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General palaeontology, systematics and evolution (Taphonomy and fossilisation)

# A new look at the Late Jurassic Canjuers conservation Lagerstätte (Tithonian, Var, France)

## *Nouveau regard sur le Lagerstätte de Canjuers, un site à conservation exceptionnelle du Jurassique supérieur (Tithonien, Var, France)*

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A B S T R A C T

The Canjuers conservation Lagerstätte represents a Late Jurassic lagoonal environment. The sedimentology and stratigraphy of the locality show three different depositional sequences. Fossils are mainly found in the basalmost layers that correspond to the first phase of deposition in the lithographic limestones *sensu stricto*. The fossil biodiversity is rich. So far, more than 1000 specimens including 38 invertebrate and 18 vertebrate taxa have been recovered from the limestones. The depositional information suggests that most invertebrates and vertebrates were not autochthonous to the lagoon, but swept in during storm events from the open sea or nearby emerged reef environments.



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R É S U M É

Le Lagerstätte de Canjuers est un gisement à conservation exceptionnelle du Jurassique supérieur, représentant un environnement de lagon. La sédimentologie et la stratigraphie du gisement montrent trois périodes de dépôt différentes. Les fossiles sont principalement récoltés dans les niveaux les plus basaux, qui correspondent à la première phase de dépôt de calcaires lithographiques *sensu stricto*. La paléobiodiversité est riche et inclut de nombreux invertébrés et des vertébrés allant de petits reptiles proches des lézards jusqu'aux grands crocodiles. Ainsi, plus de 1000 spécimens correspondant à 38 taxons d'invertébrés et à 18 taxons de vertébrés ont été découverts dans ces calcaires lithographiques. Le milieu de dépôt suggère que la plupart des invertébrés et des vertébrés ne sont pas autochtones, mais que, durant des épisodes de tempête, ils ont été introduits dans le lagon depuis la haute mer ou depuis les zones récifales voisines qui étaient émergées.



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## 1. Introduction

Scientific interest in the Late Jurassic (Tithonian) Canjuers Lagerstätte dates back to the 1970s and the pioneer works of Ginsburg and Mennessier (1970), who first mentioned the presence of well-preserved vertebrates (fishes, turtles, crocodilians) in the lithographic limestones from this locality. Indeed, this Lagerstätte contains a diverse and remarkably preserved fauna mainly composed of abundant echinoderms (e.g., echinids, ophiuroids) and different vertebrates including fishes, turtles, lepidosaurs (e.g., pleurosaurids, sphenodontids), a pterosaur, a crocodilian and a dinosaur.

Although several spectacular cases of articulated vertebrates have been described – sometimes very briefly – over the years (e.g., *Compsognathus longipes*, pterosaurs, pleurosaurids, sphenodontids; Dupret, 2004; Fabre, 1973, 1974a, b, 1981; Peyer, 2006), the palaeoenvironmental setting of the Canjuers Lagerstätte, the ecological organization of the biota and the taphonomic processes involved in the exceptional preservation of the fauna have rarely been considered. The location of the exposures, previous activity of the quarrymen and, above all, the thickness of the lithographic beds hampered previous research of the palaeoenvironmental processes. The present work shows the extension of the palaeo-lagoon and presents new stratigraphic and sedimentological data. The newly acquired field data were used to correlate the different quarries in Les Bessons stratigraphically and to locate the fossil-rich layers accurately. We revised and updated the previous inventories of the fauna and flora in the light of personal observations and recent works dealing with the systematics of the different groups. Comparisons with other Late Jurassic Lagerstätten (Cerin, Solnhofen, Wattendorf) provide a revised interpretation of the palaeoenvironment of the Canjuers Lagerstätte.

*Institutional abbreviations*. MNHN, Muséum national d'histoire naturelle, Paris; MNHN.F, palaeontological collections of the Muséum national d'histoire naturelle, Paris; CNJ, acronym for the fossil vertebrates of Canjuers.

## 2. Geological setting

### 2.1. Geographic and geological location

The Canjuers Lagerstätte lies within the military camp of Canjuers, in the Haute Provence area (Var département, SE France) (43°42′20.48′′N; 6°22′25.71′′E) (Fig. 1A). The Canjuers Lagerstätte occupies a comparatively small area within the camp, termed "Les Bessons". "Les Bessons" is the name of the ancient farm that was located near the Lagerstätte of which, today, only ruins remain. Ten quarries are identified in the "Les Bessons" area, exposing fine-layered lithographic limestone (Fig. 1B). Some of the quarries date back to when the area was explored for ornamental stone; others have been opened by MNHN scientists. The quarries cover a surface of more than 15 ha. They are separated by old quarry roads and large piles of gravel. The village of Aiguines, to which the military camp politically belongs, lies 30 km to the north. Geologically, the Lagerstätte is situated at the border of the plateau named "Petit Plan de Canjuers". This plateau is delimited by the Verdon Gorge to the north and the mountains called "Le Matelot" and "Colle Basse" to the west. The "Pilon de Fayet" and "Le Grignas" hills, separated from each other by the Artuby Gorge, define the plateaus' natural boundary to the east and the "Hubac Sandier" hill forms its southern border (Fig. 2A).

### 2.2. Biostratigraphy

The Canjuers Lagerstätte belongs to the Calcaires blancs de Provence Formation (thickness: 200 m). This formation is composed of two members: the Biolithites de Rougon (lower member) with coral bearing limestones and the Biomicrites de Sainte-Croix (upper member) exhibiting more laminated limestones and frequent traces of emersion (Atrops, 1991, 1994). The lithographic limestones from the Canjuers Lagerstätte are located at the base of the upper member (Atrops, 1991) and belong to the Early Tithonian *Mucronatum* biozone (Atrops, 1994). Compared to other Lagerstätten in western Europe, the Canjuers sediments are older than the Montsec lacustrine limestones in Spain (Barremian) (Soriano and Delclòs, 2006; Wenz, 2003) but younger than the Cerin outcrops of the French Jura (Kimmeridgian/Tithonian, *Beckeri* and *Hybonotum* biozones) (Enay et al., 1994), the Wattendorf Plattenkalk of northern Bavaria (Kimmeridgian, *Eudoxus* biozone) (Fürsich et al., 2006, 2007), the Solnhofen limestones in Germany (Tithonian, *Hybonotum* biozone) (Schweigert, 2007), and slightly younger than the Crayssac limestones in France (Early Tithonian, *Hybonotum* biozone) (Hantzpergue, 1989; Hantzpergue and Lafaurie, 1994; Mazin et al., 1997).

### 2.3. Palaeogeography

The most recent palaeogeographic reconstructions of the Late Jurassic series place the Canjuers Lagerstätte along the north-western margin of the Tethys Ocean and on the northern margin of the Provence Plateau where sedimentation is dominated by carbonate facies (Fourcade et al., 1993; Thierry, 2000). During the Early Tithonian, the northern margin of the Provence Platform is characterized by coral reefs that formed a more or less continuous barrier running east-west and separating the Provence carbonate platform from the Subalpine Basin and the Tethys Ocean. Thus, the Canjuers Lagerstätte belongs to a vast lagoon extending south of this barrier reef and is characterized by areas alternatively submerged and emerged with small coral islands (Atrops, 1994).

$\delta^{18}O$ values of ambient waters derived from thalassemydid turtles indicate that the coastal environments of Canjuers, Solnhofen, and Cerin were somewhat supplied by fresh water (Billon-Bruyat et al., 2005). Indeed, meteoric freshwater was probably present in ponds on the islands surrounding the lagoon. The closest emerged land as documented by Thierry (2000) is located around 100 km south of the Canjuers lagoon.

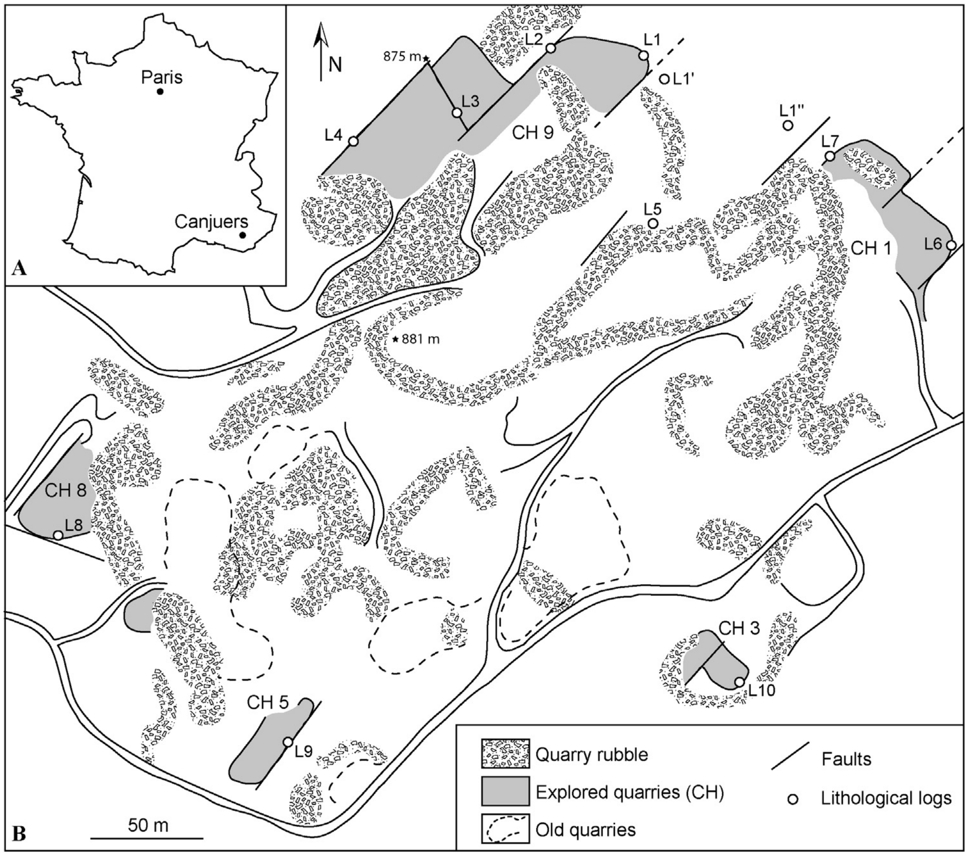


**Fig. 1.** The Canjuers Lagerstätte (SE France). **A**. Geographic location. **B**. Quarry map of the "Les Bessons" area.
**Fig. 1.** Lagerstätte de Canjuers (SE France). **A**. Localisation géographique. **B**. Carte de la carrière « Les Bessons ».

