# ICHNOFABRIC FROM THE UPPER JURASSIC LITHOGRAPHIC LIMESTONE OF CERIN, SOUTHEAST FRANCE

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ABSTRACT. The upper Kimmeridgian lithographic limestones of Cerin, France, are lagoonal deposits, remarkable for the local occurrence of invertebrate burrows. Burrows are rare in the lower, well-laminated lithographic limestones, attesting to the absence of autochtonous benthic animals and, therefore, to the unfavourable life conditions on the lagoon floor. However, burrows are frequent in the upper lithographic limestones, the most abundant being *Tubularina lithographica*. These burrows are small, partly filled by pellets and were probably inhabited by intertidal polychaete worms. They are similar to Recent burrows restricted to the intertidal area of the lagoon of Aldabra (Seychelles). *T. lithographica* is fossilized as an 'open burrow', attesting to the drying-out of the lagoon and the onset of lithification. Other trace fossils, dominated by *Thalassinoides* and *Rhizocorallium*, are restricted to certain intermediate levels between the lower and upper lithographic limestones. The resulting ichnosequence may be the result of increasing periods of emersion in the lagoon. Compared with other well known lithographic limestones (e.g. Solnhofen, Canjuers, Montsec), this rich and unique ichnofabric clearly reflects the coastal location of the Cerin site.

FEW of the well-known lithographic limestones contain trace fossils, as they were normally deposited in environments (lacustrine, more or less deep marine environments – see Bernier and Gaillard 1994) that were generally unfavourable to benthic life. For example, the intensively sampled lithographic limestones from the Solnhofen area (Bavaria, Germany) have never yielded invertebrate burrows except for a few tracks of dying animals such as crayfish and limulids (Barthel *et al.* 1990). The Cerin lithographic limestone is unusual, however, in yielding a relatively rich ichnofauna. This paper describes the most common type of trace fossil in this fauna, which is referred to *Tubularina lithographica* igen. et isp. nov. The general sequence of ichnofabrics and their environmental implications are also discussed.

## MATERIAL AND METHODS

All of the studied samples were collected during a scientific excavation at Cerin, southern Jura Mountains, Ain, France (Text-fig. 1). The excavation was made in a disused quarry, where the lithographic limestone had been worked during the nineteenth century. The site had yielded a varied range of well preserved animal and plant fossils, which have made the locality famous (Bourseau *et al.* 1984). Since 1975, a bed-by-bed study of the whole formation has been organized. This systematic investigation occurred in two areas, measuring 75 m$^2$ (upper excavation) and 150 m$^2$ (lower excavation) respectively, and produced much homogeneous palaeontological and sediment-ological data. In particular, the study of the large upper bedding surfaces yielded many ichnologic observations (Gaillard *et al.* 1991). The lithographic limestones are upper Kimmeridgian (Enay *et al.* 1994). The palaeoenvironment corresponds to the margins of a shallow, tropical lagoon, lying above a dead coral reef complex (Barale *et al.* 1985; Bernier *et al.* 1991).

The bioturbation of each bed was studied in the field. The most interesting specimens were photographed and/or sampled. Many oriented and parallel sections (vertical and horizontal) were made through bioturbated beds, making it possible to measure burrow orientation. Variations in burrow density were detected by comparing corresponding surfaces from each bed. Some of the slabs were polished to allow detailed observation and photography. Thin sections through selected burrows were made. The pellets infilling the burrows and host lithographic limestone were observed and compared by scanning microscopy.

## SYSTEMATIC PALAEONTOLOGY

### Ichnogenus TUBULARINA Gaillard, igen. nov.

*Type species.* Although ichnotaxa established at the genus-group level do not require a type species (International Code of Zoological Nomenclature, 3rd Edition, 1985), it is suggested that *Tubularina lithographica* isp. nov. be regarded as the effective type.

*Derivation of name.* From the tubular shape of the burrow.

*Diagnosis.* Small tubular open burrow with a sharply defined smooth wall, a few branches, and frequent filling by well preserved faecal pellets.

### *Tubularina lithographica* Gaillard, isp. nov.

Plate 1; Plate 2, figures 1–3; Text-figure 2

*Holotype.* Specimen number 286 300, FSL Collections of the Centre des Sciences de la Terre, University of Lyon–1 (Pl. 1, fig. 3).

*Type locality and horizon.* Quarry at Cerin-Marchamp, Ain, France. Upper lithographic limestones, bed number 274A (holotype in slab number 274A–W).

*Derivation of name.* From the lithographic nature of the host limestone.

*Diagnosis.* Small cylindrical burrow, a few centimetres long, up to 2 mm in diameter, with little

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### EXPLANATION OF PLATE 1

Figs 1–8. *Tubularina lithographica* Gaillard, igen. et isp. nov. Cerin, France; upper lithographic limestone (upper Kimmeridgian). 1, vertical section through bed 281, showing bioturbation limited to upper part of bed; ×0·3. 2, vertical section through bed 354, showing the upper part only strongly bioturbated, and the top of the bed outlined by a red-brown coloration and with prominent burrows; ×0·6. 3, holotype; vertical section through bed 274A, showing a well developed vertical tunnel, with two branches, and an incomplete filling by faecal pellets; the ichnofabric is complex, with two generations of burrows (see Text-fig. 9); ×0·6. 4, vertical section through bed 274A, showing specimen with complex branching; ×1·8. 5, vertical section through bed 274A, showing specimen with incomplete filling by well sorted and arranged faecal pellets, indicating the polarity; ×4. 6–8, vertical sections through different examples of tunnels, showing variation in the size, shape and distribution of the faecal pellet fill; 6, longitudinal section; ×8; 7–8, transverse sections; ×12.

