier et al., 2007), the duration of growth of these reefs is too long to be considered as successional. However, the phases of coral installation and reef formation at the base of the reef unit 1 are confined to a thinner interval (30–50 cm-thick; Fig. 6). According to the estimations of sediment accumulations in Upper Jurassic shallow carbonates – between 0.03 and 0.60 mm y<sup>-1</sup> (Enos, 1991; Strasser and Samankassou, 2003) – the faunal changes observed up to the realization of a reef framework at the base of the reef unit 1 may have durations in the order of decades to millennia. Such time

duration is coherent with an ecological time scale for reef systems (Aronson et al., 1998) and highlights the potential of earliest stages of reef development to record an ecological succession (Crame, 1980).

## 5.3. Ecological succession stages

### 5.3.1. Pioneer stage

The reef unit 1 overlies a ca. 50 cm-thick bioclastic interval that can be subdivided into three subunits (Fig. 6(A–D)). The first 10–15 cm-thick subunit is interpreted as the pioneer or stabilization stage preceding the coral settlement. This stage highlights a major ecological change with the record of bioclastic deposits on a soft substrate. Echinoderms with sea-urchin spines and crinoid ossicles mainly represent bioclasts, associated with sparse fragments of brachiopods, bivalves and corals, which are mainly represented by *Enallhelia*. These gracile branching corals can be easily reworked and transported. Their strong representation can however be overestimated if some fragments were originally part of the same colony (Edinger et al., 2001). Small cm-scale fragments of thin lamellar colonies of *Dimorpharea* are also observed. These colonies are known to present important phenotypic plasticity and to develop platy-shapes in relatively deep