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The lithographic limestones of Cerin (southern Jura Mountains, France). A synthetic approach and environmental interpretation

Les calcaires lithographiques de Cerin (Jura méridional, France). Approche synthétique et interprétation environnementale

Paul Bernier[a,*], Georges Barale[b], Jean-Paul Bourseau[a], Eric Buffetaut[c], Christian Gaillard[a], Jean-Claude Gall[d], Sylvie Wenz[e]

[a] *Université Claude-Bernard (Lyon-1), département des sciences de la Terre, 43, boulevard du 11-Novembre-1918, 69622 Villeurbanne cedex, France*
[b] *Université Claude-Bernard (Lyon-1), Herbiers, 9, rue Dubois, 69622 Villeurbanne cedex, France*
[c] *CNRS, UMR 8538, Laboratoire de géologie de l'École normale supérieure, 24, rue Lhomond, 75231 Paris cedex 05, France*
[d] *Université de Strasbourg, Strasbourg, France*
[e] *Muséum national d'Histoire naturelle, Paris, France*

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ABSTRACT

The lithographic limestones of the Cerin quarry (southern French Jura Mountains), of Late Kimmeridgian age, were famous during the 19th century for their quality and consequently the quarry was intensely exploited. From 1975 to 1994, scientific excavations were carried out in these limestones in order to investigate the depositional environment, the burial of organisms and their taphonomy. A large set of data was collected about various organisms, unusual locomotion tracks, microbial mats and emersion structures. This led to a new interpretation of the environment as a laguna overlying a previously emergent and eroded coral reef. This laguna was episodically connected to the sea by temporary channels, during storms. Lime mud was supplied both from the sea and from the surrounding emergent areas. Most organisms, both marine and terrestrial, were transported, trapped, mixed and buried in the laguna. After death, the preservation of the carcasses was favoured by the presence of microbial mats providing superficial anoxic conditions and protecting them from decaying.

Mots clés :
Calcaires lithographiques
Jurassique supérieur
Jura
Lagerstätten
Lagune
Taphonomie

RÉSUMÉ

Les calcaires lithographiques de la carrière de Cerin, située dans le Jura méridional français, sont datés de la fin du Kimméridgien. Ils ont été très célèbres au XIX[e] siècle, pour la qualité de leur pierre, et exploités intensément pendant cette période. De 1975 à 1994, un chantier de fouilles a été installé dans ces calcaires, afin de comprendre quel était l'environnement de dépôt et comment les organismes ont été piégés et conservés. De nombreux fossiles ont été récoltés, des pistes de locomotion originales observées, des figures d'émersion mises en évidence, ainsi que l'existence et le rôle majeur de tapis microbiens. Ces informations

* Corresponding author.
E-mail addresses: paul.bernier@free.fr (P. Bernier), georges.barale@univ-lyon1.fr (G. Barale), jean-paul.bourseau@wanadoo.fr (J.-P. Bourseau), eric.buffetaut@sfr.fr (E. Buffetaut), christian.gaillard@univ-lyon1.fr (C. Gaillard), jcgall@unistra.fr (J.-C. Gall), wenz.sylvie@orange.fr (S. Wenz).

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ont conduit à une nouvelle interprétation de ce gisement, désormais considéré comme une lagune installée dans une zone déprimée d'un ancien récif corallien émergé et érodé. Cette lagune était épisodiquement connectée à la mer par des chenaux temporaires, lors de tempêtes. La boue calcaire, à l'origine des calcaires lithographiques, provenait à la fois de la mer et des espaces émergés environnants. La plupart des organismes, marins et terrestres, ont été transportés, piégés, mélangés et ensevelis dans la lagune. L'excellente conservation des fossiles a été favorisée par la présence de tapis microbiens recouvrant les cadavres très tôt, installant des conditions superficielles anoxiques les protégeant de la décomposition.

1. Geographical location

The Cerin quarry is located between Geneva and Lyons. In this area, the Rhône River flows with a sinuous course. It crosses through the southern end of the Jura Mountains at the boundary between the folded Jura Mountains (Bugey) on its northern side and the tabular Jura (Île Crémieu) on its southern side.

The hamlet of Cerin (which belongs to the village of Marchamp and is frequently referred to as Cerin–Marchamp) is located in the first foothills of the folded Jura Mountains; it is at an elevation of 650 m, about 80 km east from Lyons, and 15 km from Belley, the main town in this area (Fig. 1).

2. Historical overview

The cliff that towers above the hamlet of Cerin was exploited to extract lithographic limestones from 1835 to 1910, used mainly for printing newspapers, advertisements and various illustrations–an activity that disappeared mainly when the advent of photography made lithography obsolete. During the exploitation period (Bourseau et al., 1984), numerous fossils were found, preserved, bought, studied and published by several authors (Lortet, 1892; Meyer, 1851; Saporta, 1873, 1891; Thiollière, 1848, 1851, 1852, 1854, 1858, 1871, 1873). Most of these fossils are kept at the Musée des Confluences, Lyons (Barale et al., 1985; Philippe et al., 2004), but others are scattered in various museums all over the world.

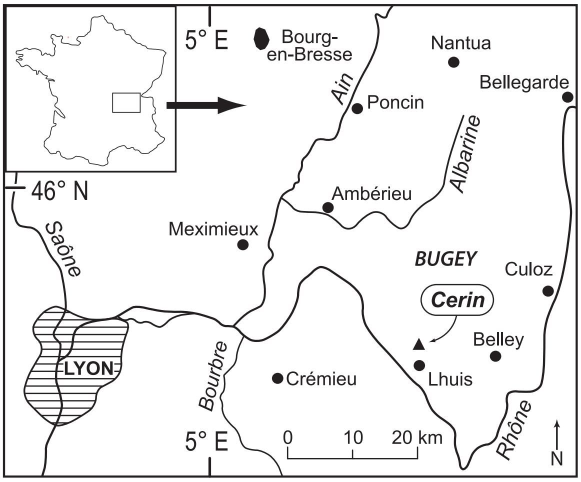

Fig. 1. Location map of the Cerin quarry (Ain, France; 45° 46′ 44″ N–5° 33′ 15″ E).

Fig. 1. Situation géographique de la carrière de Cerin (Ain, France ; 45° 46′ 44″ N–5° 33′ 15″ E).

Thereafter, the quarry was abandoned, and the studies focused more on palaeoecological aspects than on purely palaeontological problems (Enay, 1972; Gübler and Louis, 1956; Saint-Seine, 1950). Some of the Cerin reptiles were published by Cocude-Michel (1963) and by Fabre (1981).

From 1975 to 1994, the Department of Earth Sciences of the University Claude-Bernard in Lyons organized scientific excavations (managed by P. Bernier) on a small part of the quarry. During six summer weeks, every year, 15 to 20 scientists and students worked there. Each week of work was supervised in turn by scientists from the Universities of Lyons (P. Bernier, G. Barale, J.-P. Bourseau, C. Gaillard) and Strasbourg (J.-C. Gall), CNRS (E. Buffetaut) and MNHN (S. Wenz).

In the course of the excavations, more than 500 beds (each bed is 3 to 30 cm thick) were excavated. The studied cliff is about 15 m high and the upper excavated surface approximates 70 m^2. At the base of the cliff, a second, larger site (150 m^2) only a few meters thick was opened. Important technical methods (under the supervision of J.-C. Reniaud) were necessary for safety (scaffolding) and excavation (pneumatic drill, crane and bulldozer). Researchers and students were housed in an old restored sheepfold and other shelters; a well was dug and an electric line was installed.

Each bed was completely excavated before the next one was removed. Thus, the bed surfaces were clearly exposed to reveal the fossil contents and their orientation in the sediment as well as important palaeoenvironmental data. Common tracks and traces were identified that had not been observed previously. Each bed was photographed and illustrated. Sedimentary structures and the orientation of the fossils were positioned into a grid. The most interesting specimens were photographed and sampled after casting (under the supervision of G. Sirven). All data were recorded on bed data cards (Bernier et al., 1991b).

3. Questions about fossil remains

Many questions remained unanswered when the scientific excavations started in the quarry in 1975. Why were the collected fossils so diverse and originated from various environments? Why were terrestrial reptiles and terrestrial flora associated with marine fossils (e.g., fishes, echinoderms, crustaceans, molluscs)? Why did some fishes originate from the open sea (sharks, coelacanths) and others were living in coastal environments, or on the

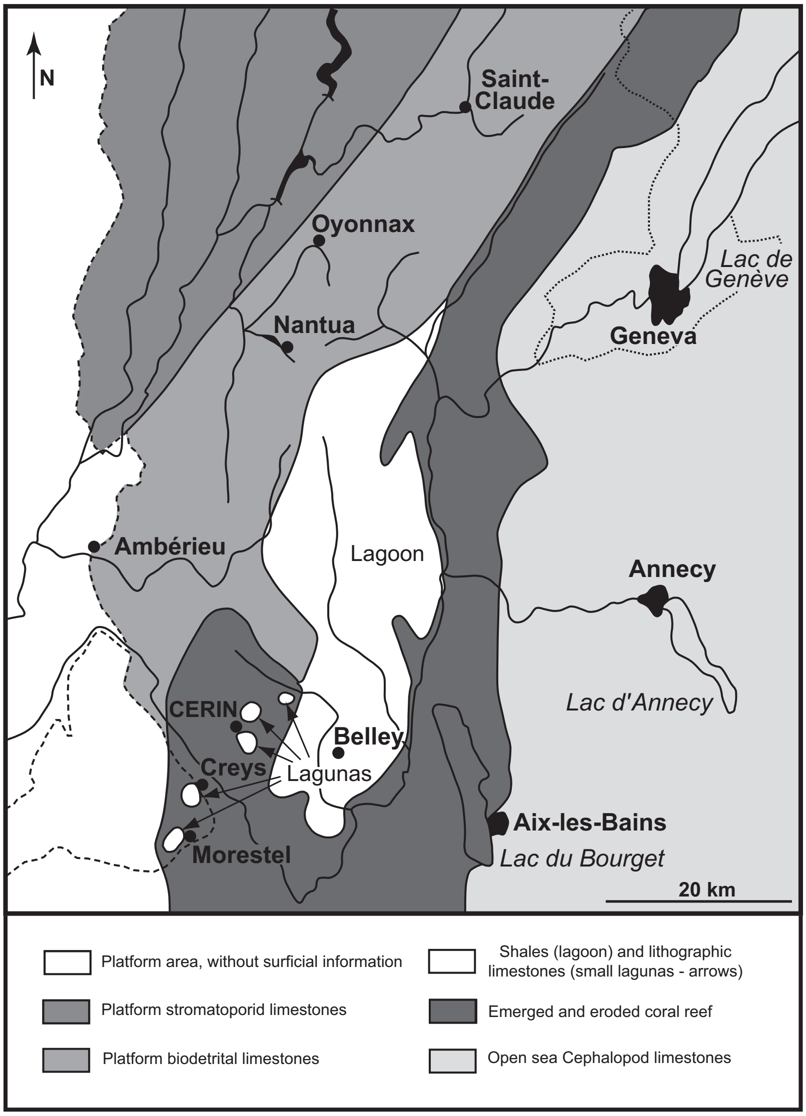

Fig. 2. Palaeogeographical map of southern Jura Mountains of the Uppermost Kimmeridgian displaying lithographic limestones sedimentation areas. The Cerin environment corresponds to a small, isolated marginal marine laguna.
Fig. 2. Carte paléogéographique du Jura méridional à la fin du Kimméridgien montrant les secteurs de sédimentation des calcaires lithographiques. L'environnement de Cerin correspond à une lagune marine bordière et isolée (d'après Bernier, 1984).
From Bernier (1984).

bottom or in coral reefs? Did all beds indicate the same environment or did they display mixed associations? Why were the fossils so perfectly preserved? Why were leaves of terrestrial flora numerous while trunks and branches were rarely found?

The aim of the excavations was to collect new samples, but also to investigate their place in the particular environment of the Cerin area and to reconstruct the conditions of life, death and burial of the organisms.