PLATE 1
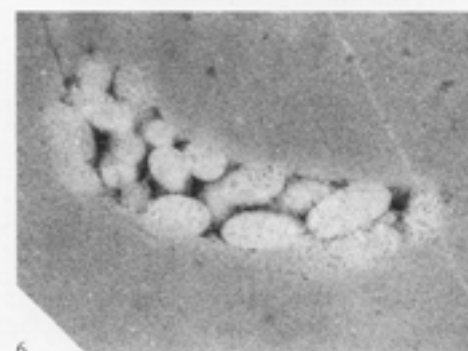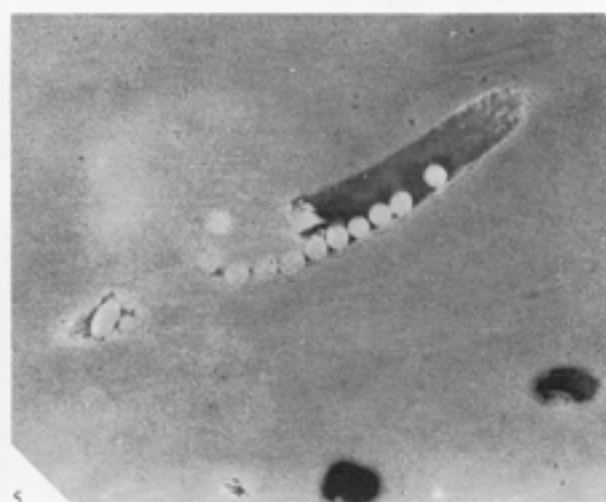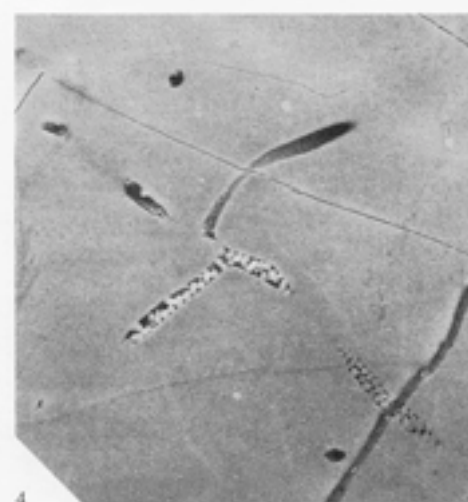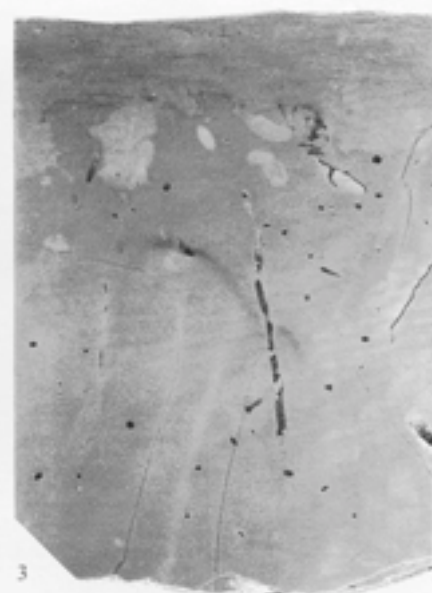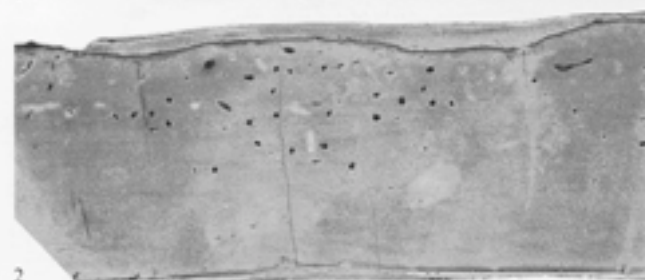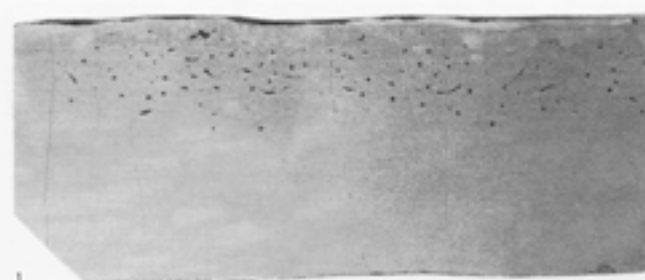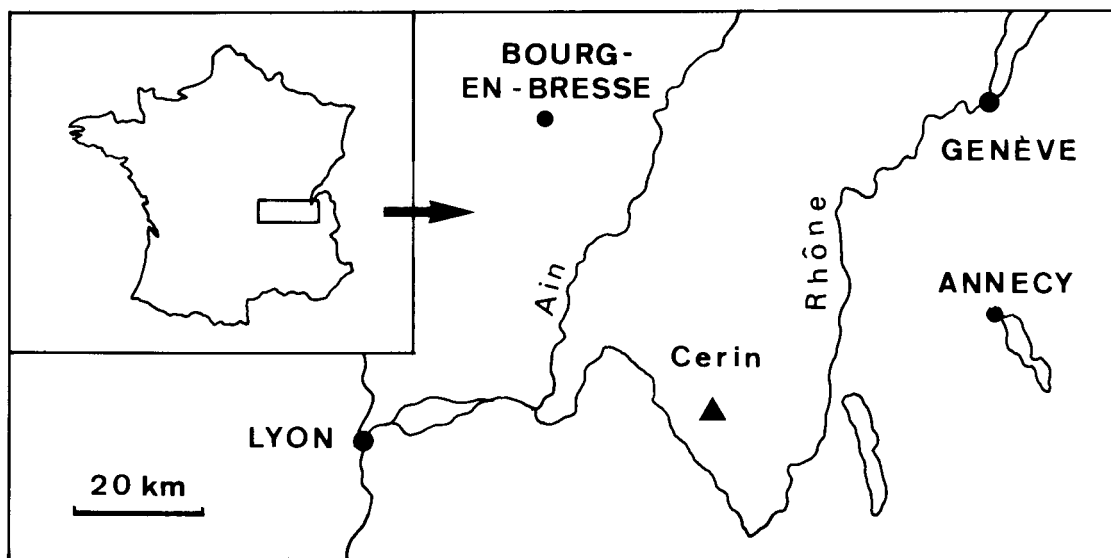
TEXT-FIG. 1. Location of the scientific excavations of Cerin (Ain, France).

branching. Tunnels sinuous and oriented in all directions relative to the bedding plane. Pellets filling it ellipsoidal, micritic, without internal structure, and up to 1 mm in diameter.

### Description

*Burrow.* The outline is generally very sharply defined (Text-fig. 2A). Transverse sections are circular (Pl. 1, figs 7–8; Text-fig. 2B), while longitudinal ones do not display any significant increase in the diameter. Diameter ranges from 0·5 mm to 2·0 mm. The total length is difficult to establish exactly but probably did not exceed 150 mm (the maximum depth of bioturbation in beds). Branching occurred but is rarely observed in section (Pl. 1, figs 3–4; Text-fig. 3). The burrow organization is rather complex. It penetrated the sediment more or less sinuously, in very different directions, but mostly with a subvertical (70°–90°) or subhorizontal (0°–20°) orientation (Text-fig. 4). From observations of vertical and horizontal parallel sections, the burrow system has been reconstructed, as shown in Text-figure 5. The wall was smooth, without ornamentation, and generally without lining. In some rare cases, thin section show a thin, dark lining which may have been detached (Text-fig. 2B–C). This possibly resulted from a mucus coating. The burrow is filled rarely by micrite, but more normally by sparite often including numerous pellets. Pellets do not line the burrow but clearly filled it.

*Pellets.* They are ellipsoidal, with a well preserved form (Pl. 1, figs 6–8; Pl. 2, figs 1–2; Text-fig. 2A–B). They are generally in contact, but not crushed. Because their diameter is approximately half the diameter of the containing burrow, no more than two rows of pellets could be observed in longitudinal section (Pl. 1, figs 5–6) and four specimens in transverse section (Pl. 1, figs 7–8). The pellets are micritic and exhibit the same homogeneous ultrastructure as the enclosing limestone (Pl. 2, figs 3, 5). In some cases faecal pellets exhibit a slight preferential dolomitization (Text-fig. 2A–B). The host rock is a very typical lithographic limestone (Bernier 1994). It consists essentially of $CaCO_3$ (99·5 per cent) and corresponds to a very pure and fine-grained micrite. The grain size of the anhedral microcrystals is less than 4 $\mu$m, frequently as small as 2 $\mu$m.

*Comparisons. Granularia* is not clearly defined. It was founded by Pomel (1849) on *Algacites granulatus* Schlotheim, 1822, a species which Brongniart (1849) had also used as the basis for the genus *Phymatoderma*; *Phymatoderma* is therefore a synonym of *Granularia*. Both genera were
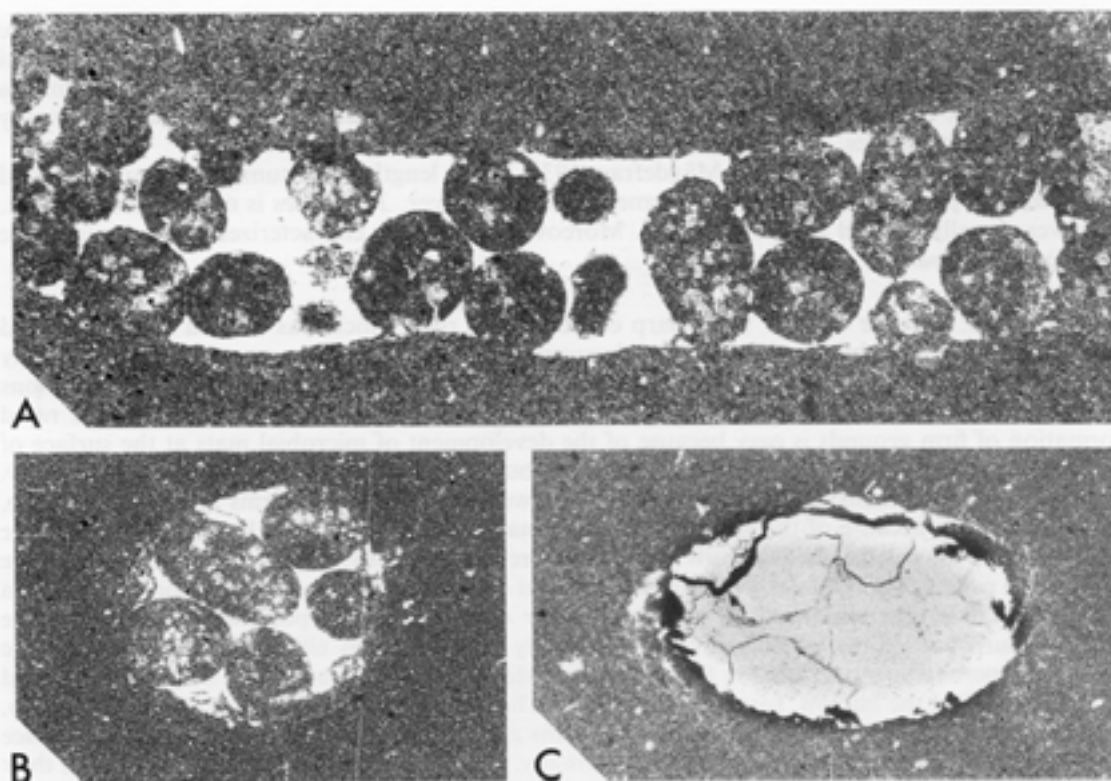
TEXT-FIG. 2. Thin sections through *Tubularina lithographica*; Cerin, upper excavation. A, longitudinal section of a typical burrow with sharp limits, sparitic filling, rounded micritic faecal pellets, and preferential dolomitization of faecal pellets; ×10. B, transverse section with faecal pellets; ×12. C, transverse section of burrow filled only with blocky calcite; an unusual detached dark lining is visible (also seen in B) which may be an ancient mucus lining; ×12.