settings where light intensity is low (Geister and Lathuilière, 1991; Insalaco, 1996; Gill et al., 2004; Lathuilière et al., 2005). In addition to a poorly illuminated setting, a position below the wave action is supported by the absence of characteristic sedimentary structures. The depositional setting of this pioneer stage is interpreted to correspond to a lower slope of a fore-reef area where gravity-reworked bioclasts were deposited in a muddy sediment (Fig. 12).

### 5.3.2. Colonization stage

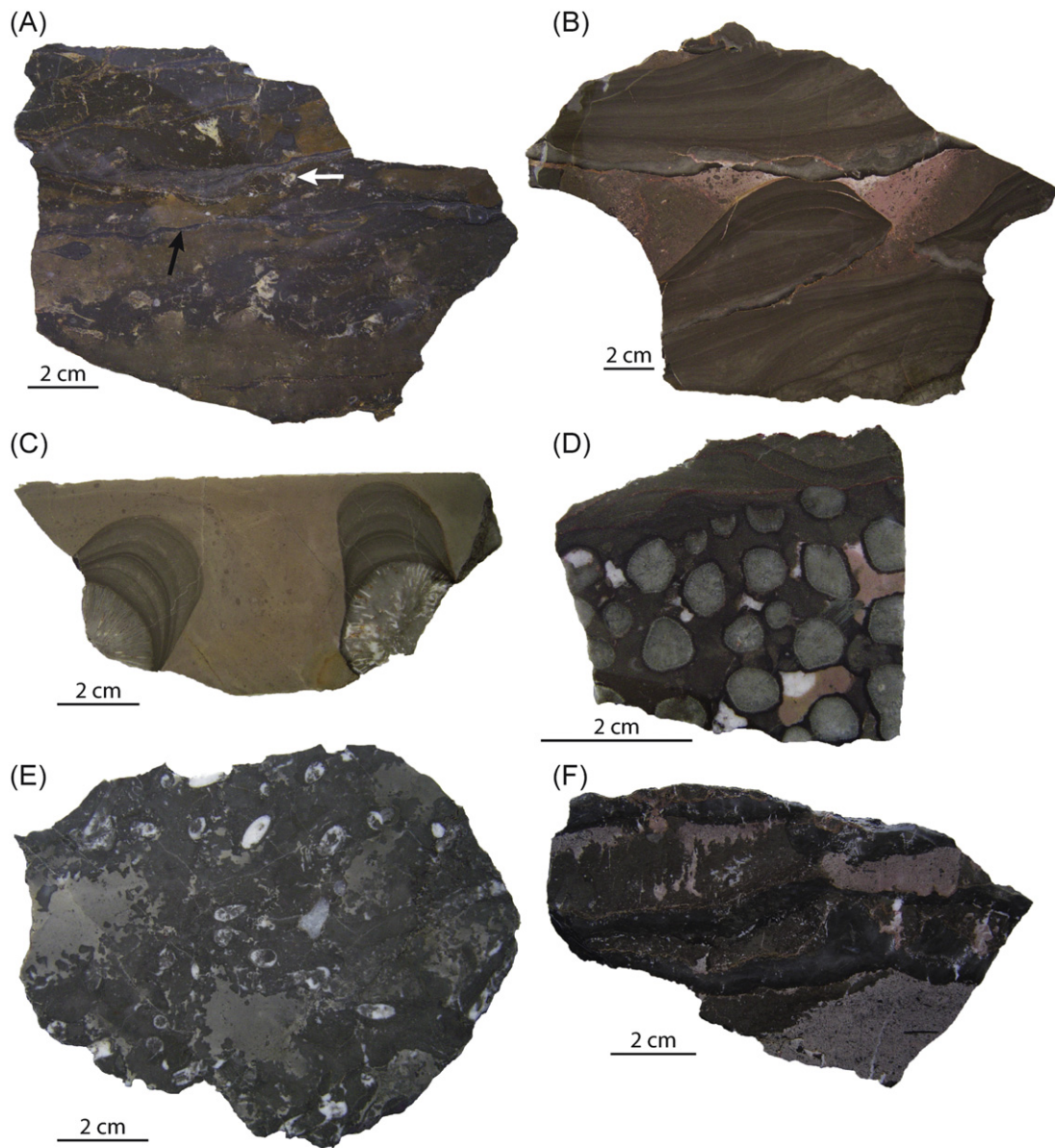
This stabilization interval progressively evolves towards another thin 10–15 cm-thick lithological subunit that represents the colonization stage (Fig. 6(C)). This stage reveals the first *in situ* coral colonies preceding the realization of a reef framework. The lack of wave-induced sedimentary structures still indicates a position below the storm wave base. The coral diversity is low (five genera) and the assemblage is mainly represented by very thin and platy colonies of *Dimorpharea* that do not exceed 2 mm in thickness and 15 cm in diameter. Platy colonies of *Dimorpharea* are also considered to represent pioneer colonies in some Upper Jurassic reef intervals (Geister and Lathuilière, 1991; Bertling, 1993; Insalaco, 1996; Martin-Garin et al., 2010). At Izwarn, the coral assemblage suggests a deep and poorly illuminated setting where coral growth initiated, but was not sufficiently efficient to form large-sized colonies. Microbialites and microencrusters are notably rare on corals, suggesting a relatively high sedimentation rate. The depositional setting of this colonization stage is interpreted to represent a deep fore-reef area (Fig. 12), where light and sedimentation rate are known to act as limiting factors for coral growth (Fabricius, 2005; Wolanski et al., 2005).