## 3. Historical context

### 3.1. Discovery of the Lagerstätte

Until the late sixties Canjuers was used by mainly two sheepherding families. When the French State initiated the construction of a military camp, the families searched for solutions to render their land more profitable. During initial military exploration of the territory, Mr. Roubault, the owner of the land south-east of the present-day quarries, discovered the lithographic limestones that outcropped on part of his land and recognized their value. The area was right away turned into a working quarry and exploited for ornamental stone. Soon, the superb limestone plates which became known to the public as "Dalles de Provence" were sold in all parts of France and all over Europe. Meanwhile, the Ghirardi family, owners of the land south and south-east of "Les Bessons," started a quarrying business of their own. In exploiting the area for ornamental stone, both families also recovered many plant, invertebrate and vertebrate fossils. The Ghirardis especially accumulated a large collection of fossils. Among them are some of the best preserved reptiles known in France, such as the little dinosaur *Compsognathus*, the crocodilian *Steneosaurus*, and the pterosaur *Cycnorhamphus*. But when Canjuers was finally declared a military bombardment range in the early 1970s, the quarry owners were deprived of their land and over the next few years relocated.

In 1983, the Ghirardi family agreed to sell their collection of fossils to the Muséum national d'histoire naturelle (MNHN) in Paris. They, however, never revealed where in the Lagerstätte and from which stratigraphic units they recovered the fossils. Some of the acquired specimens were carefully prepared and identified by researchers from the MNHN, and some were published (see below). Others were integrated into the palaeontological collections and await a complete study.

### 3.2. Scientific history

Canjuers first became known to the scientific community in the late 1960s (Ginsburg and Mennessier, 1970), around the same time when the land was in the process of being transformed into a military camp. The previous authors provided a first map and recognized the fossil richness of Canjuers. The initial phase or the "Ginsburg–Mennessier–Wenz" phase was started with a 30-day fieldtrip led by S. Wenz. Fieldtrips were consecutively repeated every year and steadily added data for a better understanding of the site (Ginsburg, 1973).

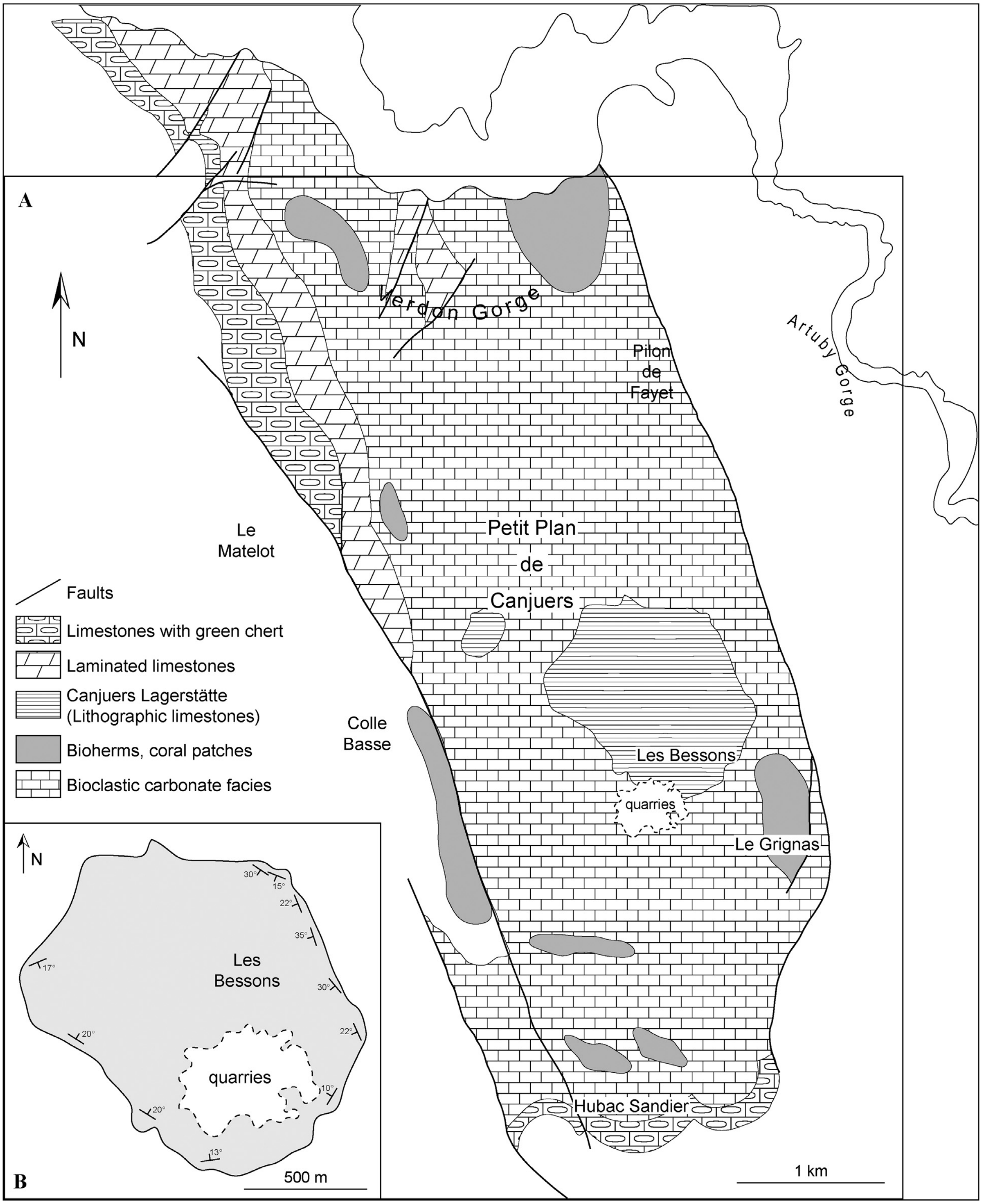


**Fig. 2.** Geology of the Canjuers Lagerstätte. **A**. Synthetic geological map of the Petit Plan de Canjuers plateau, modified from Fabre (1981), with additional field data. **B**. Extension of the lithographic limestones; note the subcircular depression indicated by the strike and dip symbols.

**Fig. 2.** Géologie du Lagerstätte de Canjuers. **A**. Carte géologique synthétique du plateau du Petit Plan de Canjuers, modifiée d'après Fabre (1981) et avec de nouvelles données de terrain. **B**. Extension des calcaires lithographiques ; noter la dépression subcirculaire indiquée par les figurés de pendage.