previously described as plant fossils, as were similar forms of *Chondrites*. According to the modern interpretation summarized by Hantzschel (1975), *Granularia* corresponds to 'Elongated fillings of burrows; long, diameter up to about 15 mm.; twig-shaped, with rather regular branching; walls originally lined with clay particles...'. *Granularia* has not been frequently used in the literature. Following the original description, *Granularia* looks a little like *Tubularina*. Compared with *T. lithographica*, ichnospecies that could be assigned to *Granularia* are of different size and more frequently branched. *Phymatoderma caelatum* Saporta (1873, pl. 68, fig. 3), which is known from the Upper Jurassic, is very probably a small burrow, 1–2 mm in diameter, filled with pellets. But these are more elongated and irregular than in *T. lithographica*. On the other hand, *Granularia repanda* Pomel (see Saporta 1872, pl. 12, fig. 1a), whose rounded grains are probably small ferruginous concretions, is very different. *Granularia lumbricoides* Heer is the most similar ichnospecies but with more numerous, straighter, larger branches (Rothpletz 1896; Reis 1910).

When algal interpretations were abandoned, *Granularia* was often used for post-depositional burrows in turbidites (Seilacher 1961; Książkiewicz 1970, 1977; Crimes 1976; Leszczynski and Seilacher 1991). These are very different from *Tubularina*. Indeed, *Granularia* occurs mainly more or less horizontally on the sole of sandy layers (hypichnial ridges) and its diameter may be very variable (Książkiewicz 1970). Moreover, the specimens described by Seilacher (1961) are lined, not filled, with mud pellets.

*Coprulus oblongus* described by Mayer (1952) corresponds to coprolites filling larger and more complex burrows. Moreover, *Coprulus* must be restricted to a special kind of coprolite (Gaillard 1978). The closely related ichnogenus *Tomaculum* Groom, 1902, is a larger burrow (10–20 mm in diameter) filled by larger elongate pellets (1–5 mm long, 0·5–1·5 mm in diameter) and commonly lying on bedding planes.

*Tubularina* resembles *Trypanites* Mägdefrau, 1932, by the length of the tunnel, its sharply defined edges, and its possible filling by the excrement of the producer. *Trypanites* is more or less straight, however, usually vertical and unbranched. Moreover, *Tubularina* characterizes a firm ground (see below) and *Trypanites* a hard ground.

*Interpretation.* Because of their very sharp contours in a rock which was formed from mud, and because they are filled by sparry calcite, the burrows related to *Tubularina* must have been typically 'open burrows' in firm ground. Pellets are also very fragile grains which require special conditions to be preserved. These taphonomic conditions may occur during emergent periods. The rapid formation of firm grounds is easy because of the development of microbial mats at the surface of the sediment (Gall *et al.* 1985; Bernier *et al.* 1991) but the formation of hard grounds is unlikely.

Worms or crustaceans may have been possible dwellers. Polychaete worms are more probable, however, mainly because of the absence of scratch marks on the wall of the burrow, and the shape and structure of pellets. Pellets from *Tubularina* are homogenous, without any structure, while crustacean pellets commonly exhibit complex internal structures. Detailed comparison with modern burrows in a similar environment provides further evidence for the polychaete hypothesis (see below). Burrow-dwelling polychaete worms usually produce such ellipsoidal pellets. They are formed by peristaltic movements in the intestine, coated with a thin mucus film, and then deposited at the opening of the burrow, forming a small pile. The well-known species *Heteromastus filiformis*, which is very abundant in modern tidal flats, forms a small mound of faecal pellets at the surface opening of its burrow (Schäfer 1952, 1972). Normally, it is destroyed and the pellets, in spite of their relative cohesion (Cadée 1979), are rolled and broken by currents. The penetration and preservation of pellets in empty branches of the active burrow is possible. Alternatively, preferentially under special conditions (e.g. during a long emergent period) worms die and the pellets remaining at the surface may be preserved. Some of them can subsequently be introduced into the open, empty, inactive burrow where they are well protected (Text-fig. 6). This seems the most probable hypothesis for the genesis of the typical *Tubularina lithographica* specimens containing faecal pellets.

## OTHER TRACE FOSSILS FROM THE CERIN LITHOGRAPHIC LIMESTONE

The following were the other main burrows found in the Cerin lithographic limestone, and occurred only at a few levels. Others were very rare and may be related to well-known ichnogenera such as *Planolites* or were indistinct traces.

EXPLANATION OF PLATE 2

Figs 1–3. *Tubularina lithographica* Gaillard, igen. et isp. nov. Cerin, France; upper lithographic limestone (upper Kimmeridgian). 1, longitudinal thin section showing faecal pellets; × 20. 2, SEM view of micritic faecal pellets and sparitic cement; × 60. 3, SEM view of detail of the micritic content of a faecal pellet; × 1300.

Figs 4–6. SEM views of Recent polychaete burrows; Dune-Jean-Louis creek shore, Aldabra. 4, longitudinal section through burrow, showing faecal pellets and showing partly consolidated lime mud; × 15. 5, detail of the faecal pellets from a similar burrow; × 50. 6, detail of the micritic content of a faecal pellet from the burrow in 4; × 1300.

