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Palaeoecologic significance of Late Jurassic trace fossils from the Boulonnais, N France

MICHAEL SCHLIRF

Institut für Paläontologie der Universität, Pleicherwall 1, D-97070 Würzburg, Germany.
E-mail: michael.schlirf@mail.uni-wuerzburg.de

ABSTRACT:

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Late Jurassic invertebrate trace fossil assemblages studied at outcrops along the coastline of the Boulonnais (northern France) are described and their palaeoenvironmental interpretations are discussed. The ichnofauna shows a high diversity (36 ichnospecies). Predominant forms are *Spongeliomorpha suevica*, *S. nodosa*, *Treptichnus*, *Asterosoma*, *Rhizocorallium irregulare*, *Rh. jenense*, *Diplocraterion*, *Teichichnus*, *Rosselia*, *Skolithos*, *Cochlichnus*, *Gyrochorte*, and *Bolonia lata*. Following Seilacher's (1967) archetypic classification the trace fossils belong to the *Skolithos* and *Cruziana* ichnofacies. In a 120 m succession of storm-dominated, nearshore, marine clastics of Kimmeridgian-Tithonian age nine frequent palaeoichnocoenoses and one exceptional palaeoichnocoenosis are identified. Their distribution is mainly controlled by hydrodynamic energy. These energy levels represented by the host rocks may differ from what the trace fossils indicate. It can be shown that a large proportion of deposit-feeding structures, such as *Teichichnus*, *Rhizocorallium irregulare*, and *Asterosoma*, indicating quiet and stable conditions, although occurring in host sediments indicating high energy conditions. This contradictory observation is attributed to non contemporaneous formation of the sediments and the trace fossils. In a sequence stratigraphic interpretation of the Grès de la Crèche at Le Portel, parasequence boundaries are detected with the help of completely bioturbated horizons. The study of trace fossil assemblages thus gives a more detailed and accurate picture of former environmental conditions than sedimentologic methods alone.

Key words: Trace fossils, Palaeoenvironmental reconstruction, Upper Jurassic, Northern France.

INTRODUCTION

Highly diverse and extraordinarily well preserved trace fossil assemblages are exposed in the Upper Jurassic (Kimmeridgian-Tithonian) rocks of the Boulonnais, northern France. Although well known for many years (Meunier 1886, Ager & Wallace 1970), their potential importance for palaeoecologic reconstructions has been neglected in most studies. The Kimmeridgian-Tithonian rocks have been the subject for various studies concerning stratigraphy (Pruvost & Pringle 1924; Pruvost 1925; Ager & Wallace 1966; Ziegler 1966; Proust & *al*. 1993, 1995), depositional environments (Hallam 1967, 1975; Gallois 1976; Gallois & Medd 1979; Tyson & *al*. 1979; Aigner 1980; Cox & Gallois 1981; Wignall 1989; Wignall & Newton 2001; Wignall & *al*. 1996; Oschmann 1985, 1988, 1990; Fürsich & Oschmann 1986; Herbin & *al*. 1991a, 1991b, 1993), micropalaeontology (Wignall 1990), and macropalaeontology (Meunier 1886; Oschmann 1985, 1988; Fürsich & Oschmann 1986).

MEUNIER (1886) first published studies on the ichnofauna of Late Jurassic age from the Boulonnais area. AGER & WALLACE (1970) made a first attempt at describing the distribution and significance of what they called most important trace fossils in the uppermost Jurassic rocks of the Boulonnais. However, none of these trace fossils were formally described or documented. SCHLIRF (2000) gave the first detailed taxonomic description of the trace fossils but without palaeoecologic interpretation.

In the present study, the palaeoecologic significance of trace fossils of the Upper Jurassic rocks in the Boulonnais is described and the value of certain ichnotaxa for facies interpretation is discussed.

A detailed review of the geologic setting and depositional environment is beyond the scope of this study. Data on the geologic history of the basin for the Jurassic period can be found in AGER & WALLACE (1966), PROUST & *al.* (1993, 1995) and WIGNALL & *al.* (1996).

LITHOSTRATIGRAPHY AND FACIES INTERPRETATION

The following lithostratigraphic data set combines the previous works of PROUST & *al.* (1993, 1995) and WIGNALL & *al.* (1996) with own field observations. The