4. General sedimentary environment of the lithographic limestones

The Lithographic Limestones of Cerin are dated to the Uppermost Kimmeridgian (Bernier, 1984; Enay et al., 1994). During this time, the sea-level fell and the long and wide coral reef complex along the Tethys Sea became emergent (Fig. 2). The exposed and eroded coral reef formed a J-shaped reef barrier that enclosed a vast back-reef laguna with calm stratified waters, where bituminous laminites were deposited. Nowadays, they are still exploited in the Orbagnoux mine and, in the past, in Saint-Champ-Chatonod and Lac d'Armailles (Bernier, 1984). Periodically, the coral environment platform emerged and then submerged again. When emerged, the coral barrier eroded and the resulting bioclastic sands were deposited upon the reef (Landaize Limestones). The resulting morphology was not smooth, but consisted of topographic irregularities and the depressions were occupied by small quiet lagunas where lime mud could accumulate.

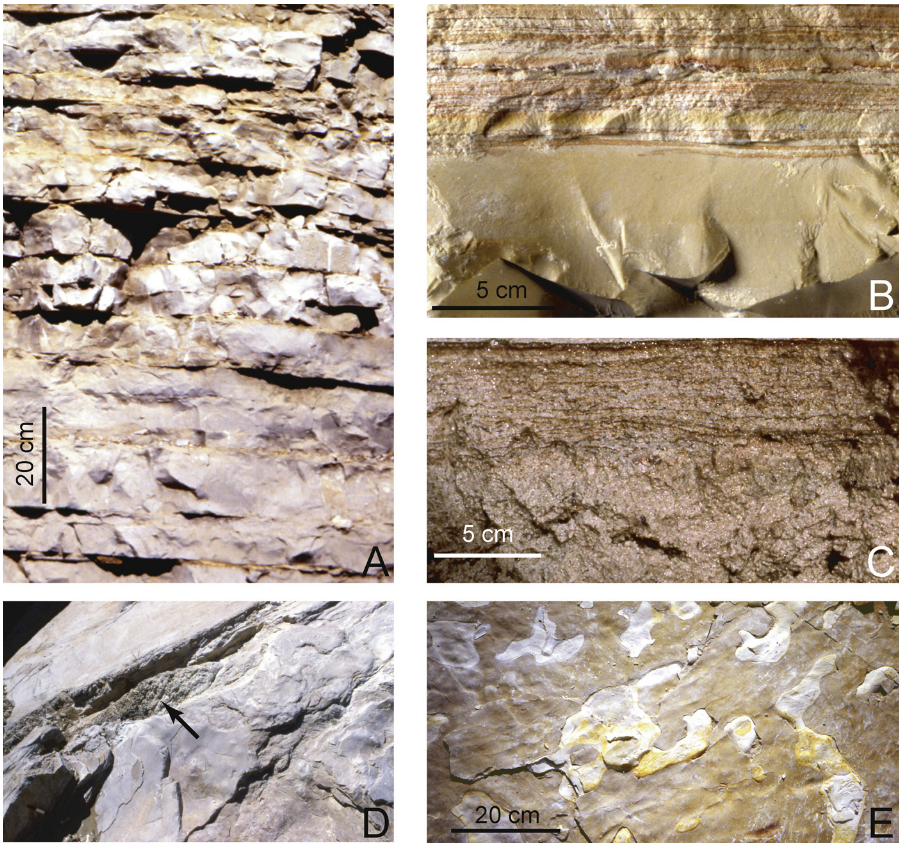

Fig. 3. (Colour online). Lithology–**A.** Lithographic limestone cliff in the Cerin quarry. Every bed displays at the top reddish laminae, microbial in origin. **B.** Lithographic limestone is homogeneous, fine-grained (micritic) and smooth to the touch. It has too conchoidal fracture and sharp edges. It is covered of reddish laminae, some millimetres to several centimetres in size, containing fossils. **C.** Lime mud from Aldabra (Seychelles) with laminated microbial films on the upper part. Aldabra lime mud is more detrital than the micritic one observed in the lithographic limestone of Cerin. **D.** The eroded substrate protrudes (arrow) through the surrounding lithographic beds, at the quarry base, displaying substratum surface irregularities. **E.** White flint level in the lithographic limestone of the lower part of the quarry.

Fig. 3. (Couleur en ligne). Lithologie–**A.** Falaise des calcaires lithographiques de la carrière de Cerin. Au sommet de chaque banc, la coloration rouille correspond aux lamines d'origine microbienne. **B.** Le calcaire lithographique est homogène, à grain fin (micritique), lisse au toucher. Il présente aussi une cassure conchoïdale et des bordures aiguës. Il est surmonté par quelques millimètres à plusieurs centimètres de laminite rouille qui renferme les fossiles. **C.** Équivalent actuel à Aldabra (Seychelles) montrant les lamines microbiennes supérieures. La boue calcaire sous-jacente est plus biodétritique que celle à l'origine du calcaire lithographique observé à Cerin. **D.** Pointement du substratum érodé (flèche), au travers des calcaires lithographiques à la base de la carrière, montrant bien les irrégularités de la surface de ce substratum. **E.** Niveau à silex, apparaissant blancs, dans les calcaires lithographiques de la partie inférieure de la carrière.

The sedimentary environment of these bituminous laminites has been studied by many authors (Bernier, 1984; Bernier and Courtinat, 1979; Bernier and Enay, 1972; Deflandre, 1941; Gübler and Louis, 1956; Pillet, 1885; Revil, 1911). The lagoonal water was stratified and provided favourable conditions for the decay of organic matter under anoxic conditions, providing bitumen and well-preserved fossil remains.

Historically, the Lithographic Limestones *sensu stricto* were interpreted by Tournier (1888), Saint-Seine (1949, 1950) and Enay (1955) as located behind the barrier reef. Gübler and Louis (1956) considered them deposited inside a huge atoll. The Cerin Lithographic Limestones are now considered later than the reef (Bernier, 1984). They were deposited in a lagunal environment, protected from the open sea, among emergent sandy reef islands overlying the buried reef.

5. Lithology of the Cerin quarry

The Lithographic Limestone of Cerin consists, from base to top, of thin micritic limestones with flints (Fig. 3E) irregularly alternating with laminites (3 m thick). These laminites are weakly bituminous but their smell is distinctive. They are overlain by lithographic limestones *sensu stricto* (18 m thick), classically referred to the Upper Kimmeridgian (Enay et al., 1994). The beds are thinner at the base (a few centimetres) and continuously thicker toward the top (25–30 cm) (Fig. 3A). The mean thickness is about 10 cm. The absence or scarcity of benthic microorganisms characterizes this member. Some beds of the upper part are bioturbated. Sedimentary structures and trace fossils indicating frequent emersion events are also observed.

The lithographic limestones lie upon a substrate with a strongly eroded surface resulting in a complicated relief

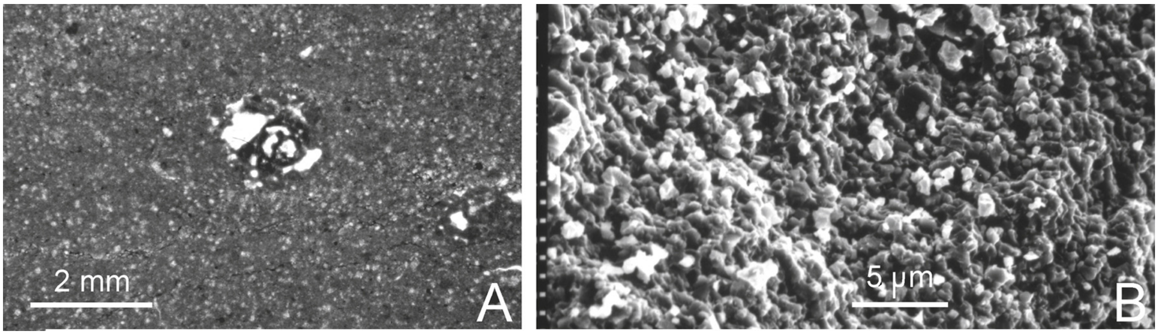

Fig. 4. Microfacies–**A.** Observed under photonic microscope, the rock corresponds to a fine micrite where foraminifera (*Everticyclammina virguliana* Koechlin) are exceptional. **B.** Micrite homogeneity and smallness are well observed under SEM. Calcium carbonate grains are of micrometric size.
Fig. 4. Microfaciès–**A.** Observée au microscope photonique, la roche correspond à une micrite fine où les foraminifères (*Everticyclammina virguliana* Koechlin) restent exceptionnels. **B.** Le microscope électronique à balayage révèle l'homogénéité et la finesse de la micrite. La taille des grains de carbonate de calcium est de l'ordre du micromètre.

perforated by lithophagous organisms (Fig. 3D). This substrate reflects bioclastic shelly sands (Bernier et al., 1994). The very thin laminites just above the substrate are variable in thickness and frequently display slope structures and slumps.

6. The lithographic limestones

A lithographic limestone is precisely defined. It is a very pure, extremely fine-grained limestone, consisting of calcite microcrystals about one micron in size, allowing its use for lithography. Its homogeneous appearance results from the grain size and from the extreme scarcity of microorganisms and detrital remains. The essential quality required by lithography is the homogeneous and fine-grained texture of the limestone. Its appearance is very smooth, with conchoidal breaking planes and sharp edges (Fig. 3B) comparable to those of flints (Barale et al., 1985; Bernier, 1994, 1997). The term lithographic is too often wrongly extended to fine-grained limestones that do not exhibit all the characteristics mentioned above.

The Lithographic Limestone of Cerin clearly adheres to these characteristics and consists essentially of $CaCO_3$ (99.5%); the calcite microcrystals are smaller than one micron (Fig. 4B). Sometimes, the base of coarser beds reveals the presence of scanty foraminifera, mainly *Everticyclammina virguliana* KOECHLIN, miliolids and ataxophragmiids (Fig. 4A) and algae: *Thaumatoporella parvovesiculifera* (RAINERI) PIA (Bernier et al., 1991a). When observed under SEM, micrite appears to be detrital, without any traces of coccoliths (Fig. 4B).

Each bed is capped by laminites, a few millimetres to several centimetres in thickness, consisting of smooth and continuous layers in which well-preserved fossils are included. These laminations are easily distinguishable by their reddish/purplish colour, which commonly stands out in contrast to the beige colour of the micrite.

7. Fossil organisms

7.1. Marine organisms

Contrary to popular understanding, fossils are not especially abundant at Cerin. Many beds are poor in fossils and many of these are neither spectacular nor large. It is only because a large volume of limestone was excavated that numerous and diverse fossils were collected.

7.1.1. Algae

Green algae are represented by dasyclads, with very frequent isolated whorls of *Clypeina jurassica* (FAVRE) and *Campbelliella striata* (RADOICIC) BERNIER (Fig. 5C). However, some bushes of complete thalli more than 10 cm long of *C. jurassica* were collected. These long axes display variation in whorl diameter along the main axis (Fig. 5B).

Two unusual species occur and are difficult to interpret. The first has long axes ending in a lengthened oblong head. This species could be attributed to *Goniolina janeti* SAPORTA (Bernier et al., 1991a), close to *Goniolina geometrica* (ROEMER) BUVIGNIER (Bassoullet et al., 1978). Usually, dasyclads are very fragile after death and very quickly disarticulated. They are complete here, indicating a short transport with feeble current and quick burial after they were uprooted. Marks imprinted into the sediment surface are indicative of a weak current and very shallow water depth (Fig. 5A and Fig. 6A). A single very long (more than 30 cm long), yet unidentified specimen was collected (Fig. 5D).

7.1.2. Invertebrates

The invertebrate fauna is not very abundant, but it is diverse. Molluscs are fairly rare and represented by small bivalves (ostreids, pectinids) (Fig. 7E). Gastropods are very scarce and cephalopods were only found at the base of the Lithographic Limestone. They are represented by ammonites: oppeliids, perisphinctids, aspidoceratids: *Aspidoceras cf. catalaunicum* (LORIOL) (Enay et al., 1994) (Fig. 7A) and belemnites (very small *Hibolites*).