PLATE 2



GAILLARD *et al.*, Jurassic ichnofabrics
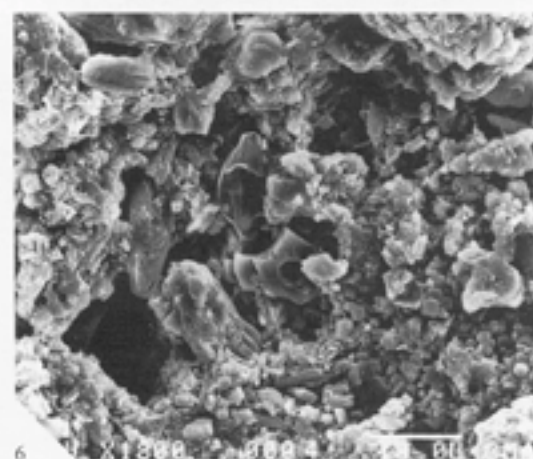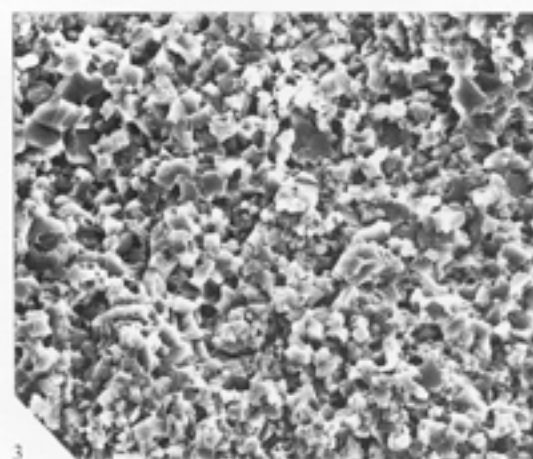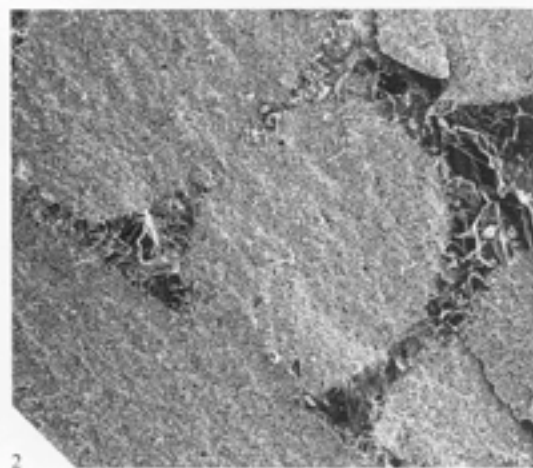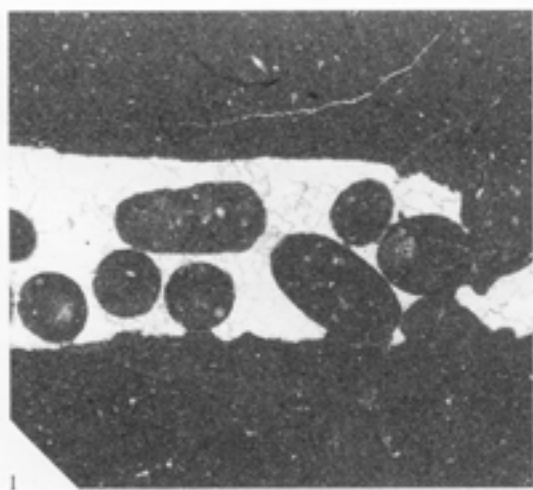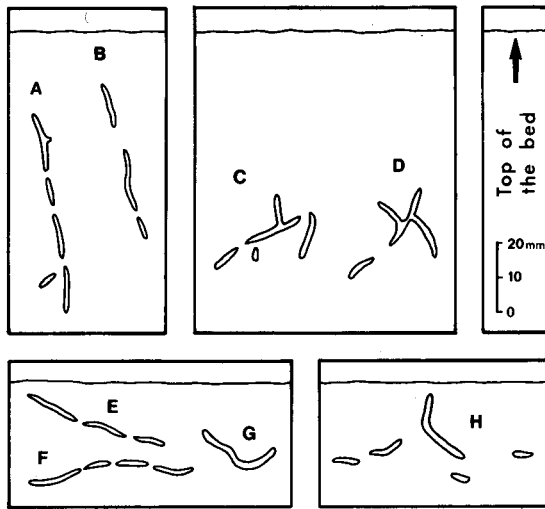
TEXT-FIG. 3. Tunnels of *Tubularina lithographica* in vertical section, drawn from polished slabs. A–B, long vertical tunnels (A—holotype). C–D, branching tunnels. E–G, long horizontal tunnels. H, burrow with upper vertical tunnel and lower horizontal branched tunnels. A, C–F, H, bed number 274A; B, bed number 306; G, bed number 296.
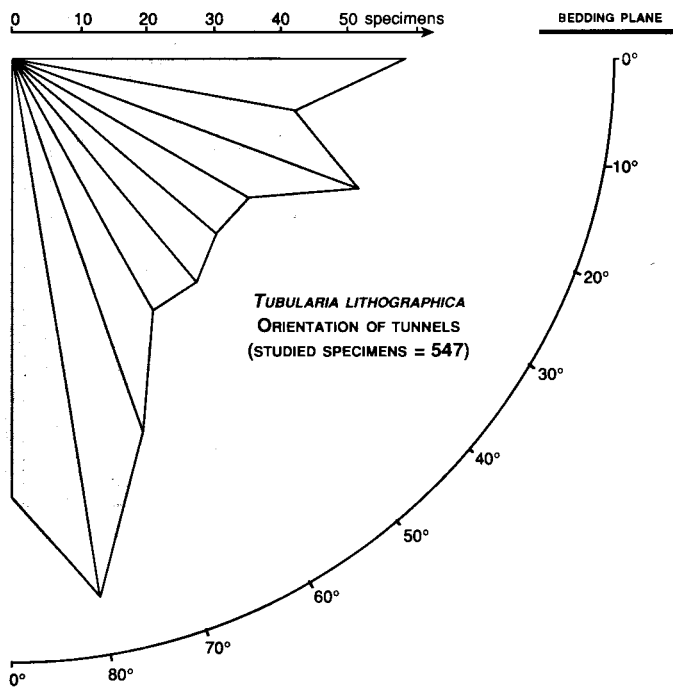


TEXT-FIG. 4. Orientation of *Tubularina lithographica* tunnels relative to the bedding plane (studied from vertical polished sections).

Thalassinoides *Ehrenberg, 1944*

This is a complex branching burrow with a horizontal network connected to the sediment-water interface by vertical shafts. Specimens from Cerin were poorly preserved (Text-fig. 7A). Only the horizontal network was visible with clear Y-shaped bifurcations and smooth walls. They are probably related to *Thalassinoides suevicus* (Rieth, 1932). The trace is usually interpreted as a feeding and dwelling burrow of a crustacean. Jurassic *Thalassinoides* containing the macrurous

TEXT-FIG. 5. Reconstruction of a complex, deep specimen of *Tubularina lithographica*.



10 mm



| SHORT EMERSION | | LONG EMERSION | SEDIMENTATION |
|---|---|---|---|
| ① | ② | ③ | ④ |
| burrow with living worm | | uninhabited burrow | fossilized burrow |
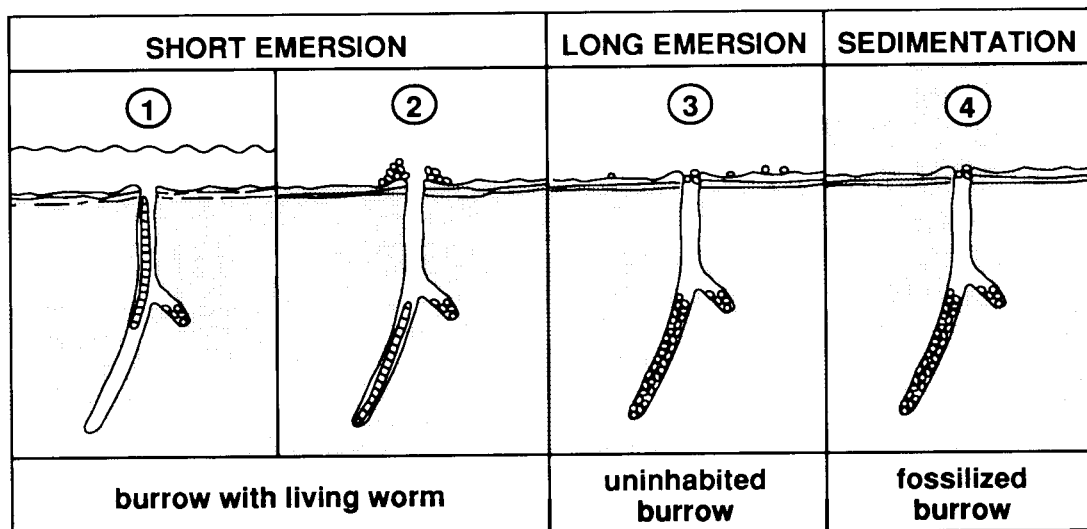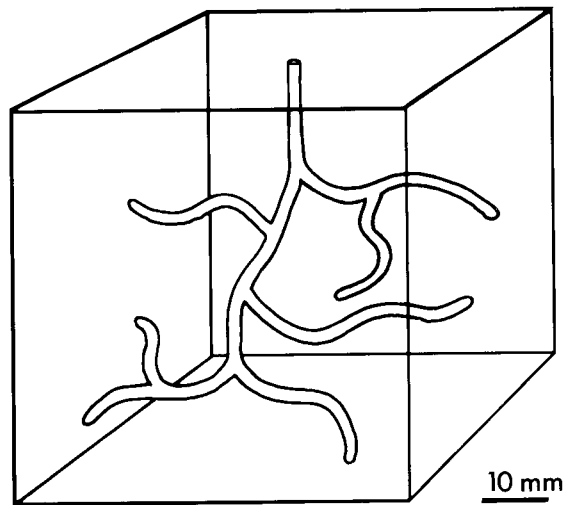
TEXT-FIG. 6. Different stages in the genesis of the fossil burrow *Tubularina lithographica*.

crustacean *Glyphaea* have been described by Sellwood (1971). *Glyphaea*, which is known as a body fossil from the Cerin lithographic limestones, is a possible excavator of *Thalassinoides*.