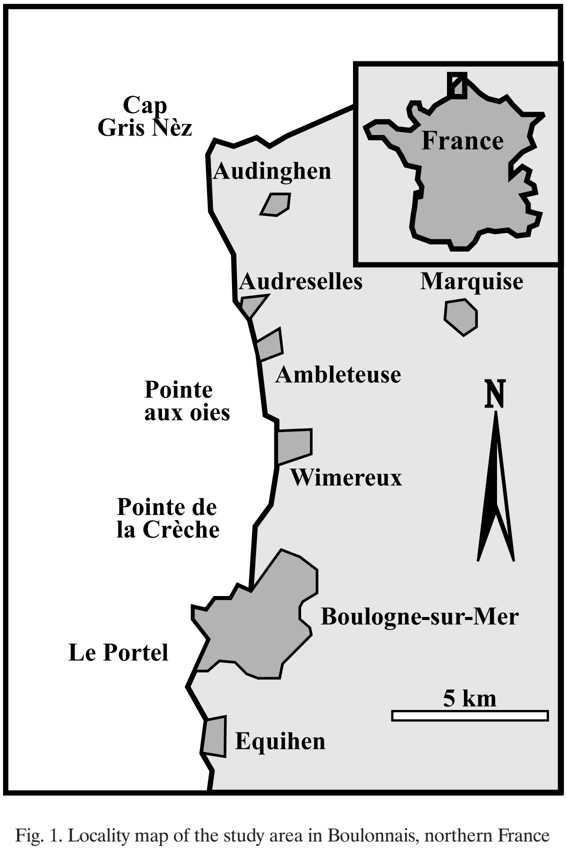

Fig. 1. Locality map of the study area in Boulonnais, northern France

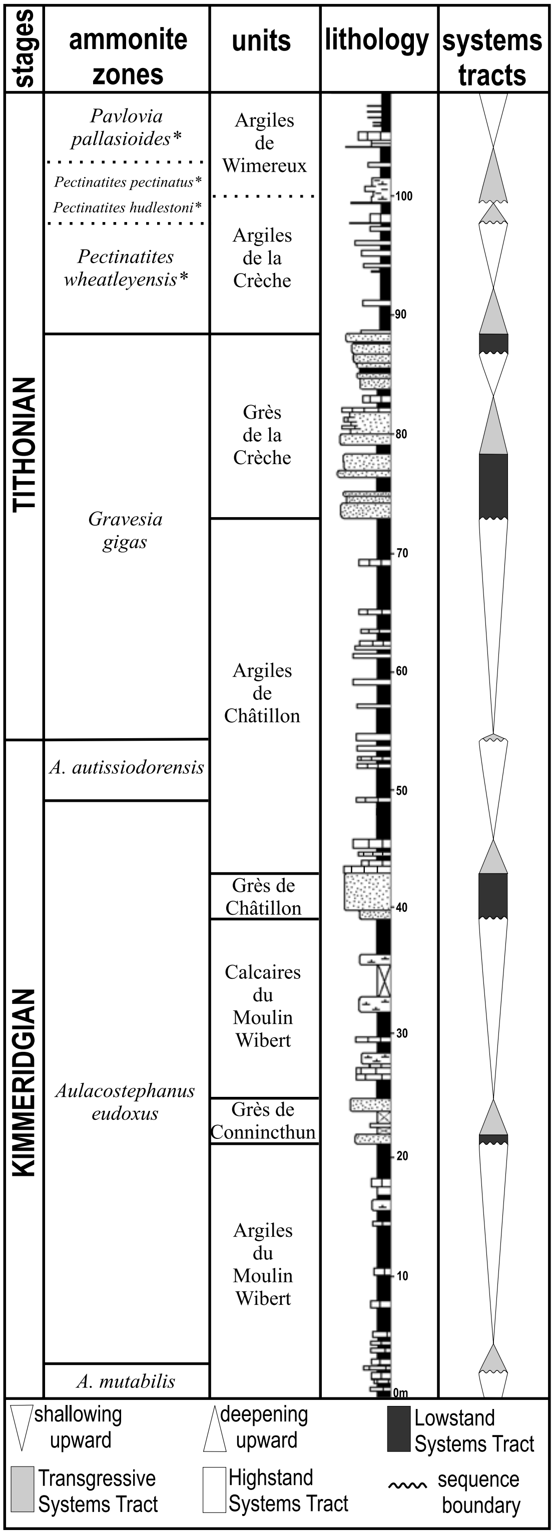

Fig. 2. Litho-, bio-, and sequence stratigraphic framework of the Upper Jurassic rocks of the Boulonnais; * indicates ammonite zones based on questionable finds; see Text-fig. 3 for legend (modified after PROUST & *al.* 1995, fig. 6)

facies interpretations for the Upper Jurassic rocks of the Boulonnais, as well as the sequence stratigraphic interpretations by PROUST & *al.* (1993, 1995) and WIGNALL & *al.* (1996) differ considerably. Unfortunately the later published work by WIGNALL & *al.* (1996) does not discuss the previously published results of PROUST & *al.* (1993, 1995). The present study is focused on the ichnocoenoses of two units at certain localities: the Grès de Châtillon exposed at Ambleteuse and Pointe de la Crèche, and the Grès de la Crèche exposed at Cap Gris Nèz, Pointe de la Crèche, and Le Portel (Text-figs 1-2). The Grès de Châtillon and the Grès de la Crèche are very similar in their sedimentology and thus were deposited in similar environments. The Grès de la Crèche are thicker and show more facies variability (Text-fig. 3). In the following the various facies types of the Grès de Châtillon and the Grès de la Crèche are briefly described and their palaeoenvironmental significance is discussed. Altogether ten major facies types (A-K) and two subtypes (J1 and J2) can be distinguished (see Table 1).