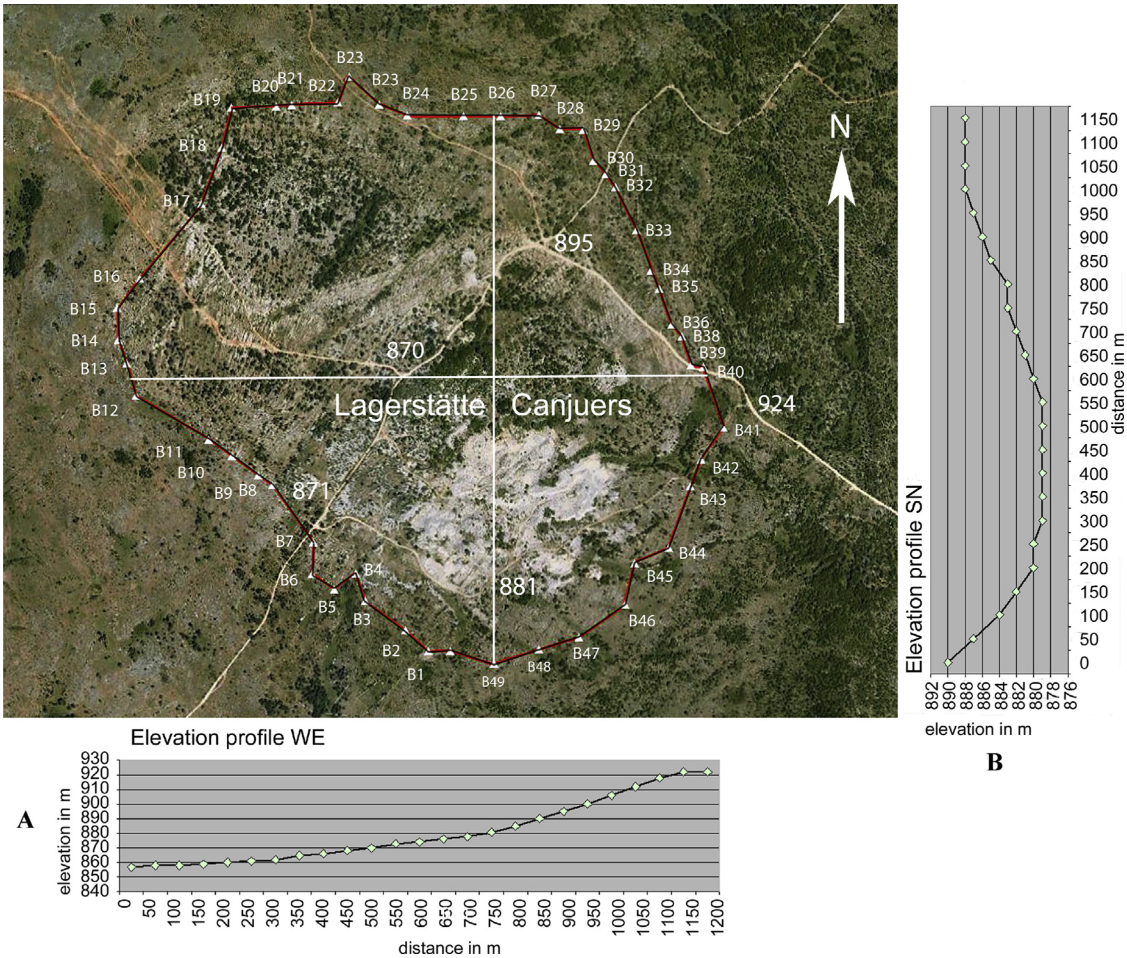


**Fig. 3.** (Colour online) Aerial map of the Canjuers Lagerstätte. Data points represent GPS markers (B1–B49) that outline the external border of the lagoon. **A**. Topographic profile east-west of the lagoon. **B**. Topographic profile north–south of the lagoon.

**Fig. 3.** (Couleur en ligne) Carte aérienne du Lagerstätte de Canjuers. Les points GPS (B1–B49) révèlent le bord externe du lagon. **A**. Profil topographique est-ouest du lagon. **B**. Profil topographique nord–sud du lagon.

During this initial phase, the original quarry owners were still permitted to quarry the site for building stones and fossils. This phase ended in the mid-1970s when quarrying was completely stopped and access was restricted to MNHN scientists. Then J. Fabre directed the palaeontological excavation and management of the site. His geological knowledge of the quarry was widely appreciated. J. Fabre published extensively on the reptile fauna of the Lagerstätte (Fabre, 1973, 1974a, b, 1976), acquired a good understanding of the palaeoenvironmental history (Fabre, 1977a, b, c), and provided the first synthesis of the Canjuers Lagerstätte (Fabre et al., 1982).

Ph. Taquet, J.-G. Michard, J.-M. Barrat, J. Roman and many other museum collaborators led the subsequent scientific teams during the second exploration phase. Now the Paris Museum was granted access to the locality only once a year during the hot summer months, when military target shooting was halted for fire safety reasons. A decade (1983–1993) of excavations led by palaeontologists of the Paris Museum to Canjuers brought to light new remarkable plant, invertebrate and vertebrate fossils, adding many specimens to the already known and formerly acquired fossils that were purchased from the Ghirardi family. In 1991, during the international conference held in Lyon (International round-table "Lithographic Limestones"; Bernier and Gaillard, 1994), the fossils of Canjuers were presented (Roman et al., 1994). The presence of ammonites (Atrops, 1991, 1994), the taphonomy of echinoderms (Roman, 1994), new fish species (e.g., *Naiathaeolon okkidion* Poyato-Ariza and Wenz, 1994), and a revision of the turtles (Broin, 1994) were presented there. In the mid-nineties, however, scientists cancelled field trips to Canjuers due to limited funding.

With the publication of the coelurosaur *Compsognathus* from Canjuers (Peyer, 2006), the Canjuers locality was finally considered again. A few years later, a new group of scientists (K. Peyer, S. Charbonnier, R. Allain, and E. Läng) reopened the Canjuers quarries. The most recent geological field seasons (2010, 2011) permitted us to understand for the first time the geology, sedimentology, and

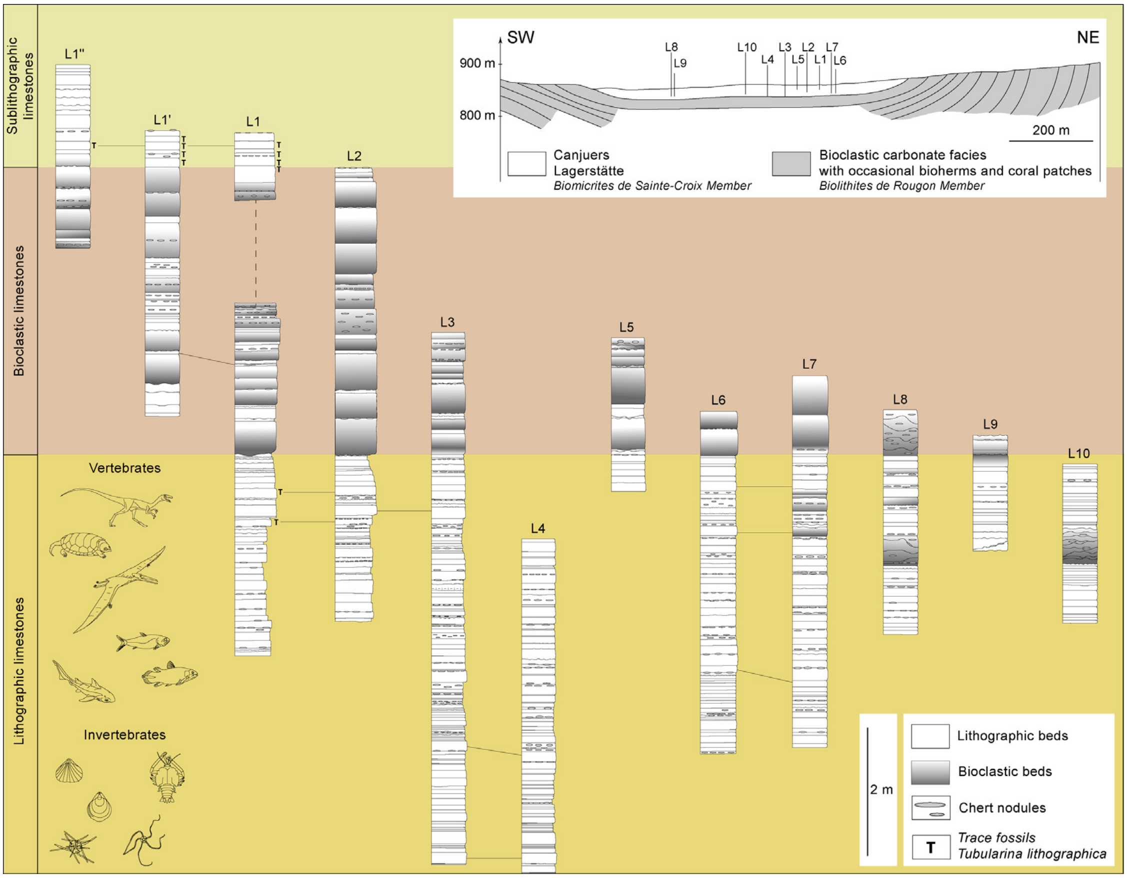


**Fig. 4.** (Colour online) Lithological logs of the Canjuers Lagerstätte with biostratigraphic correlations and fossil distribution. Note that the majority of the exceptionally preserved fossils (invertebrates, vertebrates) come from the lithographic beds of the basal unit. Their exact location in the basal unit is unfortunately not known.

**Fig. 4.** (Couleur en ligne) Coupes lithostratigraphiques du Lagerstätte de Canjuers avec les corrélations biostratigraphiques et la distribution des fossiles. La majorité des fossiles exceptionnellement préservés (invertébrés, vertébrés) provient des bancs lithographiques de l'unité basale. Leur position précise au sein de cette unité basale n'est malheureusement pas connue.

palaeoenvironmental history of the Canjuers Lagerstätte and in this respect are the stepping stones for future palaeontological field work.

## 4. Material and methods

During the first field season (July 2010), our team mapped the boundaries of the ancient lagoon, determining the position of the lithographic limestones with respect to the coral reefs (Figs. 2B and 3). The outer boundaries of the lagoon have been mapped using a GPS. From five selected quarries (CH1, CH3, CH5, CH8, CH9; Fig. 1B), stratigraphic data were collected, layer thicknesses measured, and sedimentological data compiled in logs (see Fig. 4). Within CH9, the largest quarry, seven logs were studied (L1, L1′, L1′′, L2, L3, L4, L5; Fig. 5A, B), two in CH1 (L6, L7) and one each in the other quarries (CH3: L10; CH5: L9; CH8: L8).

The past two years have also been dedicated to catalogue, digitize, and properly store the Canjuers fossils in the MNHN collections. A tentative list of invertebrate and vertebrate taxa is provided below.