Rhizocorallium *Zenker, 1836*

This is a U-shaped spreite-burrow parallel to the bedding plane. Specimens were rare at Cerin and not well preserved (Text-fig. 7B). They resembled slightly burrows from the Upper Jurassic (Fürsich 1974a) and Lower Cretaceous (Basan and Scott 1979) that are related to *Rhizocorallium irregulare* Mayer, 1954. This trace is usually interpreted as the burrow of a deposit-feeder, probably a crustacean (Fürsich 1974a, 1974b).
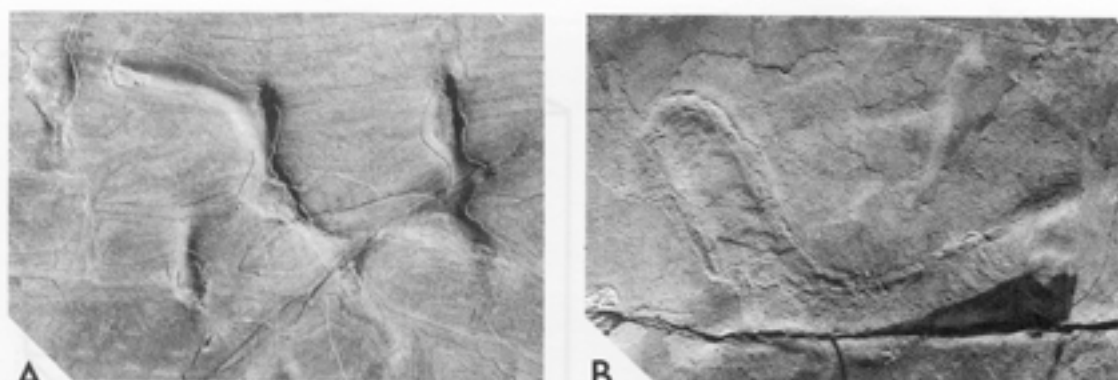
TEXT-FIG. 7. Trace fossils from the lithographic limestones of Cerin. A, *Thalassinoides*; ×0·16. B, *Rhizocorallium*; ×0·30.

## COMPARISON WITH MODERN ENVIRONMENTS

The wide distribution of Upper Jurassic lithographic limestones has no direct equivalent in the Recent. The Aldabra Lagoon (Indian Ocean, Seychelles) is probably the closest modern environment to the Cerin Lagoon (Gaillard *et al.* 1991, 1994). The lagoon of the Aldabra atoll has a surface area of 200 km², and is only a few metres deep. It communicates with the open sea through several channels. Twice a day, it is filled and emptied following a tidal rhythm. Calcareous material from benthic production and bioerosion is permanently reworked and distributed in the lagoon area according to the grain size. Consequently, a very pure lime mud is deposited along the most protected lagoon shore lines. It is frequently covered by microbial films which act as sediment stabilizers (Text-fig. 8A). These mud flats emerge for various periods of time, according to the distance from the shore. They are actively burrowed by different organisms, mainly crustaceans (Farrow 1971). The Jurassic environment of Cerin was certainly very different, principally because Aldabra is an atoll lagoon communicating easily with the open sea. Mud flats in the Aldabra lagoon are located in the most protected areas of the lagoon. The Cerin lithographic limestone was deposited in a very restricted and hostile lagoonal environment, located within an extensive tract of land. This explains the rarer benthic fauna inhabiting the Cerin lagoon. Nevertheless, there are similarities, especially in the creeks of the southern edge of the Aldabra lagoon, for example in the Dune-Jean-Louis Creek (Gaillard *et al.* 1994).

Mudflats are located along the protected southern shore of the Aldabra lagoon and are heavily burrowed by the crustacean *Alpheus crassissimus*. These burrows, which look like *Thalassinoides*, are situated near extreme low water and are covered at neap high tides. They are formed in a typical soft ground. In some more littoral and sheltered areas, mud forms a firm ground which is also intensively bioturbated. This firm ground is the result of considerable dewatering and efficient binding by microbial mats built by *Microcoleus chtonoplastes* (Text-fig. 8A–B). Different kinds of burrows are inhabited by worms and crustaceans (Text-fig. 8C). The most abundant burrows strongly resemble *Tubularina lithographica* because of their length and their filling by spheroidal faecal pellets (Pl. 2, figs 4–6). Living burrowing polychaete worms, belonging to Eunicidae (*Marphysa mossambica*) and to Nereidae (*Perinereis cultrifera*), have been found in this environment (determined by Y. Gruet and P. Gillet).

Similar environmental conditions may have occurred in the most coastal areas of the Cerin lagoon. In the centre of the lagoon, poisonous anoxic water hindered normal benthic life. Exceptionally some infaunal decapods colonized the lagoon floor (forming *Thalassinoides*) when sufficiently oxygenated. The *Thalassinoides* community may be compared to the recent *Alphaeus* community of the lagoon of Aldabra. The burrowing shrimp *Alphaeus* is common in fine-grained lime sediments, for example throughout the Florida Keys and the Bahamas (Shinn 1968). It is most
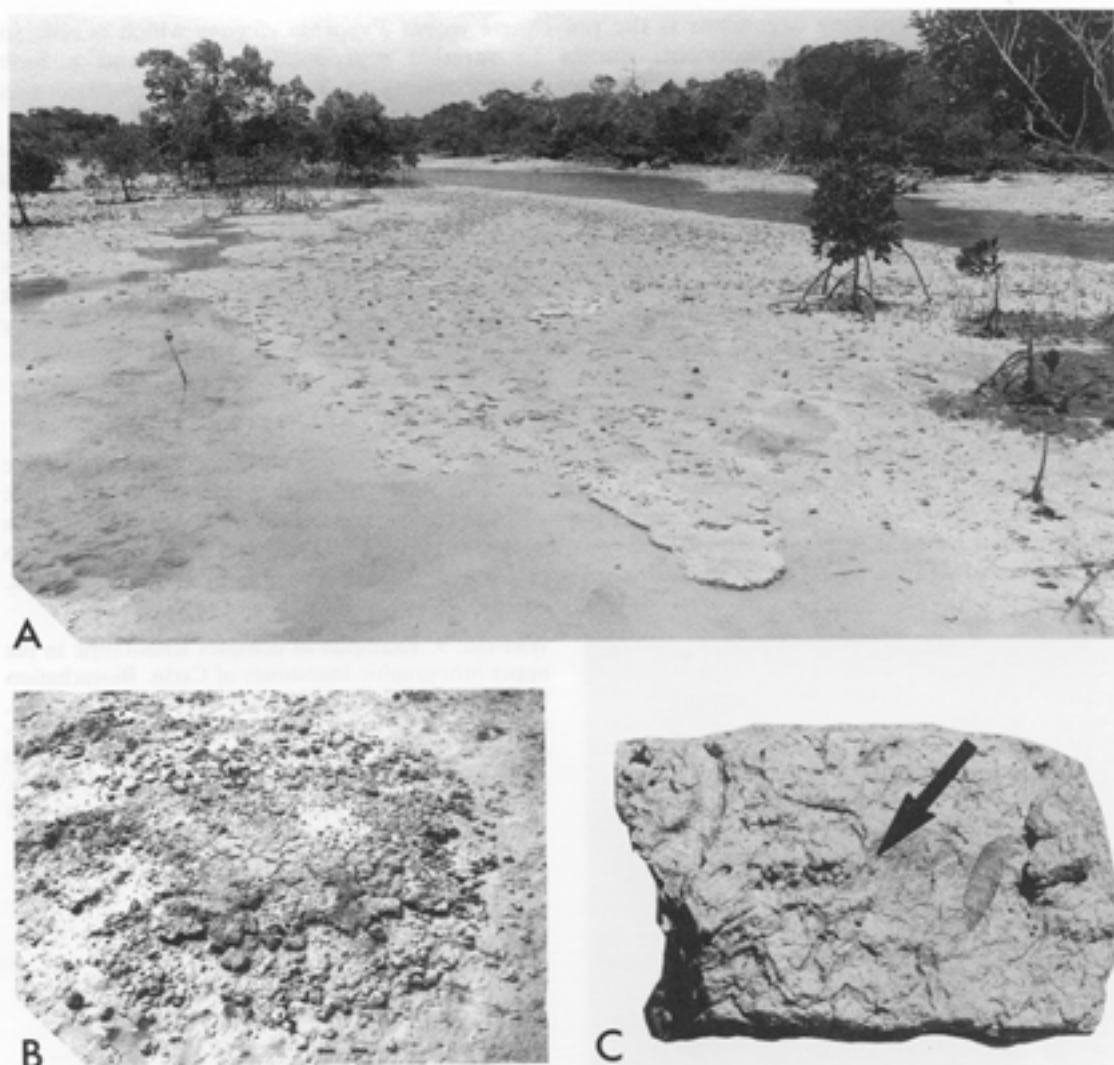
TEXT-FIG. 8. A, calcareous mud flat ('blanc d'Espagne') at low tide, partly covered by eroded *Microcoleus* mat; Abbott's creek, Aldabra. B, close-up of eroded *Microcoleus* mat; Dune-Jean-Louis creek, Aldabra. C, partly consolidated (water loss) lime mud showing, in section, many burrows sometimes including faecal pellets (arrow); Dune-Jean-Louis creek shore, area with long emersive periods, Aldabra.