### 5.3.3. Diversification stage

The colonization stage gradually gives way to the diversification stage, which is characterized by an increase in both vertical and horizontal pattern diversity (Walker and Alberstadt, 1975). Here, an increase of the coral cover, the emergence of an intense microbialitic development, and the realization of a reef framework characterize the transition between the colonization and diversification stages (Fig. 6(D, E)). The moderately diversified (11 genera) coral assemblage (Fig. 7(C)), where *Dimorpharea*, *Enallhelia*, *Stylosmilia*, and *Calamophylloipsis* are the most abundant genera (40%, 19%, 9%, and 8% of the coral assemblage, respectively), indicates a mixed phototrophic-heterotrophic mode of nutrition



**Fig. 8.** Macroscopic field views of corals and microbialites for the first (A–D) and second (E–H) reef units. **A.** Coral-microbialitic framework. Note the thin lamellar *Dimorphareae* (black arrows) encrusted by microbialites (white arrows) on their upper surfaces. Locally some solitary corals (e.g., *Montlivaltia*, dashed arrow) are also

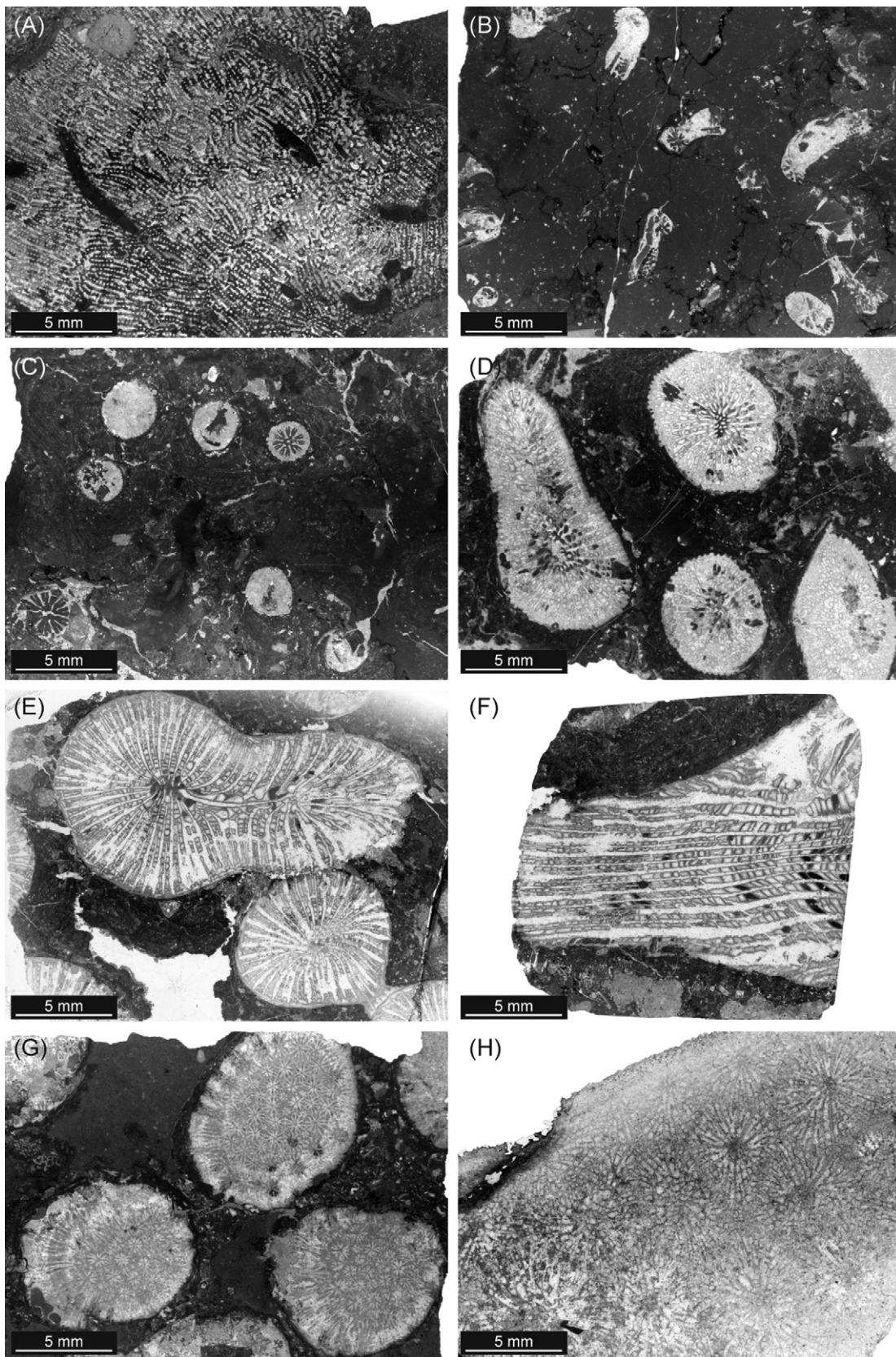


**Fig. 9.** Mesoscopic views (polished slabs) of corals and microbialitic crusts. **A.** Very thin colony of *Dimorpharaea* (black arrow) locally encrusted by microbialites. A gracile branching colony of *Enallhelia* (white arrow) is also observed between the lamella of a *Dimorpharaea* colony; base of the reef unit 1; sample MTC 49. **B.** Thick crusts of stromatolites on the upper surface of *Dimorpharaea* colony; reef unit 1; sample MTC 81. **C.** Robust branching colony of *Thecosmilia* encrusted by stromatolitic crusts; reef unit 1; sample MTC 71. **D.** Leiolites encrusting a phaceloid colony of *Calamophyllipsis*. A stromatolitic crust is observed at the periphery of the colony; reef unit 1; sample MTC 75. **E.** Gracile branching phaceloid colony of *Stylosmilia* encrusted by a dark-grey leiolitic to thrombolitic crust; reef unit 2; sample MTC 29. **F.** Platy colony of *Dimorpharaea* encrusted on its upper surface by a leiolitic to thrombolitic crust that tends to be columnar; reef unit 2; sample MTC 14.

and a low-mesotrophic regime (Dupraz and Strasser, 2002; Olivier et al., 2011). *Dimorpharaea* is still the most abundant genus, suggesting that available light was probably not optimal for coral growth. The reduced coral cover (only 14% of the reef surface) also indicates that coral growth was not very efficient. In spite of this reduced coral cover, abundant (36% of the reef surface) and thick stromatolitic crusts played a key role in the realization of reef framework (Fig. 8(C)). The appearance of some microbial