## 5. Sedimentology of the Canjuers Lagerstätte

### 5.1. Lithology of the limestones

The fossiliferous layers of the Lagerstätte crop out in the Petit Plan de Canjuers, a small plateau in the centre of the military camp. The deposits are limited to a subcircular depression and occur within a relatively short interval (ca. 12 m) (Figs. 2B and 4). They are composed of three distinct lithological units composed from base to top of:

- lithographic limestones *sensu stricto*;
- bioclastic limestones;
- sublithographic limestones (Fig. 4).

#### 5.1.1. Lithographic limestones

The basal unit (ca. 6 m) is characterized by thin limestone beds yielding the majority of the exceptionally well-preserved organisms (Fig. 5A, B). These laminated limestones and the contained fauna form the Canjuers Konservat-Lagerstätte. The basal unit can be interpreted as lithographic limestones according to Bernier (1994): they

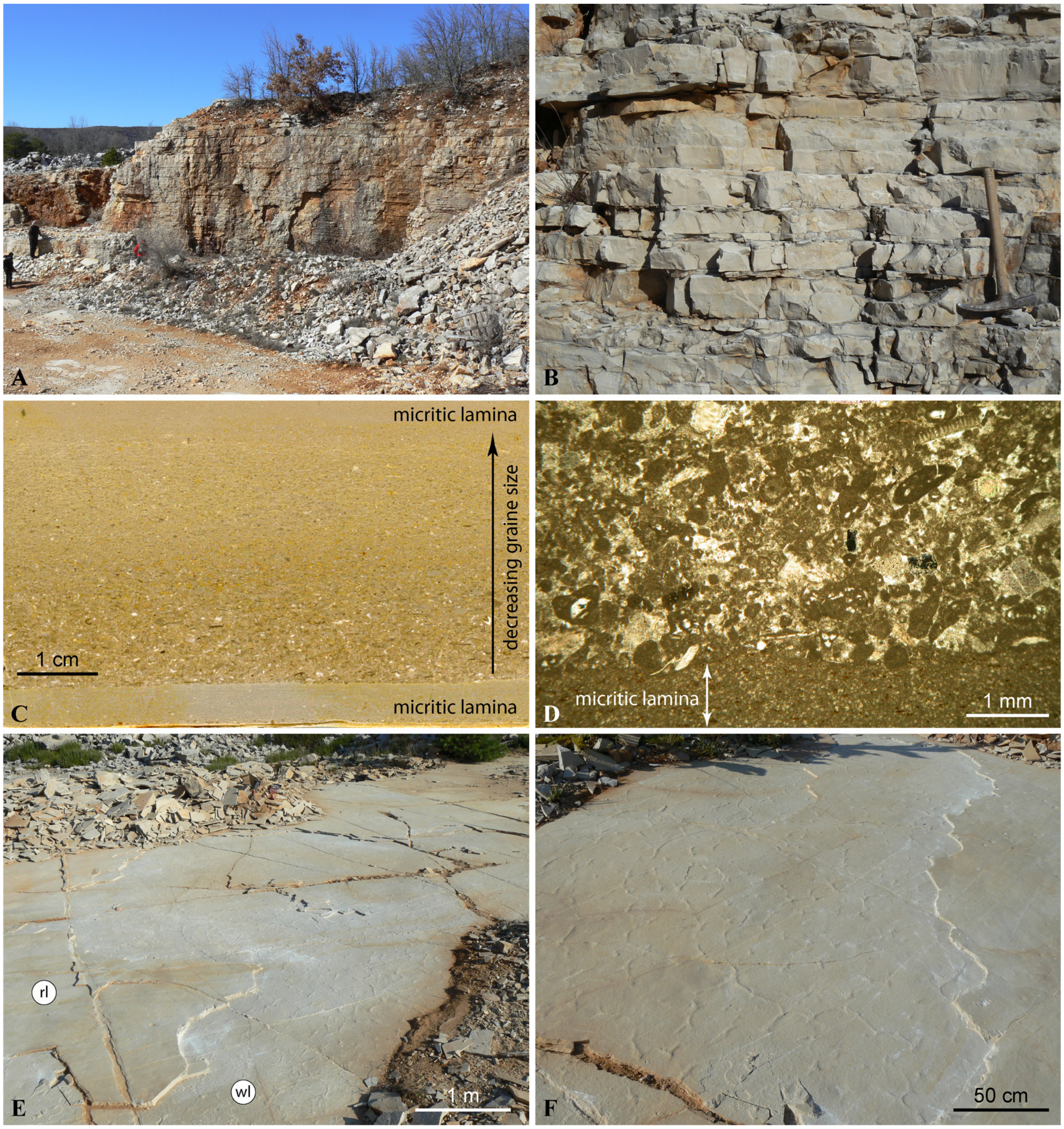


**Fig. 5.** (Colour online) Lithographic limestones from the Canjuers Lagerstätte. **A**. General view of the quarry CH9 showing the thickness of the basal unit (see log L4). **B**. Detail of some lithographic beds in quarry CH9 (pickax = 40 cm). **C**. Polished section of a bed in quarry CH3, note the two laminae composed of very fine carbonate mud. **D**. Thin-section of the same bed showing the basal micritic lamina and the core of the bed. Note the abundant bioclastic remains at the base (polarized light). **E**. Cleaned surface in quarry CH3, showing regular laminae (rl) contrasting with wrinkled laminae (wl) (evidence of microbial mat). **F**. Detail of the wrinkled surface of the microbial mat.

**Fig. 5.** (Couleur en ligne) Calcaires lithographiques du Lagerstätte de Canjuers. **A**. Vue générale de la carrière CH9 montrant l'épaisseur de l'unité basale (voir log L4). **B**. Détail de quelques bancs lithographiques dans la carrière CH9 (pic = 40 cm). **C**. Section polie dans un banc de la carrière CH3 ; noter les deux lamines composées d'une très fine boue carbonatée. **D**. Lame mince du même banc montrant la lamine micritique basale et le cœur du banc. Noter les nombreux restes bioclastiques présents à la base (lumière polarisée). **E**. Surface décapée dans la carrière CH3, montrant des lamines régulières (rl) contrastant avec des lamines plissées ou chiffonnées (wl) (mise en évidence d'un film microbien). **F**. Détail de la surface plissée montrant des polygones de dessiccation dans le film microbien.

are homogeneous, and no coarse grains, joint or vesicles are present. They exhibit conchoidal fractures and sharp edges, and are smooth to the touch. Like the Solnhofen and the Cerin lithographic limestones, they may be regarded as an obrutionary stagnation deposit (Gaillard et al., 2006; Seilacher et al., 1985). A typical lithographic limestone bed in Canjuers is generally composed of three distinct levels (Fig. 5C, D):

- a basal lamina (thickness: ca. 1–5 mm), composed of a very pure, fine micrite which probably corresponds to microbial activity (microbial film);