Brachiopods (terebratulids and rhynchonellids) are also very rare.

Echinoderms are fairly abundant. Some of them were collected and described when the quarry was exploited during the 19th century (Loriol, 1886-1889, 1895), but others were collected during later scientific excavations. Among them, a very well-preserved stalkless crinoid *Solanocrinites thiollieri* (LORIOL) (Fig. 8E) and the asteroids *Pentasteria (Archastropecten) lithographica* (Thiollière)

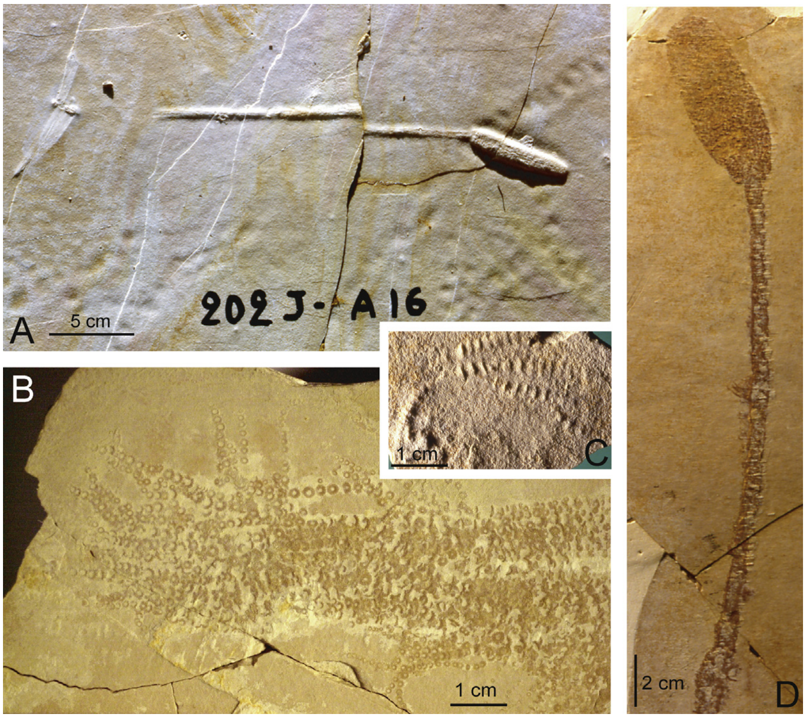

Fig. 5. (Colour online). Algae–**A**. Dasyclad alga attributed to *Goniolina janeti* Saporta. The very thin water depth and the lapping movement make the alga to oscillate and episodically touch the bottom to create small successive hollows, aligned along the weak current. Random similar hollows, scattered upon the bed, have probably the same origin. On the left top, *Zamites* fragment. Bed 202J A16. FSL 505534 (*). **B**. Dasyclad cluster of *Clypeina jurassica* (Favre). Whorls are practically connected and exceptionally well-preserved that means sudden pull-off strength and a fast burying. Bed 116C E12. FSL 505580. **C**. Dasyclad cluster of *Campbelliella striata* (radoicic) Bernier. Axes bear conical and flared whorls, fit together and well identified along the main axes. Bed 202G D11. FSL 505577. **D**. Unknown probably dasyclad alga, complete, not calcified and big-sized: the main axis is 300 mm long and the ovoid head is 80 × 30 mm. Head branches seem arranged in staggered rows. They are more difficult to be observed on the main axis but assimilatory hair is locally visible (arrow). Bed 181D Z13. FSL 505558. (*)–Acronym signification: Bed number (202J) is followed by square number on bed (A16) and collection number (FSL) of samples preserved at the "Service des collections", Université Claude-Bernard (Lyon-1).

Fig. 5. (Couleur en ligne) Algues–**A**. Algue dasycladacée attribuée à *Goniolina janeti* Saporta. La très faible épaisseur d'eau et le mouvement de clapot font osciller l'algue, qui touche épisodiquement le fond et crée les petites dépressions successives et alignées dans le sens du faible courant. Les dépressions similaires éparses et aléatoires à la surface du banc ont sans doute la même origine. Fragment de *Zamites*, en haut à gauche. Banc 202J A16. FSL 505534 (*). **B**. Touffe d'algue dasycladacée *Clypeina jurassica* (Favre). Les verticilles sont pratiquement en connexion et présentent une conservation exceptionnelle, ce qui signifie l'arrachement brutal et ensuite la préservation par un enfouissement rapide. Banc 116C E12. FSL 505580. **C**. Touffe d'algue dasycladacée *Campbelliella striata* (radoicic) Bernier. Axes portant des verticilles coniques, évasés et emboîtés, reconnaissables le long des axes principaux. Banc 202G D11. FSL 505577. **D**. Probable dasycladacée inconnue, complète, non calcifiée et de très grande taille : la tige atteint 300 mm de long et la tête ovoïde fait 80 × 30 mm. Les ramifications de la tête semblent disposées en quinconce. Elles sont plus difficiles à observer dans la tige, mais on peut voir des poils assimilateurs s'en écarter localement. Banc 181D Z13. FSL 505558. (*)–Signification des acronymes : le numéro de banc (202J) est suivi du numéro du carré sur le banc (A16) et du numéro d'inventaire (FSL) des exemplaires déposés au Service des collections, Université Claude-Bernard (Lyon-1).

(Fig. 8B) and *Comptoniaster chantrei* Breton (Fig. 8A) were collected (Breton et al., 1994). Crushed echinoid tests are attributed to *Pseudodiadema* cf. *pseudodiadema* and *Pygurus* (Bourseau et al., 1994). Sometimes, their spines are still connected to the test, other time, spines have been oriented by current. Some specimens of brittle-star ophiurids were collected (Bourseau et al., 1991). Many echinoderms (especially ophiurids and asteroids) lie on the bottom with their aboral face turned downward, indicating transportation.

Arthropods are represented by diverse decapod crustaceans. Glypheoidan lobsters are represented by *Gigacerina saemanni* (Oppel), the largest glypheid species of the fossil record (Charbonnier et al., 2013) and also by a poorly preserved mecochirid close to *Mecochirus* sp. (Fig. 7B). Polychelidan lobsters are represented by *Cycleryon bourseaui* Audo et al. and *Soleryon amicalis* Audo et al. (Audo et al., 2014) (Fig. 7C). Some astacidans and penaeidans are also probably present (Van Straelen, 1922, 1925). Two limulids *Mesolimulus walchii* (Desmarest) (Fig. 7D) were also found (Gall et al., 1996).

Finally, several beds revealed numerous well-preserved jellyfish imprints (Fig. 8D), often showing their four gonads and their tentacles (Gaillard et al., 2006). Such a quality of preservation is indicative of optimal conditions of fossilization and allowed to define new taxa: *Paraurelia cerinensis* Gaillard and Goy, *Bipedalia cerinensis* Gaillard and Goy and *Paracarybdea lithographica* Gaillard and Goy.

7.1.3. Marine vertebrates: the fishes

Fishes are very diverse and abundant. Several thousand specimens have been recorded. At least 50 species belonging to chondrichthyans, actinopterygians and actinistians were recognized (Thiollière, 1848, 1852, 1854, 1858, 1873;

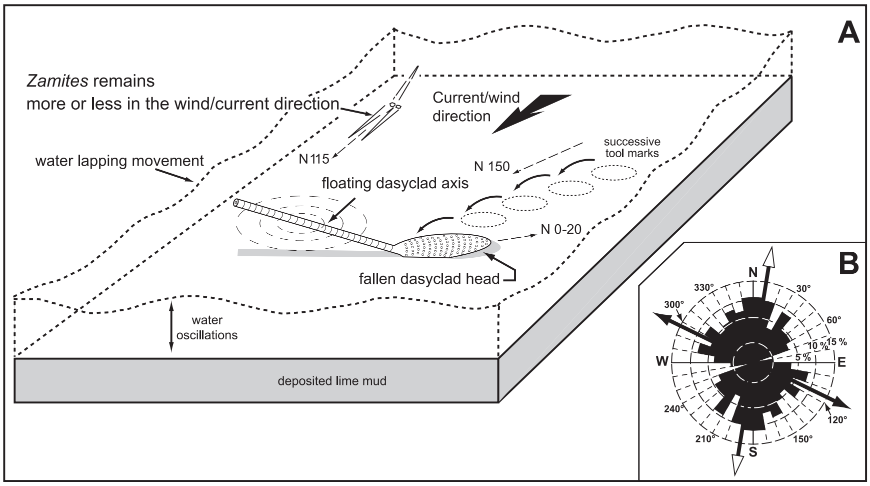

Fig. 6. **A.** Tool marks. Last lapping movements before dasyclad alga falling (bed 202J). Weak current and very thin water depth give successive hollows oriented and giving the current way. **B.** Rose diagram of dasyclad axes orientation (bed 202F, 132 data). White arrow: main direction of dasyclad axes; black arrow: approximate wind or current direction.

Fig. 6. **A.** Figures de charge. Derniers mouvements du clapot avant la chute finale de l'algue dasycladale (banc 202J). Le faible courant et la tranche d'eau très mince déplacent l'algue, qui touche épisodiquement le fond et crée de petites dépressions successives orientées dans le sens du courant. **B.** Le diagramme en rosace montre l'orientation des axes de dasycladales (banc 202F, 132 mesures). Flèche blanche : direction principale des axes de dasycladales ; flèche noire : direction approximative du vent ou du courant.

Saint-Seine, 1949; Wenz et al., 1994). Most of the collected specimens are complete or almost complete, in anatomical connections. The Cerin fish fauna is characteristic of the Late Jurassic. Some species are only known from this locality, but a large number of them are also known in the Bavarian Upper Jurassic.

Chondrichthyans (sharks and batoids) correspond to less than 5% of the fish fauna and are known by complete skeletons. Sharks (*Phorcynis* sp., *Corysodon* sp.) are of small primitive forms, not more than 45 cm in total length and rare in the Cerin quarry. Rays (*Belemnobatis* sp., *Spathobatis* sp.) (Fig. 9F) are more frequent and some reach up to 90 cm in length. They display primitive characters.

Actinopterygians comprise 95% of the Cerin ichthyological assemblage. This particular fish fauna is important and corresponds to the beginning of the considerable changes that led to the modern fish fauna (Wenz et al., 1994). During the Late Jurassic, most chondrosteans disappeared; they are absent in the Cerin quarry, while they are still present in limited numbers in the Upper Jurassic of Bavaria up to the Early Cretaceous. Neopterygians radiated explosively during the Late Jurassic while they had been poorly represented in the Triassic. The semionotids: *Oligopleurus* (Fig. 10B), *Scheenstia*, *Callipurbeckia* (Fig. 10C), amiids and pachycormids are scarce or very scarce in the Cerin quarry, while gyrodontids, macrosemids (Fig. 9E), caturids and, to a lesser extent, ionoscopids (Fig. 9B, C), are abundant and represented by a large number of species. Teleostean expansion is reflected more by the abundance of specimens than by taxonomic diversity: *Leptolepides* compose the majority of juvenile specimens found at Cerin, while *Allothrissops* and *Thrissops* (Fig. 10A) correspond to about 25% of the adult fauna.

Actinistians are represented by only one small-sized genus: *Holophagus*, making up less than 0.5% of the whole fauna.

The fish fauna consists of fishes from various environmental origins:

- sharks and rays (Fig. 9F) lived along the coast or close to the bottom and fed on molluscs and crustaceans;
- pycnodontids of the family Gyrodontidae are one of the most characteristic fishes found at Cerin. *Proscinetes bernardi* (Thiollière) (Fig. 9D) has an almost disc-shaped body and pavement-like teeth arranged in regular rows indicating a durophagous diet. The shape of pycnodontids is similar to that of parrotfish or angelfish living in coral reef context, although they are not related. This group is abundant at Cerin in terms of both number of species and number of specimens and reveals the presence of an optimal environment available close by;
- semionotids, such as *Scheenstia laevis* (Agassiz), were heavily built and poorly able to swim. They lived close to the bottom; their teeth indicate they were adapted to crushing;
- on the contrary, the hydrodynamic body shape and powerful teeth of *Caturus* suggest it being an agil and ferocious fish-eating predator, able to range far from the coast. The snake-like *Belonostomus tenuirostris* Agassiz (Fig. 9A) was a fast swimmer–at least over short distances. Its elongated snout is a frequent feature of piscivorous forms;
- microphagous nutrition is illustrated by *Leptolepides*. This very abundant small fish probably lived in shoals and fed on plankton. The high number of juvenile specimens suggests that breeding grounds were not far away.