abundant in the intertidal zone where it digs complex burrows of *Thalassinoides*-type. In the Cerin lagoon, generally only microbial mats flourished. If emergent for too long, they would be progressively altered by mechanical and biological processes. Such a relationship between microbial development and animal benthic life can be observed in many tidal environments. Gerdes and Krumbein (1986) have described the relationship between microbial mats and infaunal invertebrates in a supratidal depositional environment from the North Sea, which is a well oxygenated open sea. The texture, composition and degradation products of the microbial mats, which are dominantly formed by *Microcoleus chtonoplastes* in the most sheltered areas, are observed to control the abundance of burrowing animals. The infaunal population is low because of anaerobic conditions under the mat surface, where ammonia and sulfide concentrations are relatively high. One of the

most abundant burrowing organisms is the polychaete worm *Pygospio elegans* which is able to recolonize rapidly the fresh sediment, thanks to variable reproduction cycles and a high reproduction rate. In comparison, the burrower corresponding to *Tubularina lithographica* was probably also an opportunistic organism.

In the Cerin lagoon, greater emersion probably caused the mechanical degradation and the weathering of microbial mats, leading to mud colonization by burrowers. Indeed, desiccation cracks occur at the surface of some beds, mainly in the transition levels of lithographic limestones, although only rarely in the lower (probably because of short emersions) and upper lithographic limestones (probably because often destroyed by bioturbation). Many cases of microbial mats partly destroyed by burrowing animals can be observed in the Recent. For example, in the most sheltered parts of the Aldabra lagoon, the degradation of the *Microcoleus chtonoplastes* mats by burrowers frequently begins along desiccation cracks (Text-fig. 8B).

## RESULTING ICHNOFABRIC

The *Tubularina lithographica* ichnofabric was examined in several oriented bed sections, where burrow density and orientation could be studied. The most obvious observation was that bioturbation was more frequent in the upper part of beds (Pl. 1, figs 1–2). The lower part of beds generally had no or very few burrows. The most complete ichnofabric showed no more than two kinds of burrow (Text-fig. 9). First, indistinct irregular burrows filled by ambiant micrite occurred.
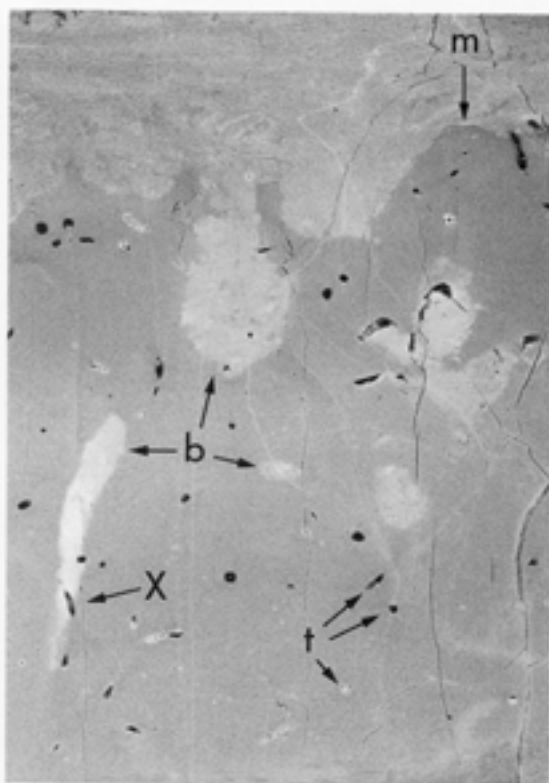


TEXT-FIG. 9. Examples of complex ichnofabric in the upper lithographic limestones of Cerin. Bioturbation by large indistinct burrows filled by light micrite (b), and *Tubularina lithographica* (t). The first are cross-cut by the second (X). On the right, the horizontal top of the initial deposit of thinner dark micrite is visible. It is probably consolidated by a thin microbial mat (m); natural size.

These early burrows excavated the superficial microbial mat, when visible, and had been subsequently cut through by *Tubularina*. This indicates that *Tubularina* was a late burrow made in a firm ground. The maximum density of *Tubularina* was always a few centimetres below the top bed
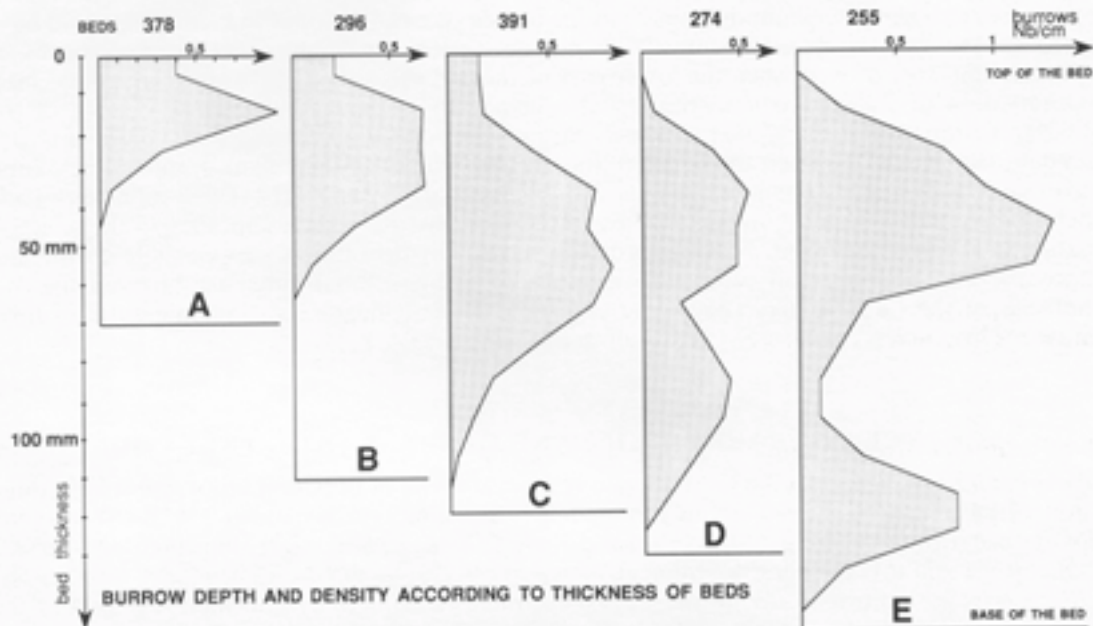
TEXT-FIG. 10. Density of burrows at different depths, in beds of Cerin lithographic limestone of different thicknesses, showing the development of bimodal distributions in the thicker beds.
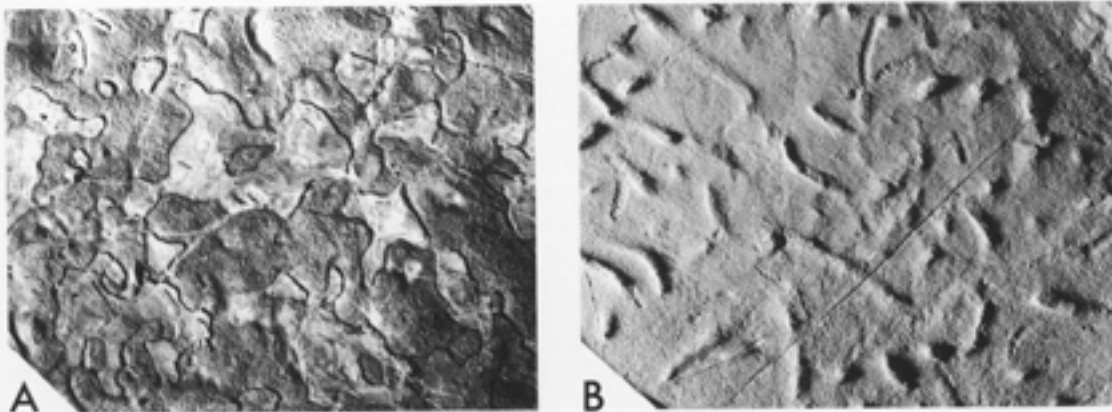