Facies A

Sharp based, highly bioturbated, shelly mudstones and siltstones with occasional plant remains. Primary sedimentary structures cannot be detected due to a high degree of bioturbation, and also the identification of trace fossils is difficult. Most common trace fossils are: *Palaeophycus tubularis* and *Planolites* ispp. WIGNALL & *al.* (1996) state that the macrofauna is highly diverse, whereas OSCHMAN (1985) comes to the conclusion that the macrofauna occurs in a strongly varying abundance and that the diversity is low to moderate. Facies A corresponds to Facies 1 of WIGNALL & *al.* (1996), and their interpretation of these rocks as deposits of unrestricted open marine conditions in a storm influenced offshore setting is supported here.

Facies B

Fine to medium sandstone, commonly argillaceous, with occasional shell gravel beds mostly made up of *Isognomon* and *Gervillella*. The sediments show a high degree of bioturbation. Most common trace fossils are: *Spongeliomorpha suevica* type B, *Rhizocorallium jenense* type 1, and *Teichichnus*. Due to the high degree of bioturbation primary sediment structures are obliterated. The sediments are interpreted as bioturbation-dominated, storm influenced upper offshore deposits (WIGNALL & *al.* 1996).

Facies C

Isolated lenses and thin-bedded, oscillation-rippled fine to medium sandstones, with plant remains; commonly with erosional base showing tool marks. Intercalated with silty clays. Bioturbation degree moderate, with *Bolonia lata*, *Gyrochorte comosa*, *Chondrites intricatus*, *Rhizocorallium irregulare*, *Rh. jenense* type 1, and *Lockeia siliquaria* as the most common trace fossils. The trace fossil content shows fully marine conditions. According to OSCHMAN (1985) and PROUST & *al.* (1995) these beds show tide influence due to the wavy and lenticular bedding (e.g., DALRYMPLE 1992). Microfaunal analyses of the mudstones imply fully marine conditions (WIGNALL & *al.* 1996). The sediments are interpreted as tide, wave, and storm influenced deposits of the transition zone between offshore and shoreface.

Facies D

Thin- to medium-bedded (with a maximum bed thickness of 20 cm), oscillation rippled, argillaceous medium sandstones, with erosional base showing tool marks and rarely gutter casts. Plant remains and shell debris common. Bioturbation degree low to high, with a diverse ichnofauna. Most common trace fossils are: *Teichichnus patens, Taenidium barretti*, *Asterosoma ludwigae*, *Spongeliomorpha suevica* type B, *Rosselia socialis*, concentrically laminated burrows, *Spongeliomorpha nodosa* type C, *Rhizocorallium jenense* type 1, *Chondrites intricatus*. These sediments are interpreted as wave and storm influenced deposits of the lower to mid-shoreface.

Facies E

Decimetre-scale trough cross-stratified bedsets of medium sandstone (foreset angle ca. 30°), with mudstone intraclasts concentrated on the toesets. Cross-beds truncated by centimetre-thick, oscillation-rippled medium sandstones with sharp base. Sandstones intercalated with thin layers of clay to silty clay. These sediments record various conditions in a wave and storm influenced upper shoreface to foreshore environment. WIGNALL & *al.* (1996) interpreted the trough cross-stratified bedsets as the result of migrating lunate dunes which were affected by erosion and wave reworking. During quiet periods fine sediments were deposited and most probably it was this quiet time when the trace fossil makers were active too. Most common ichnofossils are: *Rhizocorallium irregulare*, *Nereites missouriensis*, *Chondrites intricatus*.