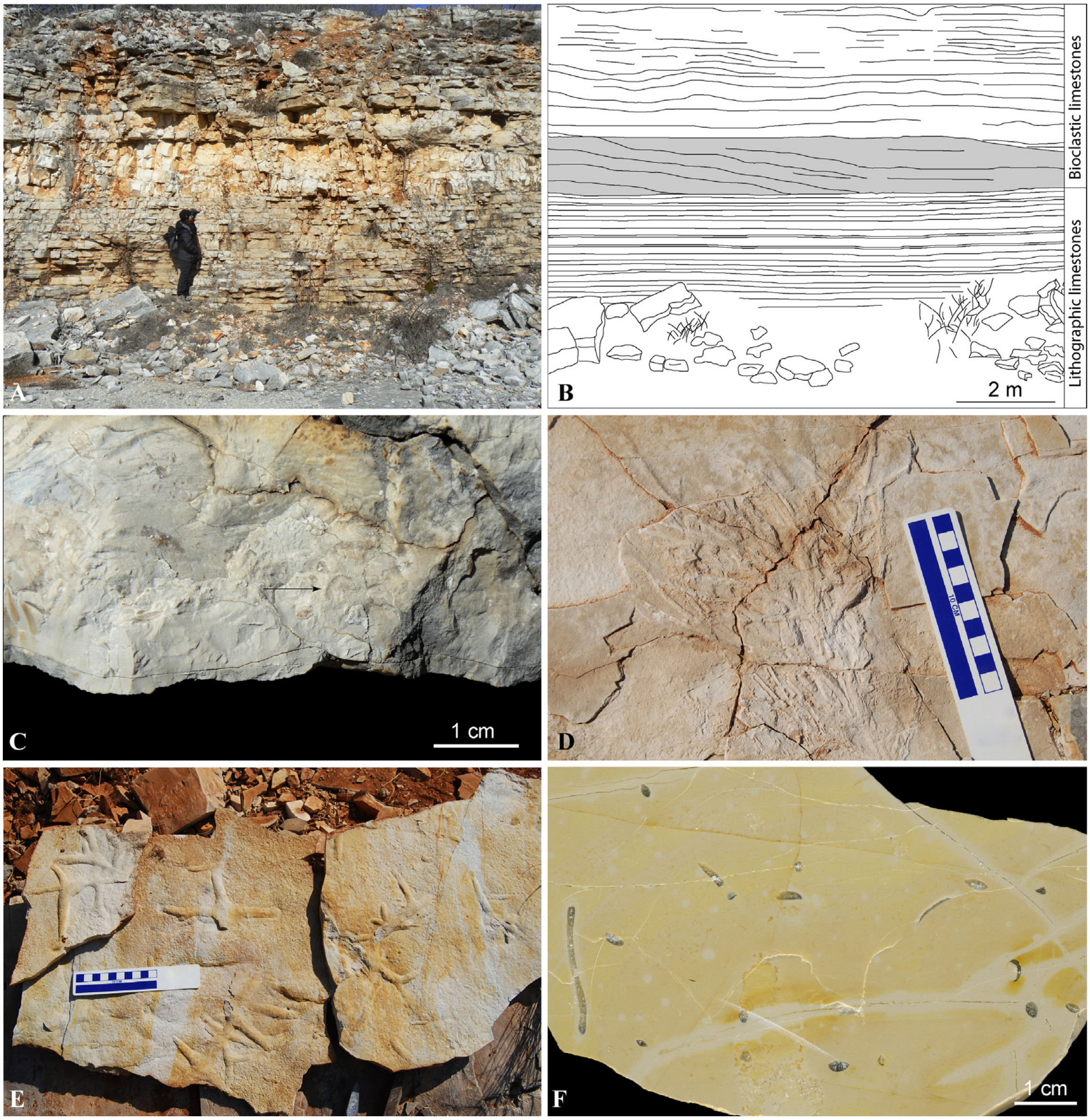


**Fig. 6.** (Colour online) Bioclastic limestones from the Canjuers Lagerstätte. **A**. General view of the quarry CH9 showing the contact between the lithographic unit and the bioclastic unit (see log L1). **B**. Interpretative drawing of the same section showing the large-scale planar cross-beds (in grey). **C**. Bioclastic bed in quarry CH9 (log L4) with an undulating base with mm- to cm-sized fragments of echinids, bivalves, brachiopods, and corals (black arrow). **D**. Plant macro-fossils on a foreset of a small megaripple in quarry CH3 (log L10). **E**. Horizontal Y-shaped burrows attributed to *Thalassinoides*, quarry CH3 (log L10). **F**. Sublithographic bed with small burrows attributed to *Tubularina lithographica* Gaillard, 1994 (polished section).

**Fig. 6.** (Couleur en ligne) Calcaires bioclastiques du Lagerstätte de Canjuers. **A**. Vue générale de la carrière CH9, montrant le contact entre l'unité lithographique et l'unité bioclastique (voir log L1). **B**. Dessin interprétatif de la même section montrant de grandes stratifications obliques tangentielles (en gris). **C**. Banc bioclastique de la carrière CH9 (log L4) avec une base ondulée, comprenant des fragments millimétriques à centimétriques d'échinides, de bivalves, de brachiopodes, et de coraux (flèche noire). **D**. Macro-reste d'une plante, déposé sur le flanc d'une petite mégaride de la carrière CH3 (log L10). **E**. Terriers horizontaux en forme d'Y, attribués à *Thalassinoides*, carrière CH3 (log L10). **F**. Banc sublithographique avec de petits terriers attribués à *Tubularina lithographica* Gaillard, 1994 (section polie).

- an intermediate normal-graded mudstone level (thickness: ca. 3–6 cm) with grain size decreasing from fine-grained carbonate mudstone at the base to very fine-grained carbonate mudstone at the top;
- a new lamina (thickness: ca. 1–5 mm), of fine micritic carbonate similar to the basal lamina.

Evidence from extracted lithographic plates shows that microbial laminae may frame all the bed, or are present only at its top, or at its base. The thickness of certain micritic laminae may be explained by the accumulation of successive thin microbial films. Some beds containing fossils exhibit an upper microbial film with


**Fig. 7.** (Colour online) Echinoderms from the Canjuers Lagerstätte (Lower Tithonian, Mucronatum biozone). **A**. *Pseudosalenia aspera* (Agassiz, 1840) (MNHN.F.A45931). **B**. *Plegiocidaris marginata* (Goldfuss, 1826) (MNHN.F.A45932), ventral view. **C**. Accumulation of plates, spines and components of Aristotle's lantern (MNHN.F.A45933, *Plegiocidaris* sp.), corresponding to probable partially digested food or regurgitation. **D**. *Geocoma* sp. (MNHN.F.R07842), dorsal view. **E**. *Pentasteria* sp. (MNHN.F.R10669), dorsal view. **F**. *Saccocoma tenella* (König, 1825), (MNHN.F.R10669), fragments of arms.

**Fig. 7.** (Couleur en ligne) Échinodermes du Lagerstätte de Canjuers (Tithonien inférieur, biozone à Mucronatum). **A**. *Pseudosalenia aspera* (Agassiz, 1840) (MNHN.F.A45931). **B**. *Plegiocidaris marginata* (Goldfuss, 1826) (MNHN.F.A45932), vue ventrale. **C**. Accumulation de plaques, de piquants et d'éléments de la lanterne d'Aristote (MNHN.F.A45933, *Plegiocidaris* sp.), correspondant probablement à des régurgitations ou à de la nourriture partiellement digérée. **D**. *Geocoma* sp. (MNHN.F.R07842), vue dorsale. **E**. *Pentasteria* sp. (MNHN.F.R10669), vue dorsale. **F**. *Saccocoma tenella*, (MNHN.F.R10669), fragments des bras.

arched-up, wrinkled surface forms termed petee structures (Fig. 5E, F). Occasionally, bioclastic layers may partly or completely erode the underlying microbial lamina.

### *5.1.2. Bioclastic limestones*

The second unit (ca. 4.5 m) is composed of relatively coarse limestones often organized in large-scale planar cross-beds (Fig. 6A, B). Sediments are bioclastic packstones


**Fig. 8.** (Colour online) Invertebrates and plants from the Canjuers Lagerstätte (Lower Tithonian, Mucronatum biozone). **A**. "*Zeilleria*" aff. *pentagonalis* (Bronn *in* Quenstedt, 1858) (MNHN.F.A45934), ventral view. **B**. *Septaliphoria obtusa* (Quenstedt, 1871) (MNHN.F.A45935), ventral view. **C**. *Dorsoplanitoides triplicatus* Zeiss, 1968, (MNHN.F.R62470), lateral view. **D**. Fragment of *Cycadopteris jurensis* (Kurr, 1846) Hirmer 1924 (MNHN.F.16640).
**Fig. 8.** (Couleur en ligne) Invertébrés et plantes du Lagerstätte de Canjuers (Tithonien inférieur, biozone à Mucronatum). **A**. « *Zeilleria* » aff. *pentagonalis* (Bronn *in* Quenstedt, 1858) (MNHN.F.A45934), vue ventrale. **B**. *Septaliphoria obtusa* (Quenstedt, 1871) (MNHN.F.A45935), vue ventrale. **C**. *Dorsoplanitoides triplicatus* Zeiss, 1968, (MNHN.F.R62470), vue latérale. **D**. Fragment d'une fronde de *Cycadopteris jurensis* (Kurr, 1846) Hirmer 1924 (MNHN.F.16640).

or grainstones containing coral fragments and skeletal fragments (e.g., echinids, bivalves, brachiopods, unidentified sponges; Fig. 6C). Some cross-beds include fragments of plants (Fig. 6D) and large burrows attributed to *Thalassinoides* Ehrenberg, 1944 (Fig. 6E). *Thalassinoides* is a complex branching horizontal burrow connected to the sediment-water interface by vertical shafts. The horizontal network of specimens from Canjuers is relatively well-preserved and recognized by its diagnostic Y-shaped bifurcations and smooth walls. Vertical shafts are rarely preserved.

#### 5.1.3. Sublithographic limestones

The third unit (ca. 1.5 m) is composed of relatively thick sublithographic limestone beds that house numerous abundant small burrows attributed to *Tubularina lithographica* Gaillard *in* Gaillard et al. (1994) (Fig. 6F).

### 5.2. Analysis and interpretation of the depositional sequences

(*1*) The depositional sequence starts with the refilling of the lagoon with sediment-laden waters from the open sea and the laying down of a fine-grained carbonate mudstone (core of the lithographic bed). During the deposition period, currents or movements were absent and the lagoon water was stagnant with anoxic conditions assumed at least for the lower part of the water column. The laminated lithographic limestone layers are undisturbed and bioturbation is absent. During these depositional times, tidal influences

**Fig. 9.** (Colour online) Undescribed limulid trackway from Canjuers (Canjuers town hall storage, Canjuers, France).

**Fig. 9.** (Couleur en ligne) Empreintes inédites de limules de Canjuers (visibles à la mairie de Canjuers, France).

were absent. On occasion, during storms or strong spring tides, the water backrush was strong enough to disturb or erode the underlying microbial films. It is assumed that during such high hydrodynamic events open marine organisms were introduced into the lagoon. Such 'violent events' were followed by calm periods of mud deposition. The majority of the open marine animals introduced into the lagoon died due to restricted hostile conditions (e.g., evaporation, hyper-salinity, anoxia) and sank to the floor where they were quickly buried and saved from further predation and fast decay. The deposition period was followed by the installation of a new microbial film at the surface of the lagoonal floor. The microbial film topping or framing the lithographic limestone layer played an important role in the preservation of organisms (Bernier et al., 1991; Gaillard et al., 2006; Gall et al., 1985). They protected organic remains in slowing down decay processes, increased cohesiveness of the sediment, and restrained erosion. Locomotion tracks such as those of horseshoe crabs (Peyre de Fabrègues and Allain, 2013) were protected by microbial films in the same way. The deformations of some of the microbial films recognized as wrinkled laminae (Fig. 5E) may indicate growth and expansion of coherent microbial surfaces, which may be the result of different physical processes such as wetting and drying, rise in water level, and wind and slope gravity (Gavish et al., 1985).