TEXT-FIG. 11. A, irregular top surface of Cerin lithographic limestone beds bioturbated by *Tubularina lithographica*, showing late selective erosion, probably by dissolution; ×0·1. B, detailed view of burrows; ×1.

surface, probably reflecting the deep development of the horizontal galleries of the burrow system (Text-fig. 10). This depth of maximum burrow density increased with bed thickness (Text-fig. 10A–C). The more that available fresh sediment was abundant, the more the burrows were developed and deeply settled. Curiously, in very thick beds (more than 120 mm in the case of the Cerin lithographic limestones), two maxima of bioturbation sometimes occurred (Text-fig. 10D–E), the upper one being the most important. This possibly illustrates two successive stages of sedimentation

in a relatively short time. Slight differences in the nature or consistency of the sediment could have controlled the vertical development of the burrow system. In some cases the two stages of sedimentation were proved when the lower part of the bed was topped by a slight microbial mat.

Observation of *Tubularina lithographica* also helped to understand the late evolution of the lithographic limestones. Only in the upper part of the formation, where *T. lithographica* was abundant (see below), the bed tops exhibit an irregular red-brown mamillate surface. Each knoll was often bristling with prominent *Tubularina* (Pl. 1, fig. 2; Text-fig. 11). These millimetre-scale reliefs corresponded primarily to holes, then to their late sparitic filling, and after to the selective ablation of the host sediment. Selective erosion, perhaps by dissolution, was possible during late diagenesis. This phenomenon could have amplified the slight initial difference between the two lithofacies of the Cerin quarry (Bausch *et al.* 1994). These ('flinze' and 'faulen') differ in their content of insolubles.

## SEQUENCE OF TRACE FOSSILS AND GENERAL INTERPRETATION

*Tubularina lithographica* was the most abundant burrow found in the Cerin lithographic limestone. It occurred at numerous levels, but only in the upper limestones (beds number 255 to 404 from the scientific excavation; Text-fig. 12). As shown earlier, *T. lithographica* clearly indicates long periods of emergence and a very cohesive sediment.

*Rhizocorallium* occurred only in rare beds (beds number 250C to 270) in the lower part of the vertical range of *T. lithographica*. In bed number 270, *Rhizocorallium* was associated with *Thalassinoides*. The association of *Rhizocorallium irregulare* and *Thalassinoides suevicus* is well-known in shallow Jurassic environments (Fürsich 1974a; Heinberg and Brikelung 1984), but according to Fürsich (1974a) the two trace-makers were probably not contemporaneous. The bioturbation by *Rhizocorallium* took place at a later stage than that of *Thalassinoides*, when the sediment became sufficiently cohesive.

*Thalassinoides* was also found in only a few beds, although more frequently than *Rhizocorallium*. It appeared lower, at the base of the lithographic limestones, and disappeared at the same level as *Rhizocorallium*.

Three levels could therefore be distinguished: (1) a lower-level without traces or with very rare *Thalassinoides*, (2) a short transition-level with *Thalassinoides* and *Rhizocorallium*, and (3) an upper-level with abundant *Tubularina lithographica*. This ichnologic succession characterizes a very precise shallowing upward sequence. The gradual increase in periods of emersion induced changes in burrowing communities, probably controlled strongly by the increase in cohesion of the substrate. This environmental interpretation is supported by other palaeontological data (Text-fig. 12). The lower level showed dominant marine influence, with the introduction into the lagoon of open-sea organisms. The fauna was characterized by the presence of ammonites and shrimps, and the dominance of fishes and algae. In contrast, the upper level showed an increase in continental influence, with the disappearance (ammonites) or reduction in abundance (fishes) of marine animals, and the dominance of terrestrial plants (*Zamites*). Microbial mats were also deformed (Bernier *et al.* 1991) but well preserved in the lower level, where bioturbation was limited or absent. They were invisible or poorly preserved in the upper level probably because it was highly bioturbated (Text-fig. 12).

Detailed ichnological sequences have been previously described from Jurassic shallow marine environments. For example, Farrow (1966) has shown a bathymetric zonation of trace fossils in Yorkshire Jurassic sections, where annelid burrows always precede crustacean burrows (*Rhizocorallium, Thalassinoides*) in the sequence, indicating a slight deepening of the water. At Cerin, the sequence culminated with the reappearance of special annelid burrows (*Tubularina*) in more coastal and restricted environments.

In the Upper Jurassic sediments from Boulonnais (northern France), Ager and Wallace (1970) have shown the following clear sequence, reflecting shallowing and emergence: (1) horizontal
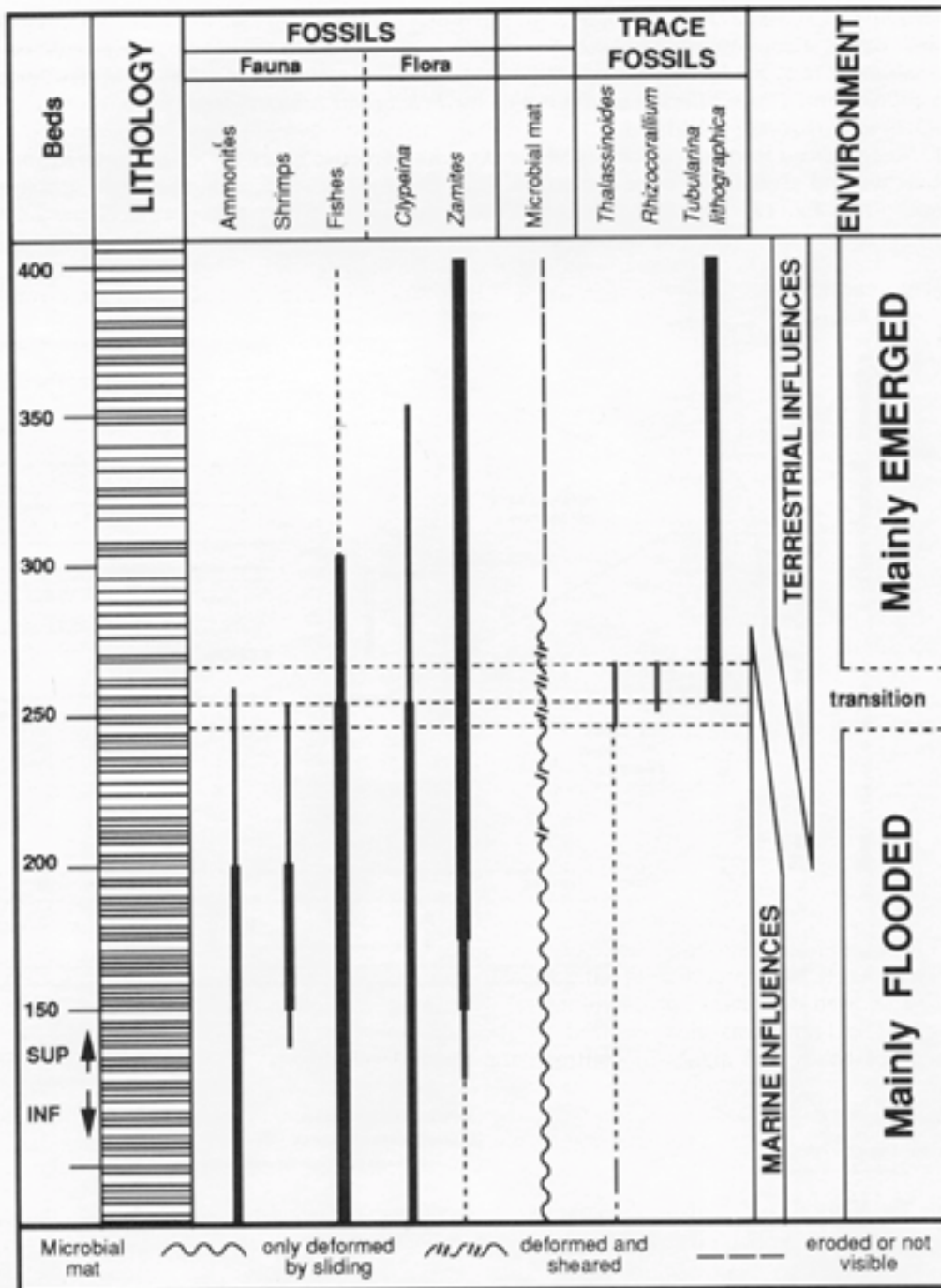
TEXT-FIG. 12. Stratigraphical distribution of trace fossils and body fossils in the lithographic limestones of Cerin, together with an interpretation of the environment.