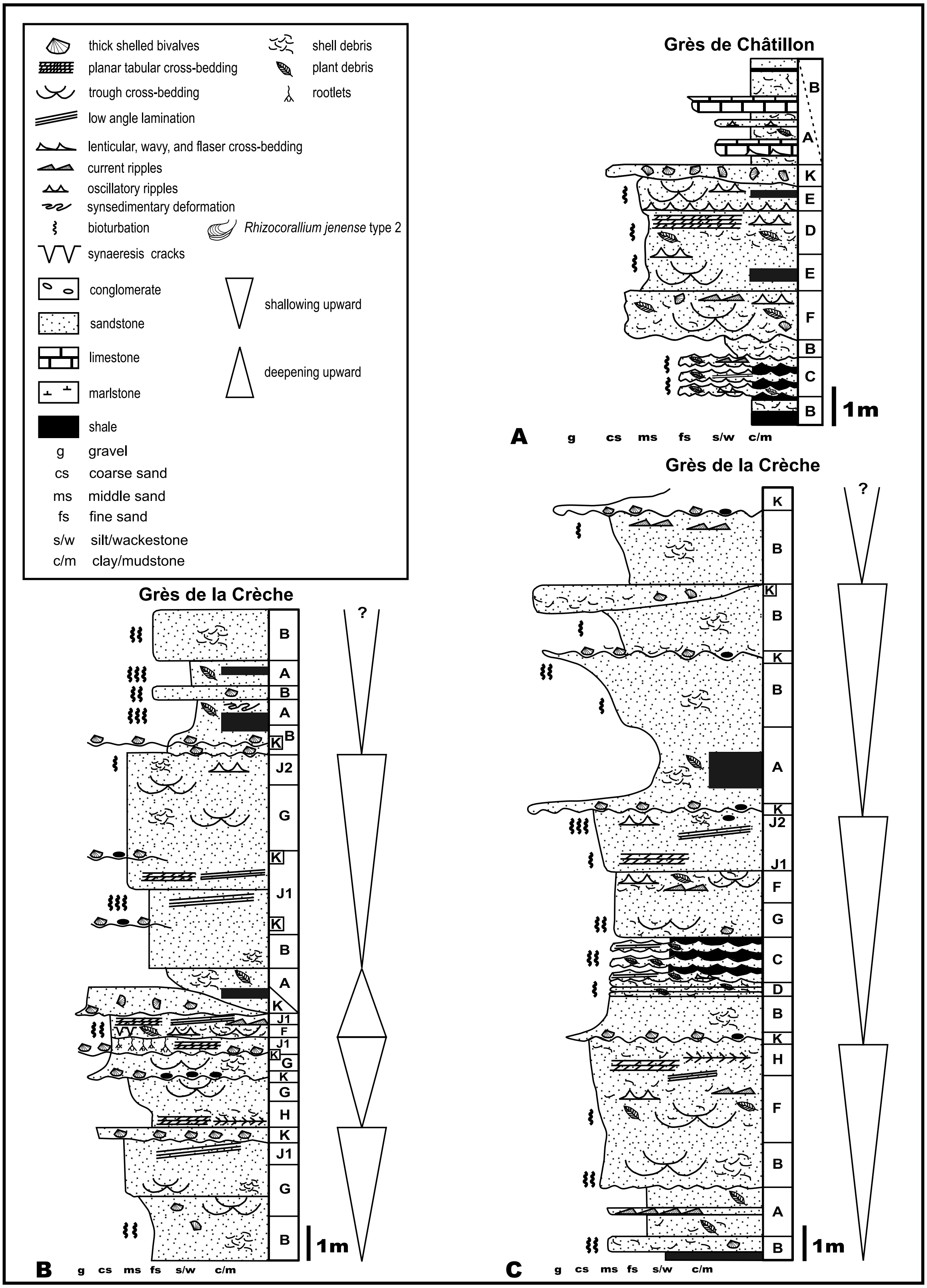

Fig. 3. Generalized graphic logs of the Grès de Châtillon (A) and the Grès de la Crèche (B, C); log B shows a proximal section, log C a more distal section (modified after PROUST & *al*. 1995 and WIGNALL & *al*. 1996)

Facies Number	Description	Palaeoenvironment	Common Trace Fossils
Facies A	sharp based, highly bioturbated, shelly mudstone and siltstone; occasional plant remains; no primary sediment structures detectable due to high degree of bioturbation	unrestricted open marine conditions; storm influenced offshore deposits	difficult to assign due to high degree of bioturbation; occasionally *Palaeophycus tubularis* and *Planolites* determinable
Facies B	fine to medium sandstone, commonly argillaceous, with occasional shell gravel beds mostly made up of *Isognomon* and *Gervillella;* highly bioturbated	bioturbation dominated, storm influenced upper offshore	*Spongeliomorpha suevica* maze, *Rhizocorallium jenense* type 1, *Teichichnus*
Facies C	isolated lenses and thin-bedded, oscillation-rippled fine to medium sandstone; plant remains; erosional base showing tool marks; embedded in silty clay; low density bioturbation	tide, wave and storm influenced transition zone between shoreface and offshore	*Bolonia lata*, *Gyrochorte comosa, Chondrites intricatus*, *Rhizocorallium irregulare*, *Rh. jenense* type 1, *Lockeia siliquaria*
Facies D	thin- to medium-bedded (max. 20cm), oscillation-rippled, argillaceous, medium sandstone with erosional base showing tool marks and rare gutter casts; plant remains and shell debris common; low to high density bioturbation	wave and storm influenced lower to mid shoreface	*Teichichnus patens, Taenidium barretti*, *Asterosoma ludwigae*, *Spongeliomorpha suevica* type B, *Rosselia socialis*, concentrically laminated burrows, *S. nodosa* type C, *Rhizocorallium jenense* type 1, *Chondrites intricatus*
Facies E	decimetre-scale trough cross-bed sets (foreset angle app. 30°) of medium sandstone with mudstone intraclasts concentrated on the toesets; cross beds truncated by centimetre-thick medium, oscillation rippled sandstone with sharp base	wave and storm influenced lower shoreface to transition zone	*Rhizocorallium irregulare*, *Nereites missouriensis*, *Chondrites intricatus*
Facies F	oscillation- and current-ripple topped decimetre-scale, trough cross-bedded medium to coarse sandstones with shell and plant remains; occasional synaeresis cracks and flat topped ripple surfaces; partially completely bioturbated	tide, storm and wave influenced upper shoreface to foreshore	*Palaeophycus tubularis*, *Spongeliomorpha nodosa* type B, *Teichichnus*, *Planolites*, *Spongeliomorpha suevica* type B, *Rosselia*, *Treptichnus*
Facies G	trough cross-bedded medium sandstone with shell material, trough heights 30 to 50 cm; coset boundaries planar, marking abrupt increase in grain size, tool marks common	shoreface	*Diplocraterion parallelum*, *Spongeliomorpha nodosa* type B & C, *Rhizocorallium jenense* type 1, *Skolithos linearis*, *Spongeliomorpha suevica* type B, *Rosselia*
Facies H	tabular cross-bedded fine to medium sandstones with shell material; herringbone cross-stratification common	wave and tide dominated shoreface	
Facies J1	swash cross-stratified medium to coarse sandstones with very low angle cross- to planar-lamination	foreshore	*Diplocraterion parallelum*, *Rhizocorallium jenense* type 1, *Spongeliomorpha suevica* type B & C, rootlets
Facies J2	partially highly bioturbated, medium to coarse sandstone with low angle- to planar-cross stratification; shell debris (*Nanogyra*) and occasional quartz pebbles; surfaces with oscillation-ripple relics	wave influenced foreshore	*Rhizocorallium jenense* type 2, *Teichichnus*, *Palaeophycus*, *Spongeliomorpha nodosa* type B
Facies K	shell gravel, up to 70 cm thick, mainly made up of thick shelled bivalves (predominantly *Laevitrigonia*) and occasionally exotic clasts; reactivation surfaces present	upper offshore to foreshore	