carbonates (e.g., *Renalcis*) during the diversification stage of an ecological succession was already documented in some Cambrian archaeocyath reefs (Zhuravlev, 2001; Debrenne, 2007). Low coral cover, low synoptic relief (ca. 1 m; Fig. 4(B)) and the sheetstone reef-growth fabric suggest that stromatolites developed at the surface of the bioconstruction. Their formation could have been favoured by periods of nutrient-rich conditions (Dupraz and Strasser, 2002; Olivier et al., 2007; Matyszkiewicz et al., 2011). The

observed. **B.** Branching phaceloid colony of *Calamophyllipsis*. **C.** Thin lamellar colonies of *Dimorpharaea* (black arrows) strongly encrusted by dark-grey microbialites. Note the presence of a thick-branching phaceloid colony of *Thecosmilia* (white arrow). **D.** Close up of (C), with a platy *Dimorpharaea* colony (black arrow) encrusted by stromatolites (see characteristic internal lamination; white arrow) on its upper surface. Note the flat truncated upper surface of the stromatolitic crust (dashed arrows) and associated stromatolitic clasts reworked into the light coloured intra-reef sediments. **E.** Reef framework made of diversified coral morphologies with a massive *Isastrea?* colony (black arrow), a dendroid *Enallhelia?* colony (white arrow), a phaceloid *Stylosmilia?* colony (dashed white arrow) and an undetermined robust branching colony (dashed black arrow). Note the low amount of dark-grey microbialitic crusts. **F.** Thick lamellar colony (*Fungiastraea?*; black arrows). Note the microbialitic crusts that tend to be columnar (white arrow). **G.** Large lamellar colony of *Dimorpharaea* (black arrow) and robust phaceloid colony of *Thecosmilia* (white arrow). **H.** Large gracile phaceloid colony of *Stylosmilia* (whole block).



**Fig. 10.** Some coral taxa of the Izwarn section (microscopic views; natural light thin sections). **A.** *Dimorpharaea*, transverse section; reef unit 1, sample MTC 73. **B.** *Enallhelia*, transverse section; reef unit 1, sample MTC 50. **C.** *Stylosmilia*, transverse section; reef unit 2, sample MTC 12. **D.** *Dermoseris*, transverse section; reef unit 2, sample MTC 30. **E.** *Thecosmilia*, transverse section; reef unit 2, sample MTC 4. **F.** *Thecosmilia*, longitudinal section; reef unit 2, sample MTC 4. **G.** Colony of *Styliina* with a branching morphology, transverse section; reef unit 2, sample MTC 21. **H.** *Isastrea*, transverse section; reef unit 1, sample MTC 120.

presence of truncated and reworked stromatolitic crusts highlights episodic events of high energy and a position above the storm wave base. In such depositional context, sediments were not continuously swept away, explaining the mudstone and wackestone textures of intra-reef sediments and the formation of a laminated microbialitic fabric.

Once the diversification stage is reached, the reef is also expected to develop a lateral zonation (James, 1983). The cover (several tens of metres) laterally explored in this reef unit 1 remains too narrow to highlight a putative zonation. However, a lateral-reef zonation has been proposed in the stratigraphically contemporaneous reefs of Cape Ghir, around 30 km west of Izwarn (Martin-Garin et al., 2007; Fig. 1). The coral assemblage described by Martin-Garin et al. (2007) in an upper slope fore-reef position is relatively close to the assemblage of the diversification stage at the base of the reef unit 1. Both are rich in microsolenids, but the predominance of *Dimorpharaea* during the diversification stage suggests a slightly deeper position and lower light level conditions compared to Cape Ghir. Thus, the diversification stage observed at Izwarn is assumed to have thrived between the storm- and fair-weather wave bases, in the uppermost part of the lower slope fore-reef area (Fig. 12).

#### 5.3.4. Upper reef unit 2: a second diversification stage?

A gap of observation did not permit sampling the base of the reef unit 2. Thus, another ecological succession with new pioneer and colonization stages that would pass into a diversified interval at the top of the reef unit 2 cannot be demonstrated. The studied interval in the uppermost part of the reef unit 2 displays a relatively well-diversified coral assemblage with 16 genera (Fig. 7(D)). It is more diversified than reef unit 1, but remains less diversified than other Upper Jurassic reefs of Morocco (Martin-Garin et al., 2007) and Portugal (Nose and Leinfelder, 1997) for the Atlantic margin, or French Jura, Burgundy, Lorraine, and Slovenia for the Mediterranean Tethys (Turnšek, 1997; Martin-Garin, 2005; Lathuilière et al., 2005; Carpentier et al., 2006; Martin-Garin et al., 2010). A reef framework is reached with a relatively high coral cover (35% of the reef volume). The laterally continuous framework over several hundreds of metres of this reef unit 2 and the presence of large-sized coral colonies suggest a more efficient coral growth compared to the reef unit 1. The coral assemblage is not still dominated by thin lamellar colonies of *Dimorpharaea*, suggesting that light conditions were no more a limiting factor. The presence of colonies with a pennular septal microstructure, such as *Dimorpharaea*, *Dermoseris* and *Microsolena*, indicates a coral association still characteristic of a mixed phototrophic-heterotrophic mode of nutrition and a low-mesotrophic regime (Insalaco, 1996; Dupraz and Strasser, 1999). The presence of more diverse robust branching colonies (*Dermoseris* and *Thecosmilia*) and solitary corals (*Montlivaltia* and *Epistreptophyllum*) may provide evidence for wave action (Olivier et al., 2004a; Lathuilière et al., 2005). Areas of intra-reef sediments show a grain-supported texture that confirms a continuous wave action.