*Rhizocorallium*, (2) large *Thalassinoides*, (3) obliquely oriented *Rhizocorallium*, and (4) *Diplocraterion*. Some elements of this sequence occur at Cerin (horizontal *Rhizocorallium* and *Thalassinoides*), but the last part is different. The replacement of the obliquely oriented *Rhizocorallium* and *Diplocraterion* communities by *Tubularina lithographica*, probably reflects the more restricted lagoonal conditions.

As *T. lithographica* seemed to be an excellent paleobathymetric index for marginal environments, its occurrence and abundance were compared from two nearby sections in the Cerin lithographic limestones (Text-fig. 13). The first (Section A) was in an area where lithographic limestones are
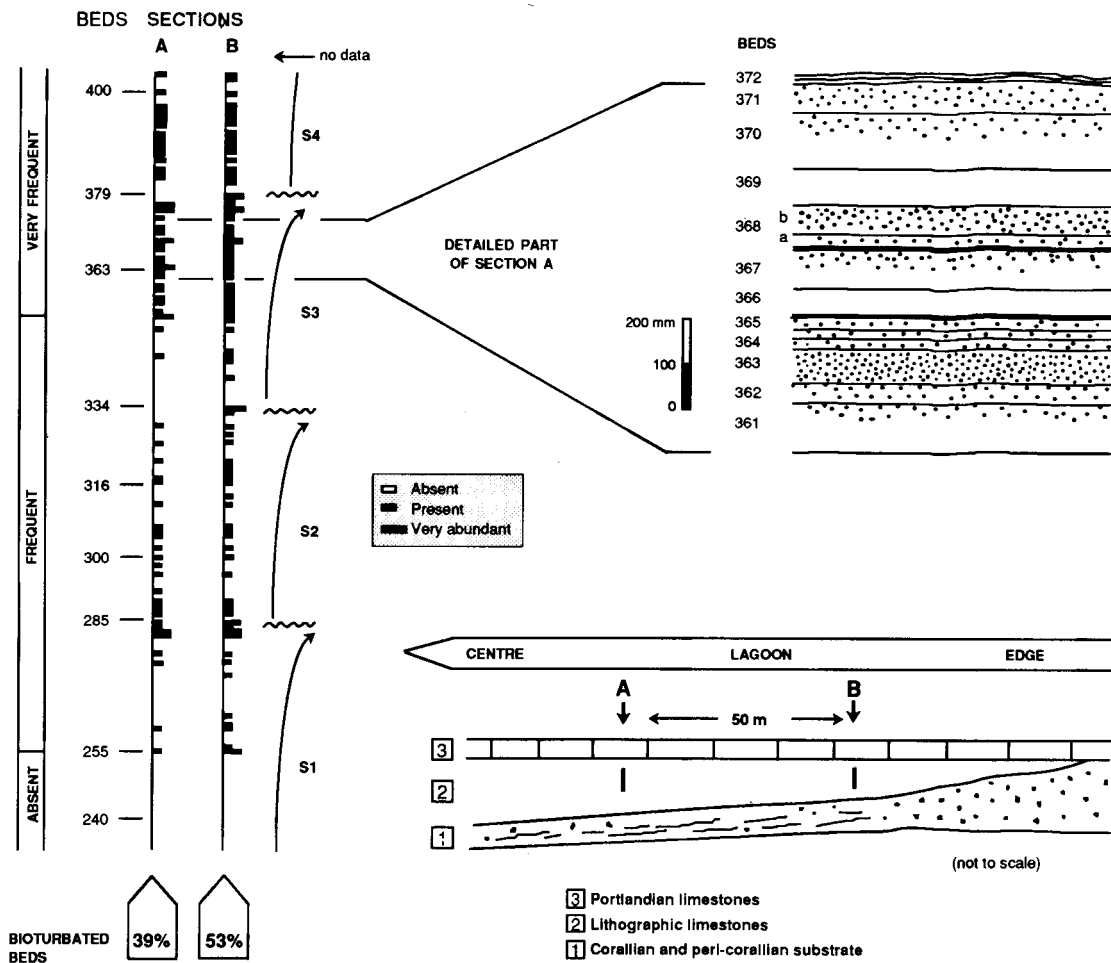


TEXT-FIG. 13. Vertical and horizontal variation of *Tubularina lithographica* bioturbation in the upper lithographic limestones in the Cerin lagoon.

thick. The second (Section B) was 50 m away and corresponded to the scientific excavation where lithographic limestones are thinner and near their rocky substrate (Bernier *et al.* 1994). In the two sections, the ichnofabric with *T. lithographica* appeared at the same level (bed number 255) and only became abundant in the upper part. Four main intervals with increasing density of bioturbation

were distinguished (S1 to S4) and interpreted as shallowing upward sequences. It was interesting, however, to note that the *T. lithographica* ichnofabric was visible only in thirty nine per cent of beds from Section A (Text-fig. 14) but in fifty three per cent of beds from section B. This probably



TEXT-FIG. 14. Detail of ichnologic sequence S3 from section A (see Text-fig. 13), showing beds 363 to 368;
×0·25.

indicates that Section A was situated nearer the centre of the lagoon, which was deeper with probably less frequent and shorter emersions than at the edge. It confirmed the very coastal situation of the scientific excavation area, where many trackways of terrestrial animals have been observed (Bernier *et al.* 1982, 1984; Gaillard *et al.* 1991).

## CONCLUSIONS

A detailed bed by bed investigation of the upper Kimmeridgian lithographic limestones of Cerin has revealed abundant but poorly diversified invertebrate trace fossils. This underlines the distinctive nature of Cerin compared with other well known lithographic limestones sites. The most abundant trace fossils (*Tubularina lithographica* Gaillard) are small, branched burrows, generally filled by spheroidal faecal pellets and sparite, indicating an emerged firm substrate. It was probably produced by a polychaete worm similar to Recent ones living in intertidal environments like the Aldabra lagoon (Seychelles). Other trace fossils, mainly *Thalassinoides* and *Rhizocorallium*, are rare and indicate 'deeper'-water conditions. The Cerin trace fossils were organized in the following shallowing upward ichnologic sequence: *Thalassinoides – Rhizocorallium – Tubularina*. The *T. lithographica* ichnofabric is probably a very precise palaeoecologic index for marginal marine environments corresponding to restricted shallow lagoons.

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