Table 1. Facies types and palaeoenvironmental interpretation of the Upper Jurassic rocks of the Grès de Châtillon and Grès de la Crèche (combined from PROUST & *al.* 1995, WIGNALL & *al.* 1996 and own observations)

Facies F

Oscillation- and current ripple-topped, decimetre-scale, trough cross-bedded medium to coarse sandstones, with shell debris and plant remains. Occasional synaeresis cracks (Text-fig. 5D) and flat-topped ripple surfaces can be observed (usually interpreted as produced during shallowing or emergence). Single troughs

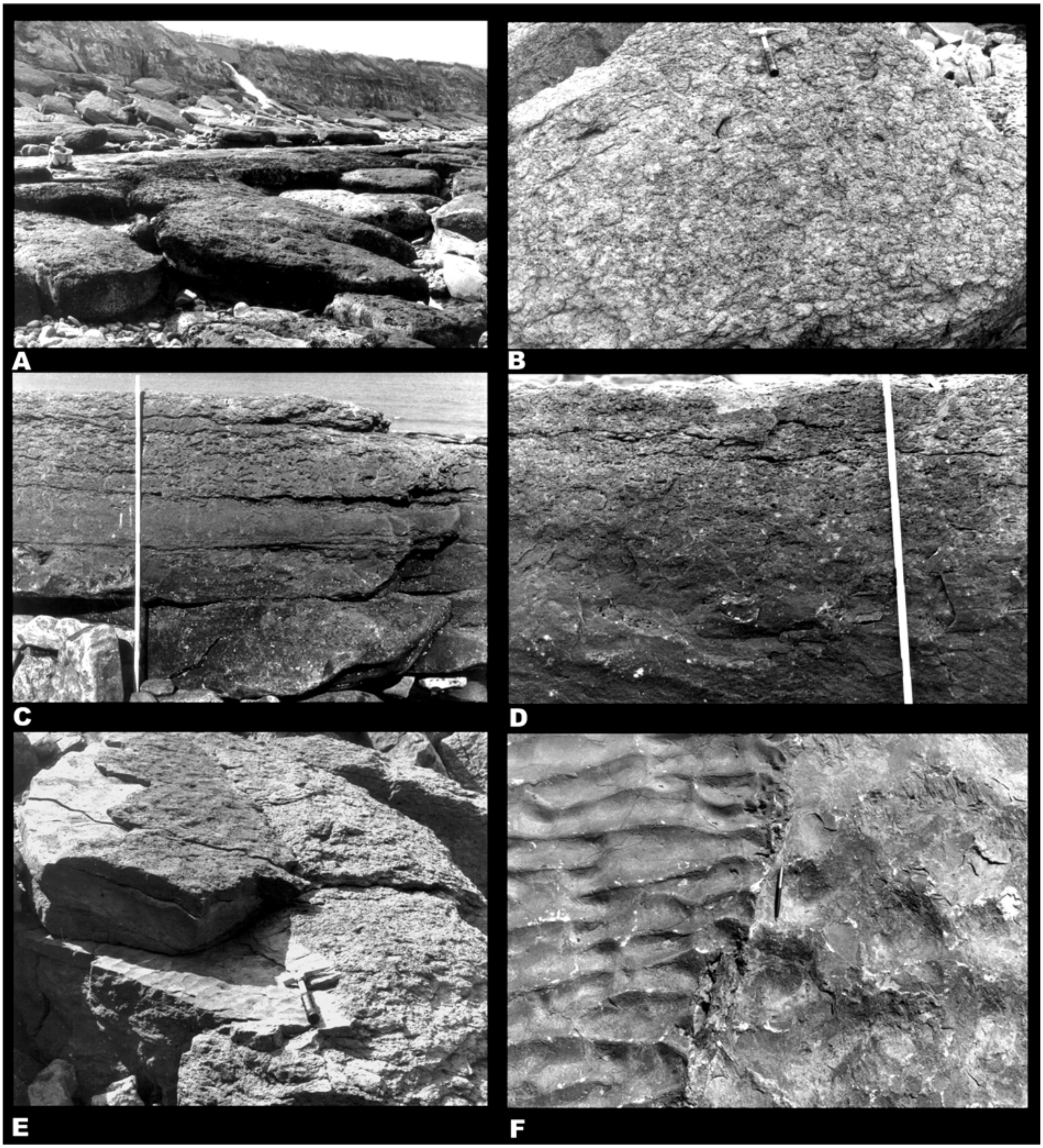

Fig. 4. A – Outcrop along the coast-line at Le Portel. Shown are ca. 15 m of the Grès de la Crèche; B – Highly bioturbated sandstone of the Grès de la Crèche at Le Portel (Facies J); C – Laminated and low angle cross-bedded sandstones with oscillatory ripple tops showing different degree of bioturbation (Facies J2). Top indicates parasequence boundary. Grès de la Crèche at Le Portel; D – Same as 3; highly bioturbated sandstones but gradual decrease of bioturbation density with depth; E – Trough cross-bedded sandstone of the Grès de la Crèche, showing highly variable degree of bioturbation. Grès de la Crèche at Le Portel (Facies F); F – Bedding plane of a channel with asymmetric ripples (left) indicating directed flow, cut into nearshore planar cross-bedded sandstones with oscillatory ripples on top. Grès de la Crèche at Le Portel (Facies F)

may be completely bioturbated (Text-figs 4E, 5C), most common trace fossils are: *Palaeophycus tubularis*, *Spongeliomorpha nodosa* type B, *Teichichnus*, *Planolites*, *Spongeliomorpha suevica* type B, *Rosselia*, and *Treptichnus*. WIGNALL & *al*. (1996) interpreted a similar facies as deposits of small (their Facies 4) to large dunes (their Facies 5) which formed in a lower shoreface to transition zone or in the mid- to upper shoreface respectively. PROUST & *al*. (1995) interpreted these trough cross-stratified beds as deposits of an outer estuary embayment or as channel mouth bar sediments, respectively. According to previous studies there is no faunal evidence of an estuarine influence in these deposits (OSCHMANN 1985; FÜRSICH, pers. commun.) and the occurring sedimentary structures are not indicative of estuaries. However, the synaeresis cracks (Text-fig. 5D) can be interpreted as a sign of fluctuating salinity. The absence of brackish water faunas does not prove absence of fresh-water influence, especially because brackish water bivalves typically have thin shells and their preservational potential is thus much lower than that of thick-shelled bivalves. Field observations of estuarine deposits of Jurassic age show that in many cases no macrofauna is present (FÜRSICH, personal communication). The trough cross-bedded sandstones show abundant plant remains as well as shell debris. Contradicting WIGNALL & *al*. (1996), the trough cross-bedded sandstones can be very well interpreted as channels. Their origin, however, remains uncertain. The erosive base and the complete bioturbation of some of the troughs appear to support a channel origin. Permanently migrating dunes do not have such a strong erosive effect, and