The Cerin fishes were diverse and originated from various ecological niches. Their association within the Cerin Lithographic Limestone suggests that most of them were allochthonous, transported from their living areas and mixed together in the Cerin laguna.

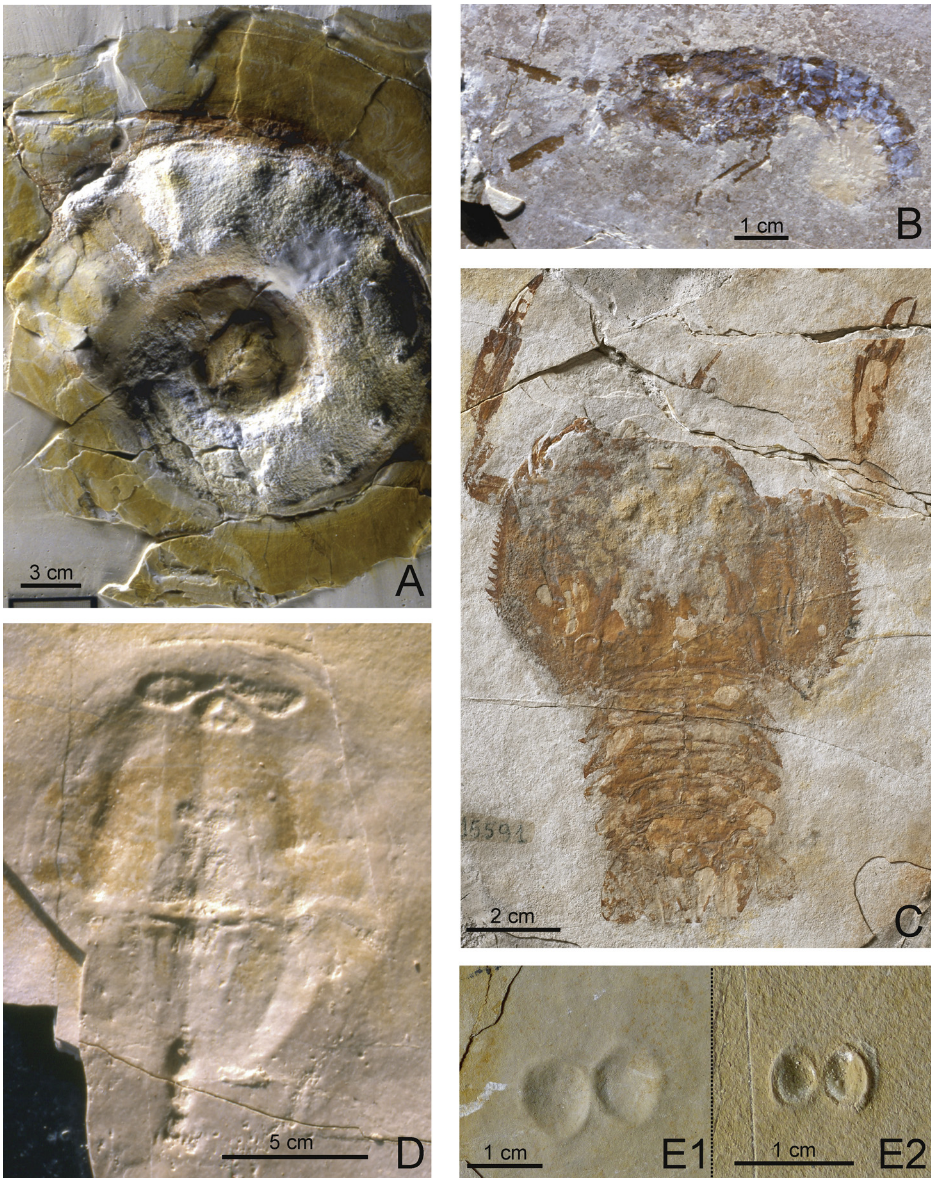

Fig. 7. (Colour online). Invertebrates (Mollusks and Crustaceans) – **A.** Ammonite Aspidoceratid. *Aspidoceras* sp. gr. *catalaunicum* (Loriol). Inner whorls of a macroconch specimen preserved with shape, strongly crushed, made in porous silica. Bed 125 Y16 (*), FSL 401805. **B.** Poorly preserved mecochirid close to *Mecochirus* sp. (Decapoda). Bed 211A Z15. FSL 501641. **C.** Eryonid lobster (Decapoda, Eryonidae): *Soleryon amicalis* Audo et al. (2014), paratype MHNL 20-015591 (*), dorsal view. **D.** Merostomata Xiphosura. *Mesolimulus walchii* (Desmarest). Bed 223D A6, FSL 401501. **E.** Bivalvia about which open shells are still connected after death, indicating a quick burial. **E1.** Bed 112 B14, FSL 500808; **E2.** Bed 258 B A14, FSL 500698. (*) – MHNL: collection number of samples preserved at the Musée des Confluences, Lyon Centre de conservation et d'étude des collections.

Fig. 7. (Couleur en ligne). Invertébrés (Mollusques et Crustacés) – **A.** Ammonite Aspidocératidé. *Aspidoceras* sp. gr. *catalaunicum* (Loriol). Tours internes siliceux d'un individu macroconque à forme conservée, très écrasée. Silice vacuolaire. Banc 125 Y 16, FSL 401805. **B.** Exemplaire altéré de mécochiridé proche de *Mecochirus* sp. (Decapoda). Banc 211A Z15. FSL 501641. **C.** Eryonidé (Decapoda). *Soleryon amicalis* Audo et al. (2014), paratype MHNL 20-015591 (*), vue dorsale. **D.** Merostomata Xiphosura. *Mesolimulus walchii* (Desmarest). Banc 223D A6, FSL 401501. **E.** Bivalve dont les valves sont en connexion, indiquant une préservation rapide après la mort. **E1.** Banc 112 B14, FSL 500808 ; **E2.** Banc 258B A14, FSL 500698. (*) – MHNL : Numéro d'inventaire des spécimens conservés au Musée des Confluences, Lyon – Centre de conservation et d'étude des collections.

7.2. Terrestrial organisms

The terrestrial flora is represented by very abundant plant remains (Barale, 1981; Saporta, 1873). Terrestrial fauna consists of various reptiles, known either from their skeletons (Cocude-Michel, 1963; Lortet, 1892; Meyer, in Thiollière, 1851) or from their footprints (Bernier et al., 1982). The lack of insects has to be noted, all the more so that they are present in the Bavarian sediments.

7.2.1. The Flora

The **herbaceous flora** corresponds to pteridophytes (fairly incomplete *Sphenopteris* fronds).

Fig. 8. (Colour online). Invertebrates (Echinoderms and Cnidarians) – **A.** Asterid. *Comptoniaster meyeri* Breton. Paratype 2 FSL 401101 a, actinal view. Bed 295A A2. **B.** Asterid. *Pentasteria (Archastropecten) lithographica* (Thiollière). Holotype MHNL 20-0015381, actinal view. **C.** Echinid. Diadematacea. Primary slender spines radiate around the test. They are not oriented by a current. Bed 295B C6. FSL 401053 a. **D.** Jellyfishes. Upper surface of bed 84, with several specimens of the jellyfish *Paraurelia cerinensis* Gaillard and Goy. Note the four central symmetrical imprints probably corresponding to gonads. Field photograph. **E.** Crinoid Comatulida. *Solanocrinites thiollierei* (de Loriol). Holotype MHNL 20-0015376, abactinal view.

Fig. 8. (Couleur en ligne). Invertébrés (Échinodermes et Cnidaires) – **A.** Astéridée. *Comptoniaster meyeri* Breton. Paratype 2 FSL 401101 a, vue actinale. Banc 295A A2. **B.** Astéridée. *Pentasteria (Archastropecten) lithographica* (Thiollière). Holotype MHNL 20-0015381, vue actinale. **C.** Échinide. Diadematacea. Les radioles primaires sont disposés de façon rayonnée à la périphérie du test. Ils ne sont pas orientés par un courant. Banc 295B C6. FSL 401053 a. **D.** Méduses. Surface supérieure du banc 84, montrant plusieurs exemplaires de *Paraurelia cerinensis* Gaillard et Goy. Les quatre dépressions centrales symétriques correspondent probablement aux gonades. Photo de terrain. **E.** Crinoïde comatulidé *Solanocrinites thiollierei* (de Loriol). Holotype MHNL 20-0015376, vue abactinale.

The **semi-arborescent flora** consists of Pteridospermales (*Cycadopteris, Pachypteris*), Cycadales (*Apoldia, Cycalacis*) and Bennettitales (*Zamites*). *Cycadopteris jurensis* Kurr (Fig. 11B) is often known by complete fronds. At the Cerin quarry, plant fossils are devoid of organic trace matter due to unfavourable environmental conditions during diagenesis. The Creys quarry, north of Morestel, just a few kilometres away from Cerin, and of the same age (Barale, 1981), allowed organic preservation. However, the very fine micritic lime mud allowed the preservation of the leaflet venation. Bennettitales are by far the most abundant order with the species *Zamites feneonis* (Pomel) Ettingshausen (Fig. 11A). *Zamites* fronds are comparable to those of

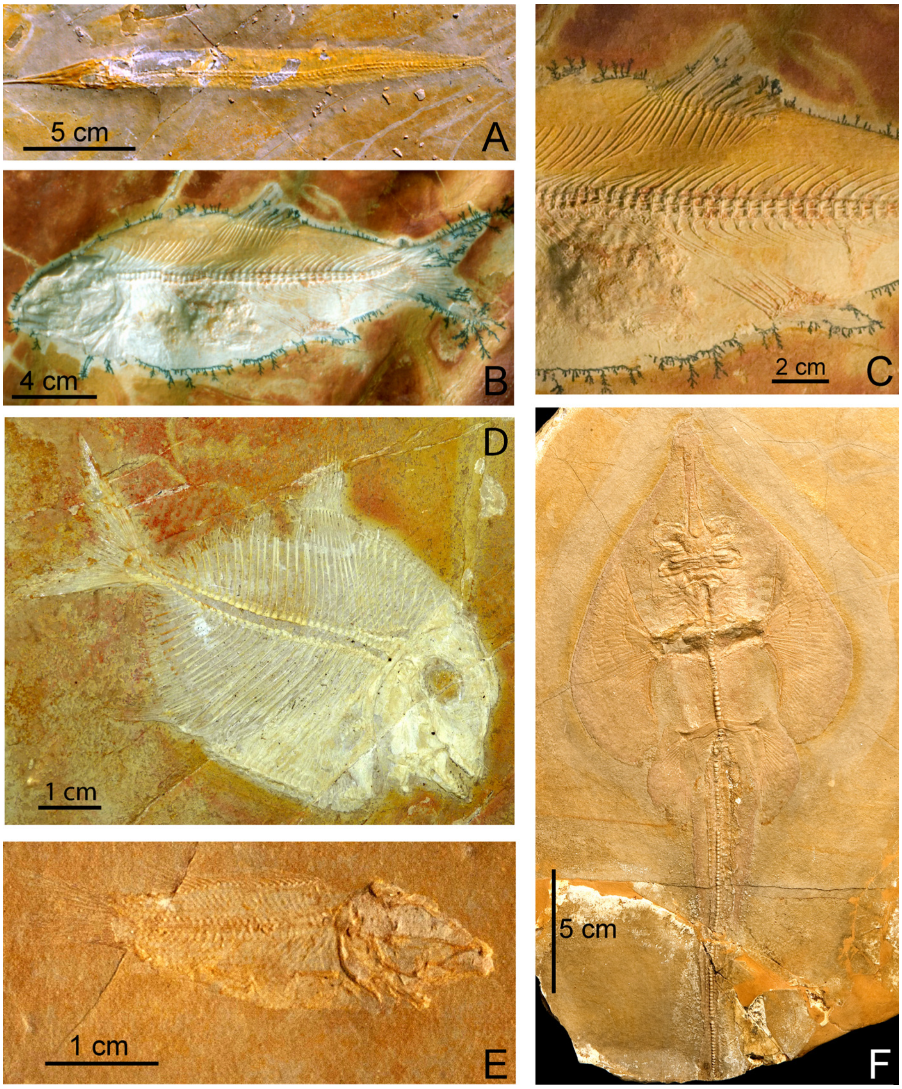

Fig. 9. (Colour online). Fishes (1) – **A.** Aspidorhynchid. *Belonostomus* sp. Bed 225C Y16. FSL 501974 a–b. **B.** Actinopterygian. *Ionoscopus* sp. Bed 59A D10. FSL 504070. **C.** Actinopterygian. *Ionoscopus* sp. Bed 59A D10. Detailed photograph displaying the high quality of preservation (skeleton and stomachal content). FSL 504070. **D.** Pycnodontid. *Proscinetes bernardi* (Thiollière). Bed 82 A7, FSL 504419. **E.** Macrosemid. *Notagogus* sp. Bed 211A B8. FSL 400047. **F.** Batoid. *Spathobatis bugesiacus* Thiollière. Holotype MHNL 20-0015307, photo P. Ageneau.