Microbialites are still observed encrusting corals, but in lower proportion (26% of the reef surface) compared to the diversification stage of the reef unit 1. A reef area covering several hundred square metres coupled to a mixstone growth fabric do not permit to clearly identify the distribution of microbialites in the framework. Contrarily to the reef unit 1, it is not sure that microbialites developed at the surface of the bioconstruction. Microbialites, which are made of thrombolites and leiolites, could have been confined within the reef framework as it is observed in some Jurassic or Holocene coral reefs (Dupraz and Strasser, 1999; Camoin et al., 1999, 2006; Searl et al., 2011). Reef-growth phases do not exceed 1–1.5 m in thickness (Fig. 4(E)). Thus, if the development of microbialites occurred in reef cavities, it was

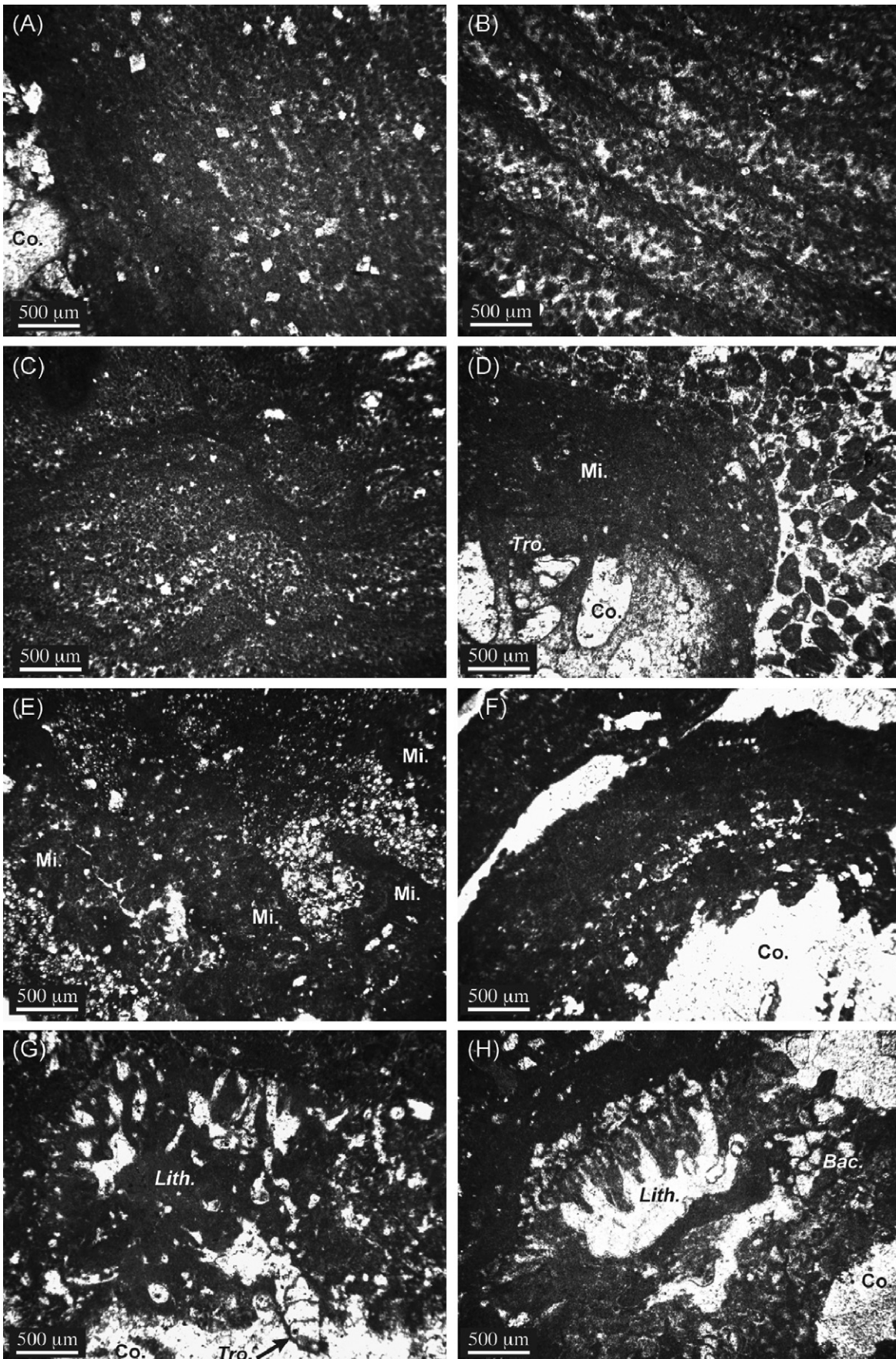
probably only few centimetres or decimetres below the living reef surface. The reef framework was probably characterized by a high porosity as suggested by the reduced coral cover (35% of the reef surface). This implies that cavities were probably not totally devoid of light. Some occurrences of *Lithocodium* and *Bacinella* in the secondary framework also indicate shallow and well-agitated waters and good light conditions (Schmid and Leinfelder, 1996; Dupraz and Strasser, 1999; Shiraishi and Kano, 2004; Lefort et al., 2011), even if Lower Cretaceous *Lithocodium* could reflect greater water depths (Schlagintweit and Bover-Arnal, 2011). Thrombolites, which are the dominant microbialitic fabric, tend to display a columnar morphology. This could reflect more favourable conditions and faster microbialite growth rate compared to stromatolites of the reef unit 1 (Olivier et al., 2004b, 2007). The almost lack of stromatolites could be explained by a lower sedimentation rate as fine sediments were probably swept away by continuous wave action. Thrombolites are indeed known to grow in shallow and well-agitated front-reef area (Feldmann and McKenzie, 1997). A position in a shallower fore-reef setting (i.e., upper slope) above the fair-weather wave base, could explain the more efficient reef-growth and the more diversified reef assemblage compared to the reef unit 1 (Fig. 12).