Fig. 5. A – High energy, nearshore, poorly lithified sandstones with planar cross-bedding with rare bioturbation (Facies H). Grès de la Crèche at Le Portel; B – Channel mouth bar facies with strongly varying degree of bioturbation (Facies F). Grès de la Crèche at Le Portel; C – Channel mouth bar facies with deeply eroding channel completely bioturbated; surrounding sediment with rare bioturbation (Facies F). Grès de la Crèche at Le Portel; D – Sole of sandstone in sandstone silt/clay intercalation with rare bioturbation and well formed synaeresis cracks indicating freshwater or brackish influence (Facies F). Grès de la Crèche at Le Portel

the high plant remains and shell debris content also favours a channel deposit origin. With the channel fill a lot of food was buried and later explored by animals, as indicated by the complete bioturbation of some of the channel fills (Text-fig. 5C). The flat-topped ripples suggest extreme shallowing or emergence. For the given reasons interpretation of the environment as a wave, storm, and tidal influenced shoreface seems justified. In parts the trough cross-bedded sandstones might be large dunes, the trough cross-bedded sandstones with erosional base, high plant remains and shell debris are interpreted as channel fills. The synaeresis cracks and the flat-topped ripples indicate some salinity fluctuations and tidal influence. Finer sediments intercalated in this facies show wavy and lenticular bedding and are interpreted as tide influenced (OSCHMANN 1985).

Facies G

Trough cross-bedded medium sandstones, with shell material, trough heights 30-50 cm. Coset boundaries planar, marking abrupt increase in grain size; tool marks common. The bioturbation degree is low to medium, the most common trace fossils are: *Diplocraterion parallelum*, *Spongeliomorpha nodosa* type B & C, *Rhizocorallium jenense* type 1, *Skolithos linearis*, *S. suevica* type B, *Rosselia*. According to WIGNALL & *al*. (1996) these deposits are interpreted as large dunes in a shoreface setting. The frequent occurrence of retrusive *Diplocraterion parallelum* indicates rapid sedimentation which the *Diplocraterion* producers tried to equilibrate by shifting their burrow upward. AGER & WALLACE (1970) ‘had little doubt in their minds’ that these beds represent an episode of intertidal emergence because of the kind of trace fossils present and the penetration depth of the trace fossils (up to 30 cm). Own field observations and the sedimentary structures do not support this view. In addition, currently no trace fossils association is known that would indicate tidal influence. However, the underlying as well as the overlying sediments show tidal influence which makes tidal influence in the ‘sandwich’ sediments not unlikely.