Fig. 9. (Couleur en ligne). Poissons (1) – **A.** Aspidorhynchidé. *Belonostomus* sp. Banc 225C Y16. FSL 501974 a–b. **B.** Actinoptérygien. *Ionoscopus* sp. Banc 59A D10. FSL 504070. **C.** Actinoptérygien. *Ionoscopus* sp. Banc 59A D10. Photo de détail permettant d'observer la haute qualité de conservation (squelette et contenu stomacal). FSL 504070. **D.** Pycnodontidé. *Proscinetes bernardi* (Thiollière). Banc 82 A7, FSL 504419. **E.** Macrosémidé *Notagogus* sp. Banc 211A B8. FSL 400047. **F.** Batoïde. *Spathobatis bugesiacus* Thiollière. Holotype MHNL 20-0015307, photo P. Ageneau.

some tropical living *Zamia*. The leaflet extremity, probably more fragile, is often missing, as a result of violent wind action.

The **arborescent flora** consists of Coniferales: *Brachyphyllum, Pagiophyllum* (close to some living Araucariaceae: presence of cones and tracheids of araucarian type) (Fig. 11C), *Cupressinocladus*, and *Cupressinoxylon* (probably Cheirolepidiaceae). Only the terminal parts of twigs are known, suggesting selective transport of the plant material.

The semi-arborescent flora is interpreted as growing close to the shore while the arborescent flora grew further away on higher ground. Coriaceous leaves, protected stomatal zones (for example *Cycadopteris* pinnules with revolute margins and numerous trichomes around stomatal apparati), and conifers with adpressed short leaves along twigs, suggest a hot and dry climate with plants that are strongly protected against evapotranspiration.

7.2.2. Terrestrial and amphibious vertebrates

They all belong to the Reptilia. Their skeletons are usually complete and rarely disarticulated. They are well preserved, but scarce. Most of them were collected during commercial excavation in the 19th century and reposited at the Musée des Confluences, Lyons (MHNL). The reptile

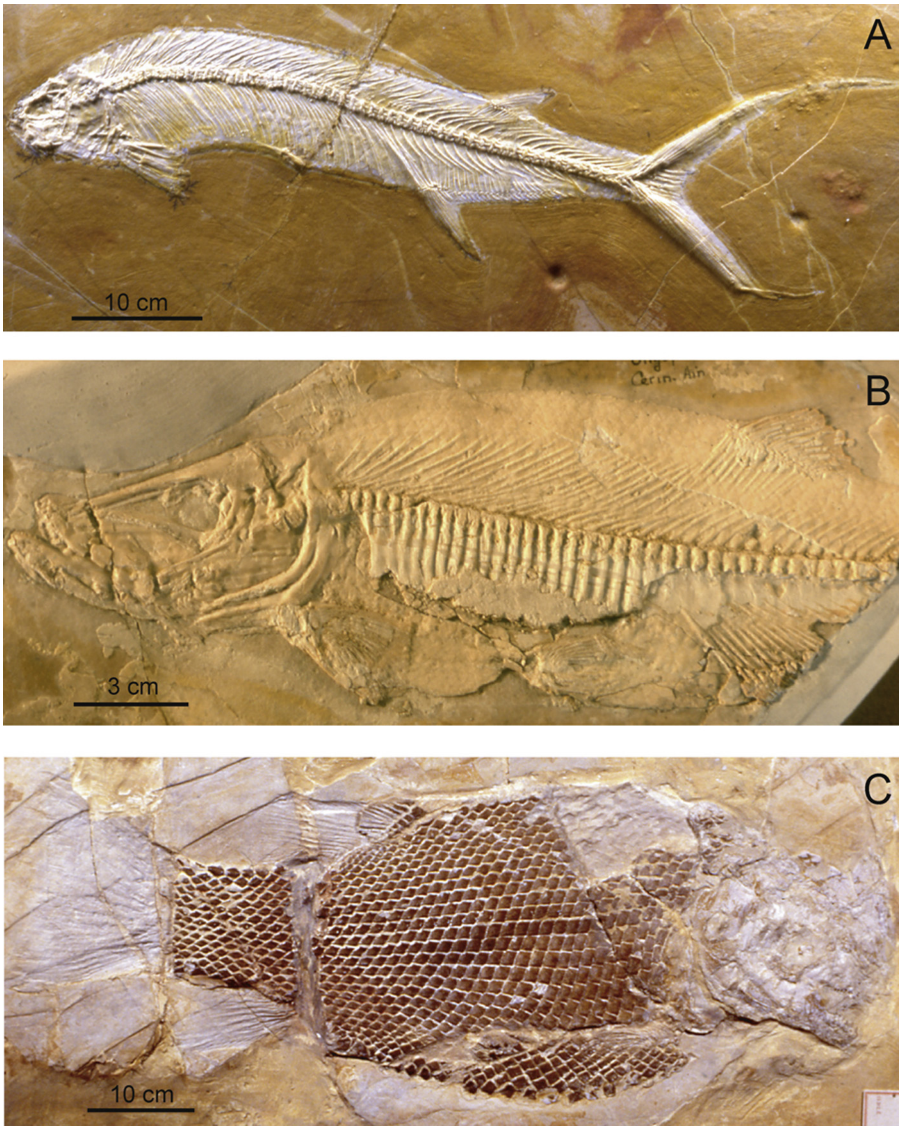

Fig. 10. (Colour online). Fishes (2) – **A**. Actinopterygian Ichthyodectid. *Thrissops formosus* (Agassiz). Bed 82 C14, FSL 503200. **B**. Actinopterygian. *Oligopleurus esocinus* Thiollière. MHNL 20-0015470. **C**. Actinopterygian Semionotid. *Scheenstia notoptera* (Agassiz). MHNL 20-0015764.

Fig. 10. (Couleur en ligne). Poissons (2) – **A**. Actinoptérygien Ichthyodectidé. *Thrissops formosus* (Agassiz). Banc 82 C14, FSL 503200. **B**. Actinoptérygien. *Oligopleurus esocinus* Thiollière. MHNL 20-0015470. **C**. Actinoptérygien Sémionotidé. *Scheenstia notoptera* (Agassiz). MHNL 20-0015764.

specimens are diverse and show adaptation to various ways of life.

Chelonians are represented by small, probably amphibious, turtles: *Idiochelys* (Fig. 12F), *Eurysternum*.

Rhynchocephalians are represented by several lizard-like genera having probably terrestrial habits: *Homoeosaurus* (Fig. 12C), *Saphaeosaurus* (Fig. 12B). Only *Pleurosaurus* is a specialized form adapted to aquatic life, with an elongate body and short limbs.

Crocodilians are mainly represented by small forms with short snouts and long limbs (Atoposauridae), which must have been essentially terrestrial: *Atoposaurus*, *Alligatorellus* (Fig. 12E), *Alligatorium*. *Crocodileimus robustus* Jourdan (Fig. 12A), known by a single perfectly preserved specimen, is a robust form of small long snouted specimen, with pointed teeth adapted for capturing fish (Buffetaut, 1994).

Pterosaurians are known only from a few isolated bones (Fig. 12D) referred to the genus *Pterodactylus* (Buffetaut et al., 1990). This is in contrast with the many complete pterosaur specimens, belonging to various taxa, known from the lithographic limestones of Bavaria (Frickhinger, 1994).

The absence of large reptiles such as ichthyosaurs, plesiosaurs and marine crocodilians is worth noting. The reptile fauna from the Cerin quarry is thus dominated by small terrestrial, amphibious or coastal species. Large reptiles are only represented by footprints.

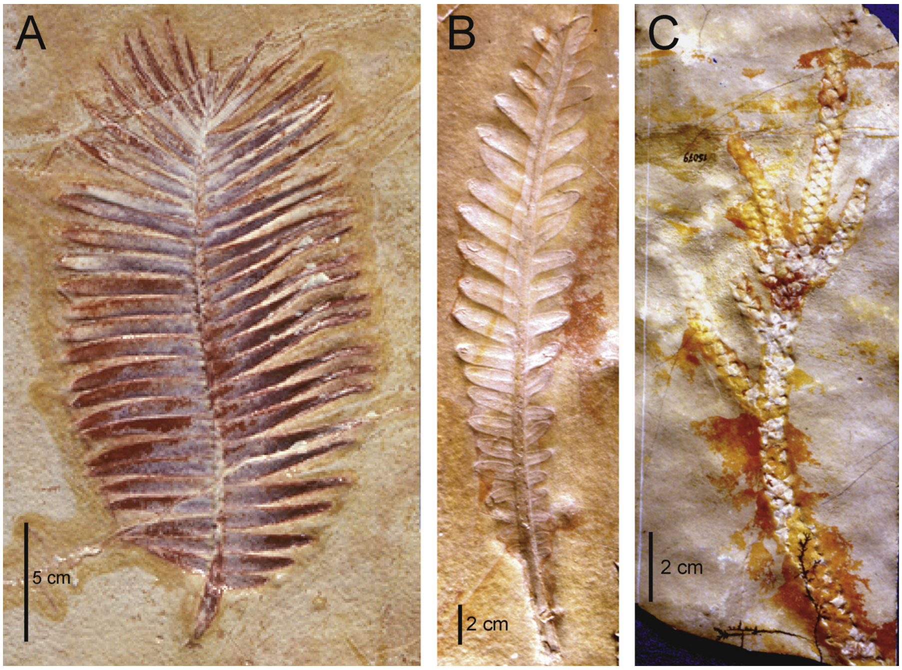

Fig. 11. (Colour online). Terrestrial Flora – **A**. Complete and very well-preserved leaf of *Zamites feneonis* (POMEL) ETTINGSHAUSEN. Lower excavation, "Hole" area, Bed 6T, FSL 506448. **B**. *Cycadopteris jurensis* (KURR) HIRMER. MHNL 20-0015078. **C**. Branch of the coniferal *Pagiophyllum cirinicum* (SAPORTA) HEER. MHNL 20-0015079.

Fig. 11. (Couleur en ligne). Flore terrestre – **A**. Fronde complète et très bien conservée de *Zamites feneonis*. (POMEL) ETTINGSHAUSEN. Fouille inférieure, secteur dit du « Trou », banc 6T, FSL 506448. **B**. *Cycadopteris jurensis* (KURR) HIRMER. MHNL 20-0015078. **C**. Rameau de coniférale *Pagiophyllum cirinicum* (SAPORTA) HEER. MHNL 20-0015079.