(*2*) The second unit indicates a change in the hydrodynamic and sedimentary regime. The Canjuers lagoon is now connected to the open sea through channels cutting across the reef barriers and reef patches. Tide currents supplied coarse, bioclastic sediments from the sea, mainly debris from the reef barriers, and also from small neighbouring coral reefs forming sub-aqueous small dunes (megaripples) that developed on the lagoon floor. Within these dunes, plant fragments are relatively abundant and confirm the presence of nearby islands. Invertebrates are common, vertebrates are rare or absent. The second unit ends with the installation of *Thalassinoides* burrows. *Thalassinoides* are often interpreted as feeding and dwelling burrows of crustaceans (Bromley, 1996; Gaillard et al., 1994; Myrow, 1995). In conclusion, the bioclastic unit contrasts with the precedent one: the lithology and the mode of deposition reflect higher water energy, shifting substrates and more open marine conditions. During this period, life could have prospered in the lagoon. The lagoon would have been constantly replenished with sea water through channels which also provided access routes for marine animals.

(*3*) The sublithographic limestones of the third unit indicate the return to calm hydrodynamic conditions, which is confirmed by the abundant burrows attributed to *Tubularina lithographica* (Fig. 6F), after Gaillard et al. (1994). These burrows were probably produced by intertidal polychaeteial worms. Like in the Cerin Lagerstätte, *Tubularina lithographica* from Canjuers is fossilized as "open burrow", attesting to early lithification that may have been associated with shallow water depth and/or the drying-out of the lagoon. According to Gaillard et al. (1994), the presence of *Tubularina lithographica* ichnofabric at the top of the Canjuers deposits is also probably a palaeoecological index of marginal marine conditions corresponding to a restricted shallow lagoonal area.

## 6. Invertebrates and plants

The Canjuers Lagerstätte contains a diverse and remarkably preserved invertebrate fauna dominated by echinoderms, brachiopods and bivalves, with also some scarce crustaceans (Table 1; Figs. 7 and 8). Among echinoderms, the echinoids dominate, including ten genera (Roman, 1991, 1994; Roman and Fabre, 1986). Most of them are preserved with their spines still attached to the tests (Fig. 7A, B), whereas test remains or *in situ* accumulations of plates and spines occur more rarely (Fig. 7C). By far, the most abundant sea urchin of the Canjuers biota is *Pseudosalenia aspera* (Agassiz, 1840) (Fig. 7A). The other echinoids are less abundant except those of the order Cidaroida (Table 1). Ophiuroids are less common in Canjuers and representatives of three families are known (Ophiuridae, Amphiuridae, and a yet unnamed family; Fig. 7D). They are found isolated but are always


A
2cm
B
10 cm
C
10cm
D
5cm
E
10cm
F
10cm
G
10cm
H
10cm

associated with sea urchins. Crinoids are represented by one large comatulid (*Comaturella pinnata* Goldfuss, 1886) and numerous small specimens of *Saccocoma tenella* (Roman, 1988, 1991; Fig. 7F). Only a single starfish assigned to *Pentasteria* Valette, 1929 is known (Roman et al., 1993; Fig. 7E). Among brachiopods terebratulids and rhynchonellids are most common with seven different species (Roman et al., 1991). Most specimens are strongly flattened and therefore have never been studied in detail (Fig. 8A, B). Bivalves in Canjuers are usually found in large numbers on bedding planes (e.g., the exogyrine oyster *Nanogyra striata*) (Smith, 1817). Some members of the genus *Chlamys* Röding, 1798 were also recovered. Crustaceans are represented by rare decapods and doubtful isopods and branchiopods. Only one specimen of decapods has been identified: *Cycleryon bourseaui* (Audo et al., in press). Chelicerata are represented with several trackways of limulids (Peyre de Fabrègues and Allain, 2013; Fig. 9).

Other macro-invertebrates from the Canjuers Lagerstätte include bryozoans (*Aspendesia* sp.), indeterminate unidentified sponges, corals (*Microsolena* sp.,?*Leptophyllia* sp.) and cephalopods (belemnites, ammonites). Corals and sponges are commonly scattered in the bioclastic beds and are almost absent in the lithographic limestones *sensu stricto*. Ammonites are relatively rare in all the Canjuers deposits. According to Atrops (1991, 1994), the presence of *Dorsoplanitoides triplicatus* Zeiss, 1968 (Fig. 8C) associated with several specimens of *Usseliceras* (*Subplanitoides*) *altegyratum* Zeiss, 1968 and *Usseliceras* (*Subplanitoides*) aff. *spindelense* Zeiss, 1968 indicate the *Mucronatum* biozone of the Early Tithonian (Late Jurassic).

Microfossils were preliminary studied by Fabre (1977a, b, c, 1981) who first mentioned the presence of foraminifera and marine ostracods. Algae and coprolites are present too.

Fossil plants are scarce and rarely well-preserved (Fabre et al., 1982; Roman et al., 1994). Pteridosperms and conifers seem to be the two most abundant fossils. According to Roman et al. (1994), numerous pteridosperm fronds and leaves belong to *Cycadopteris jurensis* (Kurr, 1845) (Fig. 8D). Small ramified axes of conifers correspond to *Brachyphyllum* Brongniart, 1828. Other axes, without ramifications, are attributed to the coniferous leaf-shoots *Cupressinocladus* Seward, 1919.

## 7. Vertebrates

The Canjuers Lagerstätte has revealed many exceptional and well-preserved fossil vertebrates including fishes, lizard-like reptiles (Rhynchocephalia), turtles (Chelonia), a crocodilian (Thalattosuchia), a pterodactyloid pterosaur, and a theropod dinosaur (Table 2).

Fishes compose the largest part of the vertebrates in Canjuers, with more than one hundred collected specimens including elasmobranchians, sarcopterygians (coelacanths), and actinopterygians. Many of them are also occurring in Cerin, Solnhofen, Eichstätt, and Wattendorf. Their preservation varies from completely preserved, articulated specimens to specimens that were preyed on or were partially decomposed, to single bone-preservations. Even coprolites and regurgitalites are found. *Undina* sp. and *Coccoderma* sp. are two representatives of the lobe-finned fish.

Sharks are very rare in the Canjuers limestones compared to the at least seven known families of sharks in the Solnhofen area (Fabre et al., 1982). An extraordinarily preserved specimen lacking only the very distal tail vertebrae can probably be attributed to *Palaeocarcharias stromeri* de Beaumont, 1960 (S. Klug, pers. comm., 2011). So far, this taxon was only known from the lithographic limestones of the Solnhofen area. The preserved Canjuers shark is 58 cm long.

The actinopterygians in Canjuers consist of two coexisting groups: the Holostei, which are diverse but not well represented, and the Teleostei, which are less diverse but very abundant (Fabre et al., 1982). Among the many actinopterygian taxa, a few well-preserved examples may be listed: *Naiathaeolon okkidion* Poyato-Ariza and Wenz, 1994 (Fig. 10A), "*Lepidotes*" sp., *Belenostomus* sp., *Proscinetes* sp. (Fig. 10B), *Gyrodus* sp., *Caturus* sp., *Ophiopsis* sp., *Tharsis* sp., and "*Pholidophorus*" sp. (see Table 2 for complete list).

*Solnhofia* is one of the three Eurysternidae-form turtles recovered in Canjuers. A second turtle was compared to *Eurysternum* by de Broin (1994) (see Fig. 10C). Newer findings have, however, shown that distinctive anatomical characters of *Eurysternum* are not well enough developed in this specimen. Until further revision the second specimen should be referred to an undetermined Eurysternidae. A third, juvenile specimen is probably closely related to *Eurysternum*. Unfortunately, the preservation of the postaxial skeleton is poor and comparisons with known adult specimens are difficult. Finally, a fourth specimen has not yet been classified and described.

The Rhynchocephalia, lizard-like reptiles, are represented in Canjuers by terrestrial sphenodontids and aquatic pleurosaurids. Three taxa of sphenodontids are known: *Homoeosaurus maximiliani* von Meyer, 1847, is the largest species of *H. maximiliani* recovered in Europe; a larger

**Fig. 10.** (Colour online) Vertebrates from the Canjuers Lagerstätte (Lower Tithonian, Mucronatum biozone). **A**. *Naiathaelon okkidion* Poyato-Ariza & Wenz, 1993 (MNHN.F.CNJ168), right lateral view. **B**. Pycnodont fish attributed to *Proscinetes* sp. (MNHN.F.CNJ3), right lateral view. **C**. Plesiochelyid turtle (MNHN.F.CNJ77), dorsal view. **D**. *Piocormus laticeps* (Wagner, 1852) (MNHN.F.CNJ68), dorsal view. **E**. *Pleurosaurus ginsburgi* Fabre, 1974 (MNHN.F.CNJ67), right lateral view. **F**. *Piocormus priscus* (von Soemmerring, 1814) (MNHN.F.CNJ78), skull in dorsal view. **G**. *Cycnorhamphus suevicus* (Quenstedt, 1855) (MNHN.F.CNJ71), ventral view. **H**. *Compsognathus longipes* Wagner, 1861 (MNHN.F.CNJ79), left lateral view.