Facies H

Tabular cross-bedded fine to medium sandstones, with shell material, herringbone cross-bedding common. In these rocks no trace fossils were found. The herringbone cross-stratification seems best to be explained by tidal influence. The sediments are typical of those encountered on modern fair-weather, wave dominated shorefaces (WIGNALL & *al*. 1996).

Facies J

Swash cross-stratified, low angle to planar cross-bedded medium to coarse sandstone, with low to high degree of bioturbation.

Subfacies J1

Swash cross-stratified medium to coarse sandstones, with very low angle to planar cross bedding. Bioturbation is low to moderate, most common trace fossils are: *Diplocraterion parallelum*, *Rhizocorallium jenense* type 1, *Spongeliomorpha suevica* type B & C. WIGNALL & *al*. (1996) also report rootlets from this facies. The sediments represent deposits of a foreshore setting.

Subfacies J2

Low angle to planar cross-bedded medium to coarse sandstones, with shell debris (*Nanogyra*), occasionally with quartz pebbles. Top 20 cm of a coset often highly bioturbated (Text-figs. 4B-4D). Bioturbated surfaces with oscillation-ripple relics. Most common trace fossils are: *Rhizocorallium jenense* type 2, *Teichichnus*, *Palaeophycus*, *Spongeliomorpha nodosa* type B. These sediments originated from a wave influenced foreshore setting. The low angle to planar cross-bedding indicates a high energy regime (upper flow regime) that rapidly deposited the sands. During quieter periods the trace fossil makers were active and wave influence played a role.

Facies K

Shell gravel, up to 70 cm thick, mainly made up of thick-shelled bivalves (predominantly *Laevitrigonia*), occasionally with exotic clasts; reactivation surfaces present. These beds represent deposits of the upper offshore to foreshore.

Sequence stratigraphic interpretation of the Grès de la Crèche at Le Portel

With a detailed study of trace fossils, the succession of the Grès de la Crèche at Le Portel can be divided into three shallowing upward cycles each representing a parasequence. The degree of bioturbation towards the top of the first parasequence boundary is 100% (Text-figs 4B, D); dominant trace fossils are *Rhizocorallium jenense* type 2, *Teichichnus* isp., and *Palaeophycus tubularis*.

The top of the following shallowing upward cycle is again characterized by a bioturbated horizon. The degree of bioturbation is 100% and the dominant trace fossils are the same as in the first parasequence. The latter parasequence boundary is the 'ravinement surface' of WIGNALL & *al*. (1996, fig. 5). At first sight this seems contradicting. However, ARNOTT (1995) states that ravinement surfaces more often coincide with flooding surfaces than commonly believed. This author reports very thin to several decimetre thick coarse grained beds (transgressive lags) at the base of a parasequence, representing the new flooding. Depending on the time available, the amount of relative sea-level rise, and the following erosion during shallowing, these transgressive lags may or may not be present at all, reaching a maximal thickness of several decimetres.

ARNOTT (1995) also observed a gradual increase of bioturbation towards parasequence boundaries, with sometimes complete bioturbation of the final bed. The two completely bioturbated beds described here are