8. Trace fossils

The ichnofauna of the Lithographic Limestones of Cerin had never been documented prior to the beginning of the scientific excavation. It shows a great diversity of very original invertebrate and vertebrate trace fossils.

8.1. Invertebrate traces

Tubularina lithographica GAILLARD is the most usual trace fossil. They are small burrows, millimeters in diameter, often filled by small ellipsoidal faecal pellets. They are the result of the burrowing activity of annelids, which occurred in the intertidal zone, withstanding long subaerial periods at low tide (Gaillard et al., 1994a). They are abundant but only observed in the upper part of the lithographic limestones. Just before the occurrence of *Tubularina* burrows, some beds display *Thalassinoides* and *Rhizocorallium* which are classically considered as crustacean burrows. The *Tubularina–Thalassinoides–Rhizocorallium* association emphazises a very clear transition period in the history of the Cerin laguna (Gaillard et al., 1994a).

A well-preserved limulid trackway is related to *Kouphichnium lithographicum* (OPPEL). This trackway is very straight, three metres long and exhibits ten successive sets of prints. It was made by a very large adult and, contrary to the famous *mortichnia* from Solnhofen, indicates a fast-moving animal on the sea-floor (Gaillard, 2011). It is similar to the limulid trackway recently found in the Tithonian lithographic limestones from Canjuers (Peyre de Fabrègues and Allain, 2013).

8.2. Vertebrate tracks

Unknown before the scientific excavations (1975–1994), they were undoubtedly the most unexpected discoveries at Cerin. They were found thanks to the excavation techniques exposing the surface, bed after bed, over a vast area.

Chelonichnium cerinense DEMATHIEU and GAILLARD is a wide trackway (Bernier et al., 1982), probably left by a giant terrestrial tortoise (Fig. 13A and Fig. 14B). It is relatively similar to those nowadays observed on the Galapagos Islands or the Seychelles Islands (Aldabra). These trace-makers were considerably larger than the small chelonids known by their skeletal remains from the same quarry. The best preserved trackway is 54 cm wide and 7 m long, a cast of which is visible in the Cerin Museum. Track analysis shows that the animal was going down a slight slope, walking on wetter and wetter mud. This tortoise was certainly moving on the edge of a sloping and wet laguna rim.

Saltosauropus latus DEMATHIEU and GAILLARD is another wide trackway (Fig. 13D and Fig. 14C) and was first interpreted as that of jumping dinosaurs (Bernier et al., 1984). Today, it is considered as giant marine turtle trackway, formed when the animals were swimming in shallow water and occasionally touched the bottom with the ends of their limbs (Gaillard et al., 2003). This conclusion results from the discovery of clear swimming traces (Fig. 13F and Fig. 14A) and intermediate forms similar to *Saltosauropus* (Fig. 13E). These marine turtles possibly approached emerged areas to lay their eggs, as they do today. Their trackways are very wide and indicate very large animals. It is an original

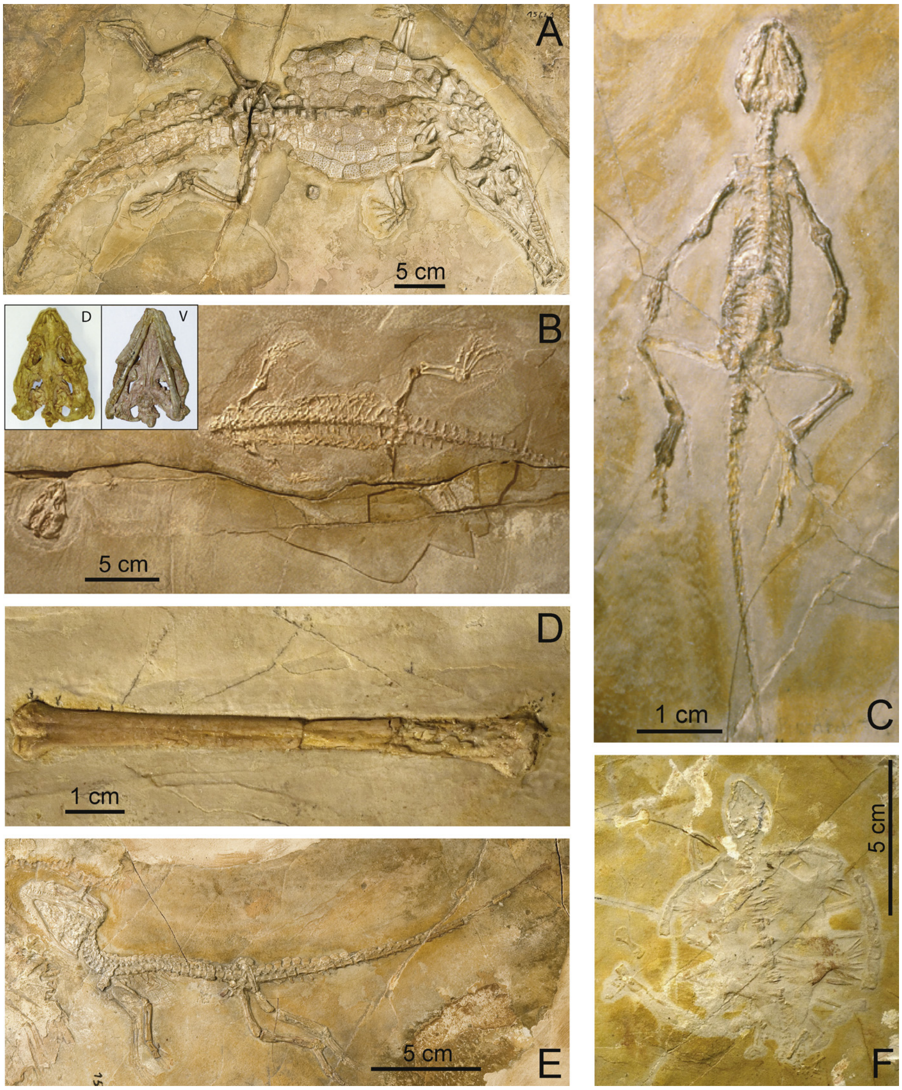

Fig. 12. (Colour online). Reptiles – **A.** *Crocodileimus robustus* Jourdan. Holotype MHNL 20-0015641. Ventral view. **B.** Sapheosaurus *thiollierei* Lortet. At the top left, dorsal (D) and ventral (V) views of the head. Bed 75 Q15. FSL 402002. **C.** *Homoeosaurus maximiliani* (Meyer). Ventral view. MHNL 20-0015677. **D.** Pterodactyloid ulna. Probable Bed 70, out of excavation. FSL 401601. **E.** *Alligatorellus beaumonti* Gervais Lateral view. MHNL 20-0015638, photo P. Ageneau. **F.** ? *Idiochelys* sp., juvenile partly disarticulated. Ventral view. Bed 80, FSL 506735a.

Fig. 12. (Couleur en ligne). Reptiles – **A.** *Crocodileimus robustus* Jourdan. Holotype MHNL 20-0015641. Vue ventrale. **B.** Sapheosaurus *thiollierei* Lortet.En haut à gauche, vues dorsale (D) et ventrale (V) de la tête. Banc 75 Q15. FSL 402002. **C.** *Homoeosaurus maximiliani* (Meyer). Vue ventrale. MHNL 20-0015677. **D.** Os de ptérodactyle entier. Ulna. Probable banc 70, hors fouille. FSL 401601. **E.** *Alligatorellus beaumonti* Gervais. Vue latérale. MHNL 20-0015638, photo P. Ageneau. **F.** ? *Idiochelys* sp., juvénile, partiellement démantelé. Vue ventrale. Banc 80, FSL 506735a.

feature of the Cerin quarry that improves our knowledge of the history of marine turtles.

Some trackways were made by other reptiles walking along the border of the laguna. Some of them are clearly quadrupedal (Fig. 13B and Fig. 14D) and others possibly bipedal (Fig. 13C). These trackways remain enigmatic because of their scarcity and poor preservation. The observed differences may result merely from taphonomic conditions (*manus* prints not preserved?).

8.3. Coprolites

As in the Solnhofen lithographic limestones, *Lumbricaria* is a very common trace fossil. This ichnogenus corresponds to white faecal strings produced by fishes. They are accompanied by regurgitation traces indicating that fishes were able to survive, probably for short periods, in the laguna.

8.4. Cyanobacterian surfaces

Cyanobacteria are not strictly marine, but, in Cerin, they occur in a marine environment and are very important in forming protective films on bed surfaces. Their presence is attested by the reddish millimetre-thick laminations and by deformation structures (slipping, folding, tearing, polygonal reliefs) (Fig. 15A–F) which affect the

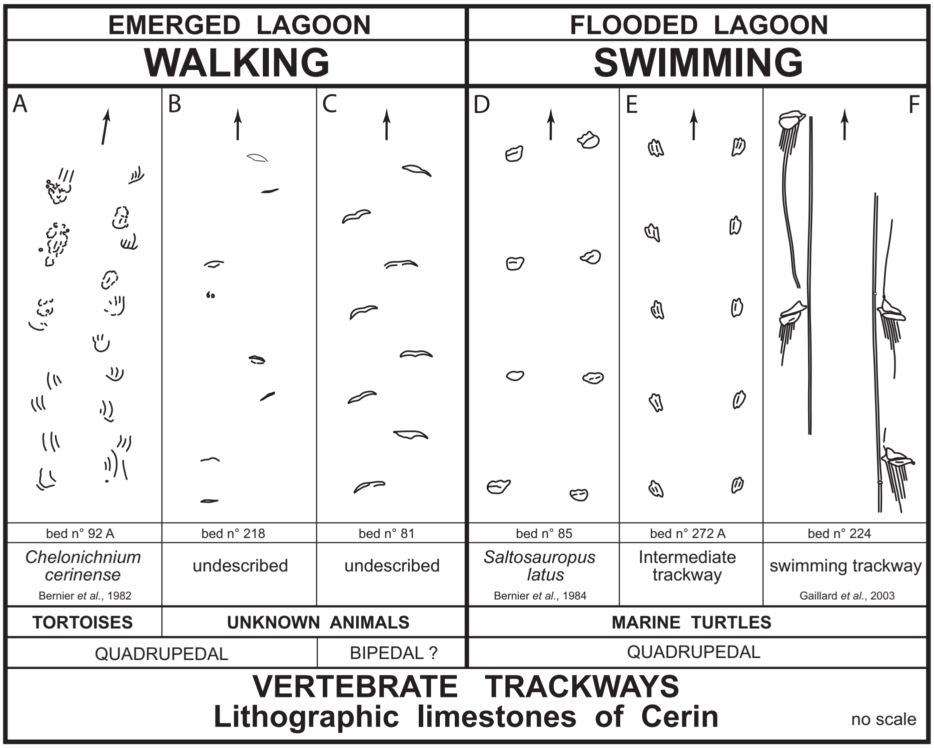

Fig. 13. Main vertebrate trackways found in the lithographic limestones of the Cerin laguna.

Fig. 13. Principales pistes de vertébrés observées dans les calcaires lithographiques de la lagune de Cerin.

laminites. Filaments are very scarce and even exceptional. However, some laminations display subhorizontal and vertical arrangements of dolomite microcrystals, linked to the filamentous framework created by cyanobacterian growth (Bernier et al., 1991c).

Bed surfaces are always covered by a few millimetres or centimetres of more or less reddish laminites, the thickness of which is independent of the underlying micritic bed. These reddish laminites are the result of cyanobacterian activity. Numerous slope structures are observed at the surface of the beds, limited to laminations and never extending to the underlying micrite. According to our interpretation, the cohesion and plasticity of these upper laminations were produced by the filamentous framework of the superficial microbial mat.