#### 5.3.5. A domination stage?

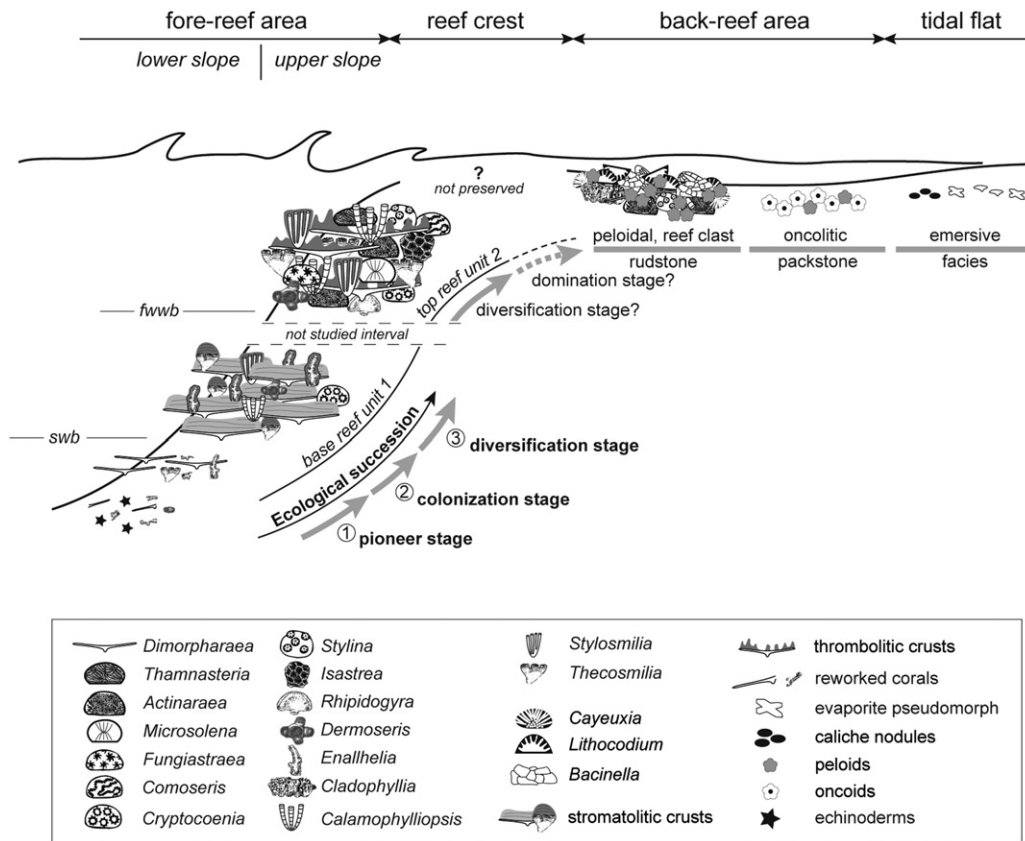
Following the diversification stage, Walker and Alberstadt (1975) defined a stage dominated by fewer taxa. This domination stage, in addition to a taxonomic restriction, is characterized by a reduction in growth-habitat diversity with a frequent domination of encrusting forms (Walker and Alberstadt, 1975). The first two beds that overly the reef unit 2 are made of abundant reworked reefal elements (Fig. 3). This rudstone facies is interpreted to represent a back-reef depositional setting (Fig. 12). Among the different elements constituting this rudstone, *Lithocodium*, *Bacinella* and *Cayeuxia* are the most abundant. Such organisms are well adapted to shallow, well-agitated waters and good light conditions (Leinfelder et al., 1993; Reolid et al., 2009; Lefort et al., 2011). Laterally continuous crusts of *Lithocodium*, associated with *Bacinella*, have already been observed at the top of some reef-growth phases in shallow Kimmeridgian coral reefs (Olivier et al., 2008). Thus, *Lithocodium*, *Bacinella*, and *Cayeuxia* probably have been reworked from an adjacent and non-preserved reef crest where a domination stage could have been reached. These encrusting organisms may have played an equivalent role to the modern coralline algae. There are numerous examples of shallowing-upward sequences that did not record reef crest zone (Vennin et al., 2004; Lathuilière et al., 2005; Martin-Garin et al., 2007). The Izwarn section does not record typical back-reef coral fauna, even though it was observed in Cape Ghir (Martin-Garin et al., 2007). This is probably explained by the paleogeographical position of Izwarn along the Moroccan margin, which displays general low angle, homoclinal ramp geometry with large north-south trending facies belts (Ambroggi, 1963; Adams et al., 1980; Bouaouda, 2004). Izwarn is located 30 km east of Cape Ghir and was situated in a shallower and more proximal setting (Fig. 1(B)). In such paleogeographic position, a reduced accommodation coupled with high salinity levels suggested by evaporite pseudomorphs at the top of the section, could reflect unfavourable conditions for the development of a back-reef coral fauna.