**Fig. 10.** (Couleur en ligne) Vertébrés du Lagerstätte de Canjuers (Tithonien inférieur, biozone à Mucronatum). **A**. *Naiathaelon okkidion* Poyato-Ariza & Wenz, 1993 (MNHN.F.CNJ168), vue latérale droite. **B**. Poisson pycnodonte attribué à *Proscinetes* sp. (MNHN.F.CNJ3), vue latérale droite. **C**. Tortue plésiochélyide (MNHN.F.CNJ77), vue dorsale. **D**. *Piocormus laticeps* (Wagner, 1852) (MNHN.F.CNJ68), vue dorsale. **E**. *Pleurosaurus ginsburgi* Fabre, 1974 (MNHN.F.CNJ67), vue latérale droite. **F**. *Piocormus priscus* (von Soemmerring, 1814) (MNHN.F.CNJ78), crâne, vue dorsale. **G**. *Cycnorhamphus suevicus* (Quenstedt, 1855) (MNHN.F.CNJ71), vue ventrale. **H**. *Compsognathus longipes* Wagner, 1861 (MNHN.F.CNJ79), vue latérale gauche.

**Table 1**
List of fossil macro-invertebrates from the Canjuers Lagerstätte (Early Tithonian, Mucronatum biozone).
**Tableau 1**
Liste des macro-invertébrés fossiles du Lagerstätte de Canjuers (Tithonien inférieur, biozone à Mucronatum).

- ECHINODERMATA
  - ECHINOIDEA
    - Cidaroida
      - *Plegiocidaris marginata* (Goldfuss, 1826)
      - *Rhabdocidaris nobilis* (Münster *in* Goldfuss, 1826)
      - *Diplocidaris gigantea* (Agassiz, 1840)
    - Hemicidaroida
      - *Hemicidaris crenularis* (Lamarck, 1816)
      - *Acrocidaris nobilis* Agassiz, 1840
      - *Hessotiara florescens* (Agassiz, 1840)
    - Salenioida
      - *Pseudosalenia aspera* (Agassiz, 1840)
    - Phymosomatoida
      - *Pleurodiadema stutzi* (Moesch, 1867)
    - Arbacioida
      - *Acropeltis aequituberculata* Agassiz, 1847
      - *Magnosia nodulosa* (Goldfuss, 1826)
  - ASTEROIDEA
    - Paxillosida
      - *Pentasteria* sp.
  - OPHIUROIDEA
    - Ophiuridae
      - *Geocoma canjuersensis* Roman, Breton & Vadon, 1993
      - *Geocoma* aff. *carinata* (Münster *in* Goldfuss, 1826)
    - Amphiuridae
      - gen. et. sp. uncertain
    - Family uncertain
      - *Ophiurella* aff. *speciosa* (Münster *in* Goldfuss, 1826)
  - CRINOIDEA
    - Comatulida
      - *Comaturella pinnata* Goldfuss, 1886
    - Roveacrinida
      - *Saccocoma tenella* (Goldfuss, 1831)
- BRACHIOPODA
  - RHYNCHONELLIDA
    - *Torquirhynchia guebhardi* Jacob & Fallot, 1913
    - *Septaliphoria obtusa* (Quenstedt, 1871)
    - ?*Somalirhynchia* sp.
  - TEREBRATULIDA
    - *Juralina insignis* (Schübler, 1820)
    - *Moeschia* aff. *foraminata* (Rollier, 1918)
    - *Ismenia pectunculoides* (von Schlotheim, 1820)
    - "*Zeilleria*" aff. *pentagonalis* (Bronn *in* Quenstedt, 1858)
- MOLLUSCA
  - BIVALVIA
    - *Modiolus* (*Modiolus*) *imbricatus* (Sowerby, 1818)
    - *Entolium* (*Entolium*) *corneolum* (Young & Bird, 1828)
    - *Chlamys* (*Chlamys*) *textoria* (von Schlotheim, 1820)
    - *Spondylopecten* (*Spondylopecten*) *subpunctatus* (Münster, 1833)
    - *Nanogyra striata* (Smith, 1817)
    - *Actinostreon gregareum* (Sowerby, 1815)
  - CEPHALOPODA
    - *Dorsoplanitoides triplicatus* Zeiss, 1968
    - *Usseliceras* (*Subplanitoides*) *altegyratum* Zeiss, 1968
    - *Usseliceras* (*Subplanitoides*) aff. *spindelense* Zeiss, 1968
    - *Usseliceras* (*Subplanitoides*) cf. *schwertschlageri* Zeiss, 1968
    - *Usseliceras* (*Usseliceras*) cf. *franconicum* Zeiss, 1968
    - *Hibolites* sp.
- CRUSTACEA
  - DECAPODA
    - *Cycleryon bourseaui* Audo et al., in press
- CHELICERATA
  - XIPHOSURA
    - *Kouphichnium lithographicum* Oppel, 1862

**Table 2**
List of fossil vertebrates from the Canjuers Lagerstätte (Early Tithonian, Mucronatum biozone).
**Tableau 2**
Liste des vertébrés fossiles du Lagerstätte de Canjuers (Tithonien inférieur, biozone à Mucronatum).

- ACTINOPTERYGII
  - AMIIFORMES
    - CATUROIDEA
      - Caturidae
        - *Caturus* sp.
        - *Eugnathus* sp.
        - indeterminate taxa
  - PYCNODONTIFORMES
    - Gyrodontidae
      - *Gyrodus* sp.
      - Pycnodontidae
      - *Proscinetes* sp.
      - Indeterminate taxa
  - PACHYCORMIFORMES
    - Pachycormidae
      - Indeterminate taxa
  - PHOLIDOPHORIFORMES
    - Pholidophoridae
      - *Pholidophorus* sp.
  - LEPTOLEPIFORMES
    - Leptolepidae
      - *Leptolepis* sp.
      - *Tharsis* sp.
      - Indeterminate taxa
  - *IONOSCOPIFORMES*
    - Ophiopsidae
      - *Ophiopsis* sp.
      - Indeterminate taxa
  - ELOPIFORMES
    - Elopidae
      - Indeterminate taxa
  - *LEPISOSTEIFORMES*
    - Lepidotidae
      - *Lepidotes* sp.
  - ASPIDORHYNCHIFORMES
    - Aspirorhynchidae
      - *Belonostomus* sp.
  - ELOPOMORPHA
    - *Naiathaelon okkidion* Poyato-Ariza and Wenz, 1994
    - Indeterminate taxa
- SARCOPTERYGII
  - *ACTINISTIA*
    - *Undina* sp.
    - *Coccoderma* sp.
- CHONDRICHTHYES
  - LAMNIFORMES
    - *Palaeocarcharias* sp.
- REPTILIA
  - CHELONII
    - Plesiochelydae
      - *Solnhofias* sp.
      - *Eurysternum* sp.
      - Indeterminate taxa
  - RHYNCHOCEPHALIA
    - Pleurosauridae
      - *Pleurosaurus ginsburgi* Fabre, 1974
      - *Pleurosaurus goldfussi* von Meyer, 1831
    - Sphenodontidae
      - *Homoeosaurus maximiliani* von Meyer, 1847
      - *Leptosaurus pulchellus* (von Zittel, 1887)
      - *Piocormus laticeps* Wagner, 1852
  - MESOEUCROCODYLIA
    - Teleosauridae
      - *Steneosaurus priscus* (von Soemmering, 1814)

Table 2 (*Continued*)

| | | |
|---|---|---|
| PTEROSAURIA | | |
| | Pterodactylidae | |
| | | *Cycnorhamphus suevicus* (Quenstedt, 1855) |
| DINOSAURIA | | |
| | Compsognathidae | |
| | | *Compsognathus longipes* Wagner, 1861 |

sphenodontid *Leptosaurus pulchellus* (von Zittel, 1887); and finally the toothless *Piocormus laticeps* (Wagner, 1852) (Fig. 10D). Two members of the aquatic pleurosaurids have been recovered. *Pleurosaurus ginsburgi* Fabre, 1974 (Fig. 10E) is represented by a nearly complete specimen measuring almost 2 m (Fabre, 1980). A second specimen, *Pleurosaurus goldfussi* von Meyer, 1831, differs from the former by much shorter forelimbs, different number of presacral vertebrae, and dissimilar skull proportions (Dupret, 2004).

A specimen of *Steneosaurus priscus* (von Soemmerring, 1814) (Fig. 10F), a teleosaurid crocodiliform of 3.5 m length is the largest fossil found in Canjuers (Buffetaut, 1980). The skull and a superbly preserved postaxial skeleton are present. A representative of the same species but much smaller specimen is also known from Solnhofen, Germany (von Soemmerring, 1814).

The French pterodactyloid pterosaur *Gallodactylus canjuersensis* Fabre, 1974, was recently referred by Bennett (1996, 2010, 2013) to *Cycnorhamphus suevicus* (Quenstedt, 1855) from the Nusplingen lithographic limestones in Germany. *Cycnorhamphus suevicus* from the Canjuers Lagerstätte is one of the best preserved pterosaurs known in France (Fig. 10G). The French subadult specimen has a wing span of 1.4 m.