During emersion periods, the boundary between microbial mat and lime mud functioned as a drainage zone. The irregularities of the bottom resulted in gentle slopes, gas production and water flow detached the microbial mat from the underlying micrite, producing various warpings (Bernier et al., 1985, 1991c; Gall, 1989). It was thus possible to distinguish: *(1)* slope structures such as crescentic wavy, radial and torn structures (Gall et al., 1985), *(2)* polygonal peetees structures resulting from microbial growth on a limited surface and sometimes associated with mud volcanoes (Fig. 15D), *(3)* mixed structures combining several of the above-mentioned structures. All these structures have recent counterparts (Bernier and Gruet, 2011; Gavish et al., 1985; Gerdes and Krumbein, 1987; Reineck et al., 1990).

9. Taphonomy

Fossils are mainly found on the bed surface, inside the microbial laminites.

The presence of very fine detrital micrite without any fossil remains contrasts with the covering microbial laminites containing well-preserved fossils.

The dead bodies settled upon the lime mud after the end of sediment deposition. They always lie on their wider surface, which indicates a fundamentally quiet environment (Fig. 8C). However, some small and elongate organisms or organites (in particular, echinoid spines) are sometimes displaced and oriented by weak currents. Current directions were measured (Bourseau et al., 1994) (Fig. 6B), often repeatedly similar from one bed to another. Exceptionally, a few fossils were found included inside the bed, for instance *Zamites* fronds.

Skeletal remains are usually articulated and very well-preserved. The reason is that they were deposited on a very fine-grained substrate and were quickly covered by a protecting microbial film that prevented organisms from being destroyed by oxidation and/or scavenging.

The good preservation of shrimp tests shows that they were buried very quickly, as recent experiments suggest. When exposed on the bottom after death for longer than a few weeks, shrimp skeletons are quickly decayed by oxidation (Baas et al., 1995; Briggs, 1995, 2003; Briggs and Kear, 1994; Wilby et al., 1996).

The development of cyanobacterian filaments constituting the laminites provided a very dense mesh that

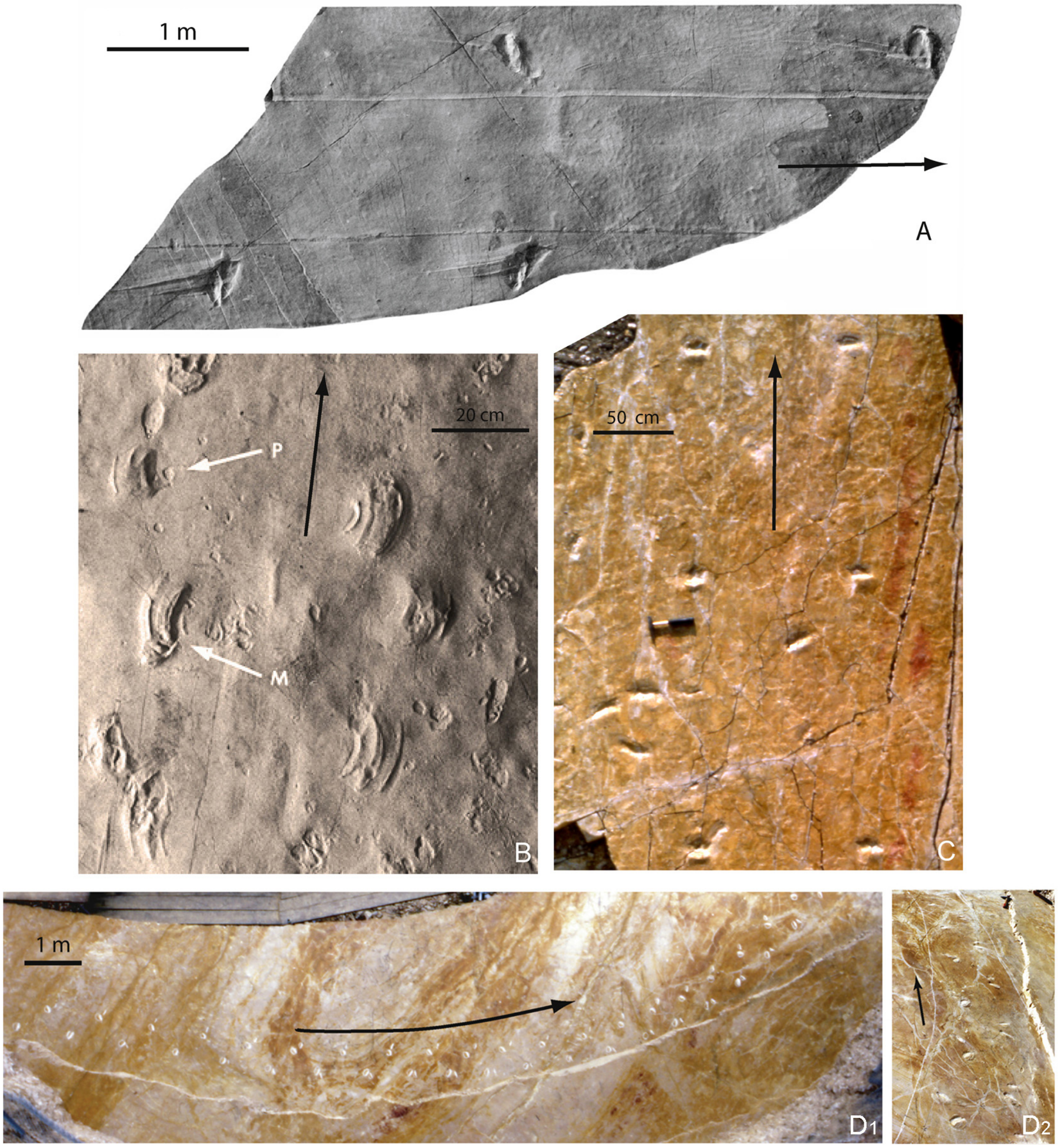

Fig. 14. (Colour online) Trackways – **A**. Swimming trace of a probable giant marine turtle. Bed 224 (Fig. 13F). Photo of the whole trackway cast. Opposite large imprints correspond to manus and right parallel grooves correspond to inactive pes. **B**. *Chelonichnium cerinense* Demathieu and Gaillard. Walking trace of a giant tortoise. Bed 92A (Fig. 13A). Photo of a part of the trackway cast. Arrows correspond to holotypes of manus imprint (M) and pes imprint (P). **C**. *Saltosauropus latus* Demathieu and Gaillard. Possible swimming trace of a giant marine turtle. Field picture. Bed 285. Opposite imprints correspond to manus. **D**. Long trackway of an unknown quadrupedal animal. Bed 133. **D1**. Field picture in plane view. Manus and pes imprints are underlined with white chalk. **D2**. Field picture of the same trackway. A part of the original trackway is exposed in the Cerin Museum. The arrows indicate the walking direction.
Fig. 14. (Couleur en ligne). Pistes – **A**. Trace de nage d'une probable tortue marine géante. Banc 224 (Fig. 13F). Photo du moulage d'une partie de la piste entière. Les grandes empreintes opposées correspondent aux mains, tandis que les sillons parallèles rectilignes correspondent aux pieds inactifs. **B**. *Chelonichnium cerinense* Demathieu et Gaillard. Traces de pas d'une tortue géante. Banc 92A (Fig. 13A). Photo d'une partie du moulage de la piste. Les flèches correspondent aux holotypes d'empreinte de main (M) et d'empreinte de pied (P). **C**. *Saltosauropus latus* Demathieu et Gaillard. Trace de nage possible d'une tortue géante marine. Photo de terrain. Banc 285. Les empreintes opposées correspondent aux mains. **D**. Longue piste d'un animal quadrupède inconnu. Banc 133. **D1**. Photo de terrain en vue surplombante. Les empreintes de mains et de pieds sont soulignées en blanc à la craie. **D2**. Photo de terrain de la même piste. Une partie de l'original de cette piste est exposée au musée de Cerin. Les flèches indiquent le sens de la marche.

rapidly became colloidal beneath the surface providing anoxic conditions (Gall et al., 1985). Thus, even soft bodies or soft parts of bodies were preserved such as fish intestines, fish scales or jellyfishes (Gaillard et al., 2006). Iron sulphurs are present inside the laminites, which were oxidized during Tertiary and Quaternary times by freshwater circulation, producing their characteristic reddish colour.

Trace fossils are abundant on bed surfaces (with numerous and various trackways) but also inside some beds (burrows). Burrows, in particular, are indicative of an autochthonous life. Trackways indicate a very shallow

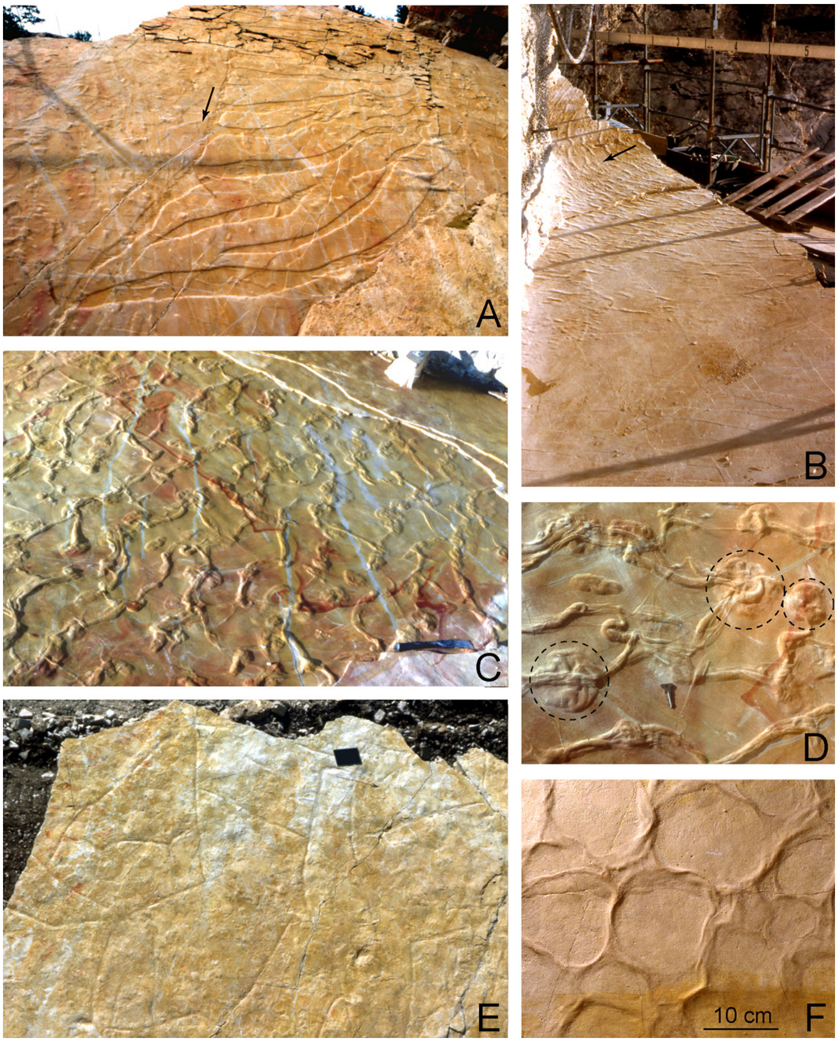

Fig. 15. (Colour online). Microbial surfaces – **A**. Partial view of bed surface 280 exhibiting, on the right, torn microbial film and the stream channel position at the extremity scouring the surface (arrow). **B**. Curved small foldings of microbial mat which slid between two more stable areas. The arrow indicates the movement direction. Bed 247A. **C**. Distorted "peetee" structures twisted by the slope, and mud volcanoes. Bed 69D. A part of this bed is preserved under the number: FSL 402005. **D**. Detail view of the preceding bed surface. Mud volcanoes (circles) linked to twisted "peetee" structures. Scale given by the small key (5 cm long). Bed 69D. **E**. Big-sized mud-cracks. Each crack corresponds to a small hollow *vs.* "peetee" structures which exhibit a slight relief. Scale given by black card (15 × 10 cm). Bed 278. **F**. "Peetee" structures regularly developed in all directions (isotropic), of polygonal shape. Their border appears in relief. Unknown bed, sampled out of the excavation area, FSL 402004.