#### 5.4. Ecological successions in Late Jurassic reefs

Walker and Alberstadt (1975) in their description of Ordovician to Cretaceous ecological successions observed in reefs did not provide any example for the Jurassic times. Kiessling (2002) states that complete ecological successions were observed in Late



**Fig. 11.** Some microbialitic crusts and associated microencrusts of the Izarn section (microscopic views; natural light thin sections). **A.** Stromatolitic crust on a branching coral (Co) made of a clotted to peloidal micrite. Clots and peloids tend to be aligned, emphasizing a discrete lamination. Dolomite crystals are common; reef unit 1, sample



**Fig. 12.** Schematic illustration showing inferred palaeoenvironmental settings and ecological succession during the deposition of the studied reefs along the Izwarn section (swb: storm wave base; fwwb: fair-weather wave base).

Jurassic reefs, but also did not give any example. Several studies illustrate pioneer coral communities in some Upper Jurassic reef intervals (Geister and Lathuilière, 1991; Bertling, 1993; Insalaco, 1996). However, these studies do not document different stages of a putative ecological succession in reefs and thus do not touch on this concept. Other studies on Jurassic reefs reveal shifts in reef components during their growth – e.g., sponges to corals or corals to microbialites (Leinfelder et al., 1993; Werner et al., 1994). However, such stratigraphic successions highlight extrinsically-controlled community replacements rather than ecological successions. The only Jurassic ecological succession that is clearly mentioned in the literature concerns Oxfordian coral reefs of the French Paris Basin (Delance, 1984). These Oxfordian reefal units in the upper Yonne valley (Burgundy) show a pioneer stage mainly made of brachiopods, and probably the transition to a colonization stage (Menot, 1967; Delance and Menot, 1968). However, the stratigraphic thickness (15–20 m) of this putative colonization stage is incompatible with the duration of an ecological succession (Aronson et al., 1998). The stratigraphic succession described by Bill et al. (2011) in the Oxfordian Liesberg beds of the Swiss Jura probably records the first stages of an ecological succession. These authors recognize recurrent dm-thick intervals along which four fossil communities colonized the substratum. These four communities are annelids and soft-bottom bivalves, ostreids and isolated

small-sized corals, calcareous sponges, and large-sized corals with an increased morphological diversity. If the succession of the first two fossil communities could be interpreted as stabilization and colonization stages, the formation of a persistent and diversified reef framework did not occur. Along their entire stratigraphic interval, only two dm-thick biostromal levels are present and the absence of a diversification stage could be explained by periodic siliciclastic influx in a turbid environment (Bill et al., 2011), leading to an arrested reef succession (Copper, 1988).