The most celebrated specimen of the Canjuers Lagerstätte is the coelurosaurian dinosaur *Compsognathus longipes* Wagner, 1861 (Fig. 10H). It was discovered in 1971 by the Ghirardi family and subsequently described by various authors (Bidar et al., 1972a, b; Michard, 1991; Peyer, 2006). The specimen is almost completely preserved and only lacks some phalanges and the extremity of its tail. It had a hip height of 33 cm, a total length of 1.4 m (Peyer, 2006). The French *Compsognathus* was preserved with its gastrointestinal contents, of at least two partly digested small reptiles.

## 8. Palaeoecology and palaeoenvironment

### 8.1. Invertebrates

Ophiuroids are particularly useful to understand the dynamics of the Canjuers palaeoenvironment. Like those from the Cerin lithographic limestones (Bourseau et al., 1994), the Canjuers ophiuroids are probably allochthonous. This was inferred from the apparent rigidity of their bodies (Roman, 1988) as well as the absence of bioturbation traces. Further evidence comes from several taphonomic experiments that tried to quantify the speed of decay from present-day regular echinoids under various physical conditions (Kidwell and Baumiller, 1990).

All the echinoids from Canjuers are regular and lived classically on hard substrate very different from the fine carbonate mud that constituted the original bottom of the Canjuers lagoon. They might have lived on the nearest coral reefs and/or reef patches, and were carried across the barrier reef into the lagoon during storms that were particularly frequent in intertropical areas or during strong spring tides. According to Bourseau et al. (1991) and Roman (1994), the ophiuroid probably arrived alive into the lagoon. The transport must have been fast, because generally the spines are still attached. The ophiuroids were fixed by prolific microbial films. Concerning the *in situ* accumulations of plates and spines, they probably correspond to partially digested food or regurgitations of diverse marine predators such as fishes (see Miller, 2007 for details).

The little exogyrine oyster *Nanogyra striata* (Smith, 1817) is very abundant in Canjuers. *N. striata* occurs in fine-grained low-energy sediments of the Jurassic European epicontinental sea (Fürsich and Oschmann, 1986). It is interpreted as having lived cemented to hard substrates during early juvenile stages, but commonly reclining on soft, muddy substrates in the adult stage. This could suggest that adult specimens were autochthonous to the lagoon. Their orientation in the sediment (they lay flat in a convex down orientation) and the absence of bioturbation in the sediment suggests, however, that the Canjuers oysters *N. striata* were probably introduced from neighbouring water areas during storms and settled out of suspension (as proposed by Fürsich et al., 2007 for the taphonomy of benthic fauna of the Wattendorf Plattenkalk). Brachiopods would have suffered a similar faith.

Atrops (1994) noted that all the ammonites (*Dorsoplanitoides*, *Usseliceras*) from the lithographic limestones belong to the family Ataxioceratidae, probably lived in open marine waters and would not have tolerated the hostile conditions in the lagoonal waters; their empty shells were washed into the Canjuers lagoon post-mortem too.

### 8.2. Flora

The plant fossils indicate an open forest environment, on more or less developed coral islands close to the lagoon. The semi-arborescent flora (Pteridospermales, Cycadales) may be pictured as growing close to the shore, with the arborescent flora (Coniferales) further away, on higher ground. According to Barale (1981) and Roman et al. (1994), the presence of relatively coriaceous leaves, strongly protected against evapotranspiration, suggests a hot, dry climate, at least during a large part of the year. *Cupressinocladus* belongs to the extinct conifer tree family Cheirolepidiaceae Takhtajan, 1963 (Watson and Alvin, 1999) that is also known to have grown at the edge of a shallow hypersaline lagoon, under strongly seasonal climate during the Late Jurassic all over south-western Europe (Philippe et al., 2010). A similar palaeoenvironment could be expected in the Canjuers area.

### 8.3. Vertebrates

The fossil vertebrate fauna of the Canjuers Lagerstätte originates from both terrestrial and different marine habitats. Evidence from newly discovered vertebrate fossils, the acquired stratigraphical data from the past two field

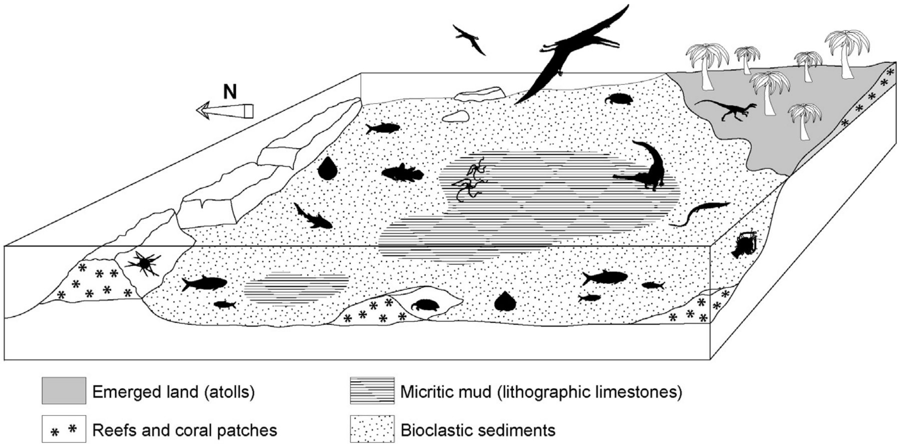


**Fig. 11.** Palaeoenvironmental reconstruction of the Canjuers lagoon and associated fauna. Animals and plants not to scale.
**Fig. 11.** Reconstitution paléoenvironnementale du lagon de Canjuers avec la faune associée. Animaux et plantes ne sont pas à l'échelle.

seasons, and the re-evaluation of the already existing Canjuers specimens in the MNHN collections strongly suggest that all vertebrates must have been embedded in the first depositional sequence *(1)*; the lithographic limestones *sensu stricto*. This sequence corresponds to a time when the lagoon was isolated from the open sea and not periodically replenished with seawater. Changing water levels in the lagoon led to unstable water temperature and salinity.

Some of the fossil fish preserved in the Canjuers lagoon originate from deeper off-shore waters. $\delta^{18}O$ values of corresponding fish from Cerin suggest just that, as the low isotopic water temperatures of their analysed bones correspond to values found in those from deeper marine waters (Billon-Bruyat et al., 2005). The $\delta^{18}O$ values of bones of the coral reef dwellers Pycnodontiformes and "*Lepidotes*" from Canjuers and Cerin imply much warmer water temperatures and may indicate that they did not live in the lagoon but near the coral reefs surrounding the lagoon (Billon-Bruyat et al., 2005).

The aquatic Canjuers eurysternid turtles probably lived close to the coral reefs surrounding the lagoon while *Pleurosaurus* and the thalattosuchian crocodilian *Steneosaurus* were more adapted to near-shore or open marine environments.

The occurrence of terrestrial vertebrate fossils in these limestones indicates the presence of an emerged, supratidal zone or islands in close proximity to the lagoon. These small islands are thought to have been overgrown with plants such as pteridosperms and conifers and created habitats for various small reptiles such as lizard-like reptiles (rhynchocephalians), and possibly small dinosaurs (*Compsognathus*) and pterosaurs. With the exception of the pterosaur, reptiles are generally completely articulated. This implies that transport before final burial on the lagoonal floor was short and that their natural habitat must have been close to the Canjuers lagoon. The pterosaur *Cycnorhamphus* may have lived on emerged land located around 100 km south of the Canjuers lagoon as documented by Thierry (2000). With some pterosaurs reaching soaring speed up to 90 km per hour (Witton and Habib, 2010), it would have been plausible that the Canjuers pterosaur could easily travel 100 km to reach the Canjuers region when looking for prey.

Different scenarios are possible to explain the ways that vertebrate animals arrived at the lagoon. Both the open marine fish taxa and the reef-dwelling fish must have been washed into the lagoonal basin during storm events (Fabre et al., 1982). Not adapted to the unsuitable lagoonal environment (too warm, elevated salinity, oxygen depleted bottom water-mass), they died quickly. The small terrestrial reptiles (terrestrial rhynchocephalians) probably arrived either dead into the lagoon when storm waves swept over the exposed surrounding and overgrown coral reefs, or alive followed by subsequent drowning. The larger terrestrial reptiles such as *Compsognathus*, *Cycnorhamphus*, and *Steneosaurus* were probably swept into the lagoon post-mortem.

## 9. Conclusions

The Late Jurassic palaeo-lagoon of Canjuers had an area of 1 km$^2$. The connection of the lagoon with the open sea varied over time and these different environmental conditions are recorded in the lagoonal sediments. Considering the three different depositional sequences, it is the first one which is of most palaeontological interest. Here the thin-layered lithographic limestone beds contain various well-preserved plant and animal specimens from different habitats. The soft muddy floor of the lagoon and the oxygen-poor conditions of the bottom water body proofed to be ideal for their preservation. The water level in the lagoon probably fluctuated with higher water levels after storm events, followed by decreasing water levels due to evaporation. A constant tidal influence is not assumed and seawater, containing sediments from the sea and surrounding exposed coral reefs, replenished the lagoon only periodically.

A more open connection to the sea, which occurred during the second depositional sequence, would have replenished the lagoon with well-oxygenated water rendering it favorable to turtles, aquatic reptiles (pleurosaurids), crocodilians, sharks, and a variety of fish and invertebrates. This scenario is depicted in a reconstruction of the lagoon (Fig. 11).

With the installation of the third, hydro-dynamically calm depositional sequence, the lagoon was again largely cut off from the open sea.

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