Fig. 15. (Couleur en ligne). Surfaces microbiennes – **A**. Vue partielle de la surface du banc 280 montrant, à droite, le voile microbien déchiré, et l'emplacement du ruisselet à son extrémité qui indique une pente et le sens de l'écoulement (flèche). **B**. Plissements arqués du voile microbien qui a glissé entre deux zones plus stables. La flèche indique le sens du mouvement. Banc 247A. **C**. Structure en « peetees » déformés et torsadés et volcans de boue. Banc 69D. Une partie de ce banc est conservée sous le n° FSL 402005. **D**. Vue de détail de la surface du banc précédent. Volcans de boue (cercles) liés à des « peetees » torsadés. L'échelle est donnée par la petite clé (longueur : 5 cm). Banc 69D. **E**. Fentes de dessiccation de grande taille. Chaque fente correspond à une dépression au contraire des structures en « peetees » qui montrent un léger relief. L'échelle est donnée par l'ardoise noire (15 × 10 cm). Banc 278. **F**. Structures en « peetees » régulièrement développées dans toutes les directions (isotropes), à aspect polygonal. Les bords apparaissent en relief. Banc inconnu, prélevé hors fouille, FSL 402004.

marginal marine environment where either marine animals (limulids, marine turtles) or terrestrial animals (tortoises) alternatingly occurred. On the other hand, body fossils undoubtedly indicate a mixed origin. Organisms that lived in very diverse, terrestrial and marine environments are associated in the same beds. There are not strictly terrestrial or marine beds: fossils are generally mixed within them. However, considering the very good state of preservation, the original life environments were probably close by and transportation was short. Some organisms were possibly still alive when arriving in the laguna but died quickly because of high water temperatures and lack of food.

10. Laguna environment

The studied Cerin area is interpreted as a landscape on the edge of a small tropical laguna inside a shallow reefal depression, far from the open sea and communicating with a vast quiet reef lagoon (Fig. 2). This laguna had

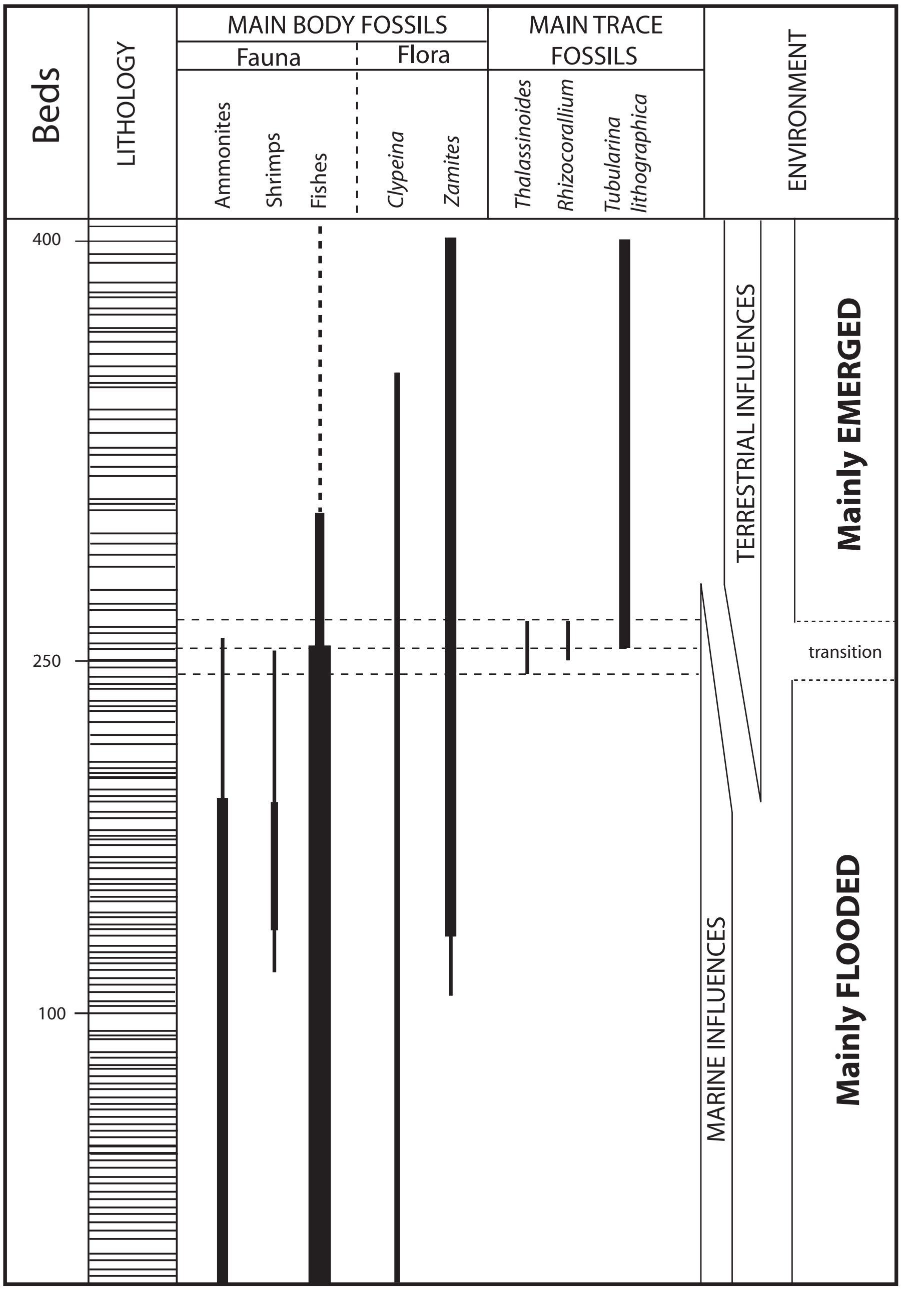

Fig. 16. Stratigraphical and environmental distribution of trace fossils and body fossils in the lithographic limestones of Cerin.

Fig. 16. Distribution stratigraphique et environnementale des fossiles et des pistes récoltés dans les calcaires lithographiques de Cerin (d'après Gaillard et al., 1994a, 2003, 2006).

From Gaillard et al. (1994a, 2003, 2006).

temporarily stagnant waters, poorly oxygenated and certainly hostile to life. During storms, the lagoon and laguna communicated together and with the open sea, bringing oxygenated marine waters until the laguna. At the same time, various organisms could be carried away, swept by wind or pushed and dragged into the laguna, from which they could not escape.

Detrital lime mud coming from the normally quiet laguna, and causing turbidity, was very quickly deposited thus forming a more or less thick mud layer, depending of the storm duration and strength. Each mud layer was produced from a single source within a few hours or days. The animals could survive for some time before dying. Their bodies lay over the mud and were rapidly covered by a microbial film, providing exceptional anoxic preservational conditions. Water depth was certainly very shallow and the bottom very frequently exposed, particularly on the laguna edge. During emergent periods, terrestrial

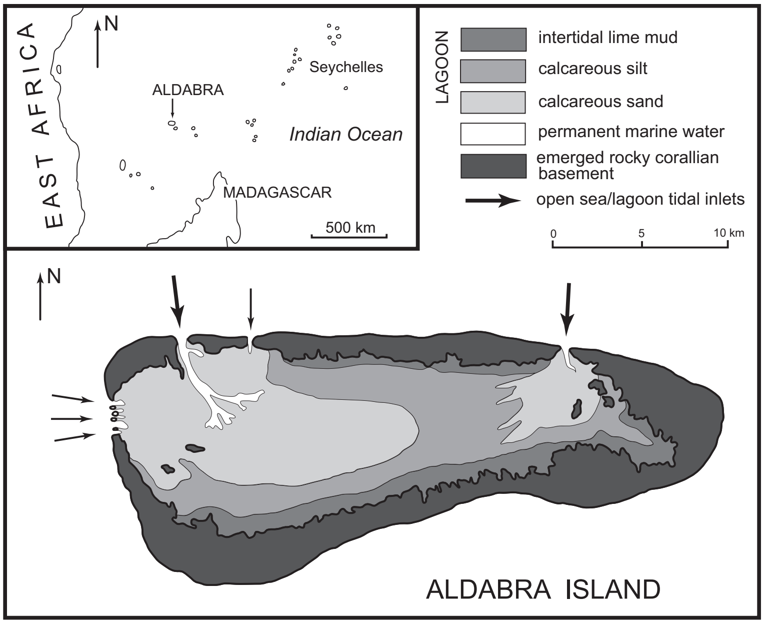

Fig. 17. Location and sediment distribution of the Aldabra atoll (Seychelles).
Fig. 17. Situation et distribution des sédiments de l'atoll d'Aldabra (Seychelles) (d'après Gaillard et al., 1994b).
From Gaillard et al. (1994b).

animals could occupy this area while during periods with higher water levels, marine animals are predominant.

The homogeneous and very fine-grained lime mud originates from the erosion of emergent reef substrate that provided 98% of calcium carbonate.

According to the results obtained during the scientific excavation, the fauna, flora and trace fossils occur in various positions along the outcrop of the lithographic limestones. The lower lithographic limestones contain frequent marine animals (fishes, ammonites and shrimps) and algal whorls (*Clypeina*), but marine burrows and terrestrial flora are not or poorly represented (Fig. 16). Marine influences were dominating and the laguna was frequently flooded. The upper lithographic limestones contain numerous terrestrial leaves (*Zamites*), while tree trunks and branches were rarely sampled. Very shallow marine burrowing structures (*Tubularina*) are present, but other marine organisms are poorly represented. The emergent periods were longer and more and more frequent. All these observations indicate an infilling and emerging tendency of the Cerin laguna.

11. The Aldabra laguna, a recent model to explain the Cerin environment

Aldabra is a coral island belonging to the Seychelles (Indian Ocean) and the most southern island of the archipelago. It forms a large laguna (34 km long and 14.5 km wide). This corallian environment displays interesting similarities with the Cerin deposits (Gaillard et al., 1994b).

The Aldabra laguna is very shallow and communicates by several straight channels with the Indian Ocean (Fig. 17). The tidal range is relatively high (more than 3 m) and the laguna is emptied at every low tide. Sediments inside the laguna originate from island erosion, and are transported and distributed by tide currents. The corallian origin of the island provides lime mud and more or less coarse grains deposited according to their hydrodynamic location. Very pure lime mud is deposited along the internal laguna edge corresponding to the most protected areas. These are frequently exposed and regularly covered by cyanobacterian films (Fig. 3C). These films contain various organic remains such as coprolites similar to those observed in the Cerin site, known as *Lumbricaria*. In the same areas, annelids produce burrows similar to *Tubularina*, from Cerin. Numerous and various fishes (sharks, parrot-fishes, rays, etc) and others animals are actively or passively (currents) introduced into the laguna, from the littoral or from the open sea. They are trapped in the laguna, die there and may later be preserved. Numerous (estimated number: 150,000) giant terrestrial tortoises, as *Aldabrachelys gigantea* (Schweigger), are living on the island and when they walk on the mud of the inner island edge their footprints are very similar to those described at Cerin like *Chelonichnium cerinense* Demathieu and Gaillard. Marine turtles are occasionally present to lay their eggs into beach holes. Such behaviour may explain the large swimming traces observed on some Cerin beds (Gaillard et al., 2003).

In spite of these numerous similarities, the Aldabra lagoon is really significantly different from the Cerin laguna, especially in its geographical context. Environments resembling Cerin do not exist today. In tropical lagunas along the sea (Persian Gulf, eastern Mediterranean Sea), the skeletons of organisms may occasionally be preserved within superficial microbial developments, but the observed similarities are less complete than those observed within the Aldabra laguna.

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All the numerous samples collected during the scientific excavations are deposited, listed and curated into the “Collections du département des sciences de la Terre”, Université Claude-Bernard (Lyon-1), and preserved thanks to its director A. Prieur, now assisted by E. Robert. The previous samples, collected during the 19th century, are kept at the “Centre de conservation et d’étude des collections du musée des Confluences de Lyon” and preserved thanks to D. Berthet.

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