### 5.5. Depth-dependant ecologic succession

Most studies dealing with ecological successions in reefs give a detailed description of the faunal shifts between successive ecological stages, but do not really discuss the sedimentary context that allowed their record (Walker and Alberstadt, 1975; Copper, 1988; Debrenne, 2007). These studies argue that stable environmental conditions are necessary to allow the record of intrinsically-controlled successions. However, stabilization and colonization stages have generally a short duration (Walker and Alberstadt, 1975), implying an exceptional potential of preservation in a specific sedimentary context. Lasemi and Amin-Rasouli (2007) assimilated the skeletal grain accumulation of a stabilization stage observed in Cambrian archaeocyathan buildups to

MTC 71. **B.** Stromatolitic crust. The lamination corresponds to the alternation of peloidal and clotted layers. Locally some thin biofilms are observed within the clotted layers; reef unit 1, sample MTC 75. **C.** Stromatolitic crust made of peloidal to clotted micrite. The planar to wavy lamination is marked by thin layers of dense micrite; reef unit 1, sample MTC 66. **D.** Thin crust of dense to peloidal micrite (Mi) on a branching coral (Co) bored by *Troglotella incrustans* (Tro); first limestone bed above the reef unit 2, sample MTC 33. **E.** Microbialitic crust made of columns of dense to clotted micrite (Mi). Inter-columnar area are unfilled by dolomite crystals; reef unit 2, sample MTC 28. **F.** Columnar stromatolitic crust on a branching coral (Co). The crust is made of dense to clotted micrite and the lamination is locally outlined by *fenestrae*; reef unit 2, sample MTC 12a. **G.** Encrusting *Lithocodium aggregatum* (Lith) and boring *Troglotella incrustans* (Tro) on a branching coral (Co); first limestone bed above the reef unit 2, sample MTC 35. **H.** *Lithocodium aggregatum* (Lith) and *Bacinella irregularis* (Bac) on a branching coral (Co); reef unit 2, sample MTC 10a.

transgressive lag-storm deposits. Most Jurassic coral reefs are observed in shallow settings (Leinfelder et al., 1996). In these depositional settings, coral reefs display sharp basal surfaces where colonizing agents are not preserved or not recognizable, due to the erosive wave action. Examples of relatively deep and distal coral reefs, located between fair-weather and storm wave bases, do not record any phase of reef installation (Olivier et al., 2011). Deeper sponge bioherms, which are located below the storm wave base, can show a basal interval where numerous small sponges represent pioneer elements (Gaillard, 1983; Reolid et al., 2005; Reolid, 2011). A depositional environment below the storm wave base allowed the record of successive coral reef fossil communities colonizing the substratum (Bill et al., 2011). Thus, the record of ecological succession in fossil coral reefs is linked to a specific depth window, where corals were protected from the storm wave action and sufficiently exposed to the light for an efficient coral growth (Fig. 12).

## 6. Conclusions

The Izwarn section (High Atlas, Morocco) improves the knowledge of Late Jurassic reefs in the poorly documented North Atlantic realm. This section reveals two reef units, mainly made of corals and microbialites, included in a progradational shallowing-upward succession. A moderately diversified coral assemblage (11 genera), adapted to relatively low light levels with abundant thin platy colonies of *Dimorpharaea*, characterizes reef unit 1. This reef unit is interpreted to have developed in the lower slope of a fore-reef area. A more diversified (16 genera) coral assemblage characterizes reef unit 2 and is interpreted to reflect shallower and well-agitated waters of the upper slope of a fore-reef area. Overlaying these reef units, a set of facies indicates shallow back-reef settings. A putative reef crest is not recorded.

At the base of the reef unit 1, a phase of reef installation is observed, reflecting an ecological succession with pioneer, colonization, and diversification stages. Bioclastic deposits, mainly echinoderms and sparse corals, brachiopods and bivalves characterize the pioneer stage. A poorly diversified coral assemblage with first coral colonies preserved in life position reflects the colonization stage. The realization of a reef framework made by a more diversified coral assemblage and thick stromatolitic crusts marks the diversification stage. It is the first well-described example of an ecological succession in Late Jurassic coral reefs.

The preservation of such ecological succession in Jurassic reef systems is clearly depth-dependant, explaining its rarity in the sedimentary record. Preservation was only possible into a specific depth window where corals were not reworked by wave action, but were sufficiently exposed to light for an efficient growth leading to a purely autogenic depth change. At Izwarn, these favourable conditions probably occurred in a lower slope fore-reef area.

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