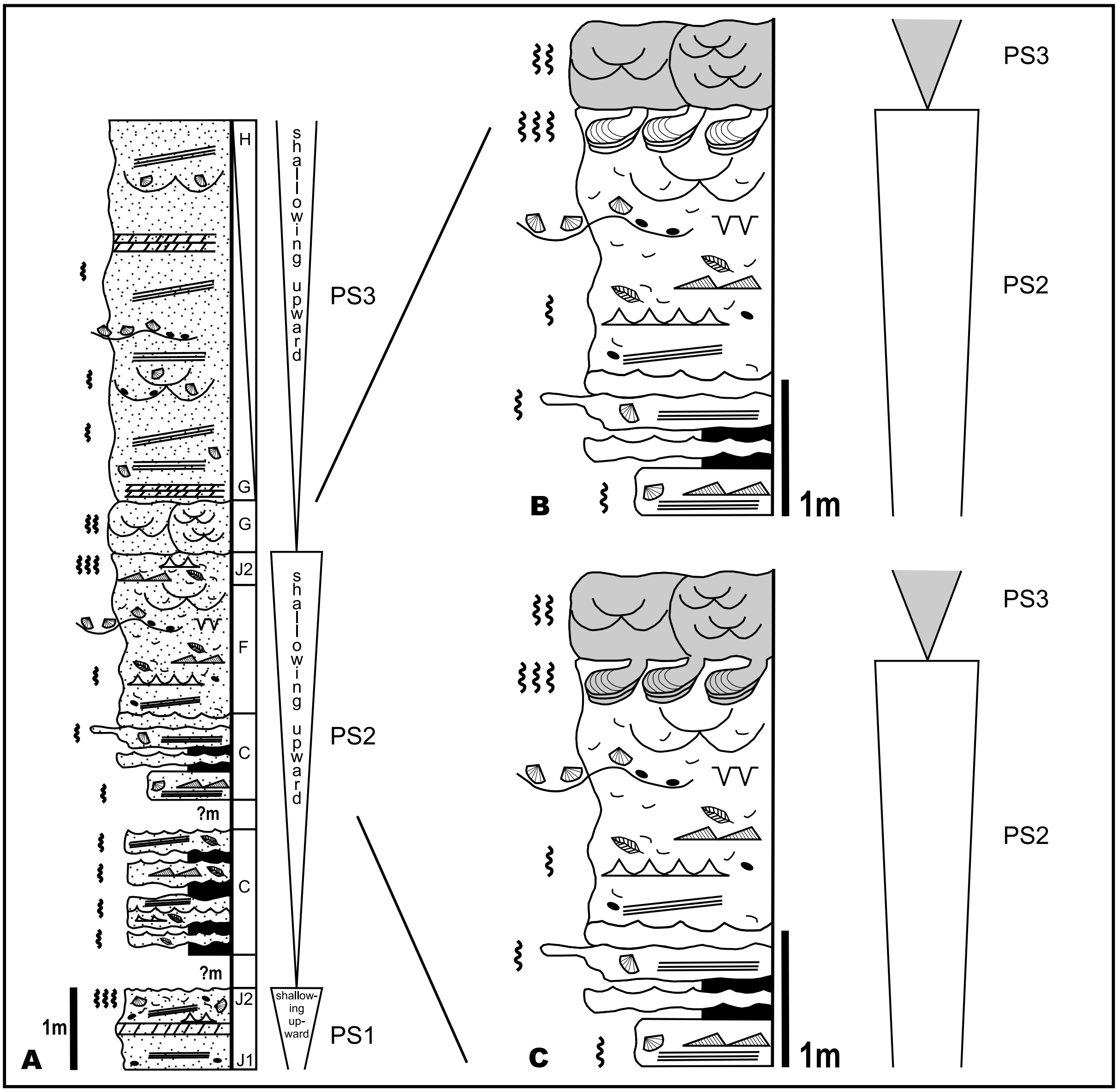

Fig. 6. A – Graphic log of the Grès de la Crèche at Le Portel and sequence stratigraphic interpretation; B-C – Enlargement of a part of the section: B - Interpretation of the trace fossils being produced at the end of a gradual shallowing, thus belonging to PS2; C - Interpretation of the trace fossils being produced at the beginning of a renewed shallowing development, thus belonging to PS3 and representing a "lag-ichnofauna"; PS1-3: parasequences 1-3; legend given in Text-fig. 3

inferred to indicate stable conditions favourable for deposit-feeders. During the rise of the sea-level the sands were exposed for relatively long periods of time, and could thus be penetrated by many organisms which lead to a complete bioturbation. Basis for this assumption is the interpretation of *Rhizocorallium jenense* type 2 as a deposit-feeder structure. Using only morphological analysis, the ethology of *Rh. jenense* type 2 is difficult to define (SCHLIRF 2000). However, under the light of a sequence stratigraphic interpretation of the studied rocks a deposit-feeding interpretation seems plausible. As shown by SAVRDA (1995) surfaces with a dominance of traces such as *Diplocraterion*, *Rhizocorallium jenense* type 1, *Skolithos*, *Gastrochaenolites*, and/or *Arenicolites* can be used as indicators of sequence boundaries and/or transgressive surfaces. DAM (1990) and TAYLOR & GAWTHORPE (1993) interpreted especially *Diplocraterion parallelum* and other suspension feeder structures as made by opportunistic tracemakers. Following this interpretation *Rh. jenense* type 2 should be interpreted as produced by suspension-feeders, and in analogy to *D. parallelum* the *Rh. jenense* type 2 traces would represent an opportunistic community being active under shallow water conditions. In addition, this would also imply that the trace fossils were produced during the final phase of the parasequence, and thus characterize the end of a gradual shallowing development (Text-fig. 6B). This, however, would contradict an opportunistic interpretation, because opportunists are the first to colonize an ecosystem and are then gradually replaced by specialists. Another interpretation, favoured here, is that *Rh. jenense* type 2 is the result of deposit-feeding behaviour. This would imply that the trace fossils in the terminal beds of the two parasequences belong genetically to the overlying parasequence since they should have been produced in non-mobile substrates, and thus under the most quiet hydrodynamic conditions, i.e., after flooding, which means at the beginning of a shallowing upward sequence (Text-fig. 6C). Taking into account the observations made by ARNOTT (1995) the trace fossils in the uppermost bed of the underlying parasequence represent the time after renewed flooding and before the new shallowing. Such particular trace fossil coenoses may be called 'lag-ichnofauna'.

Highly bioturbated beds often indicate environmental changes (MACEACHERN & *al.* 1992; PEMBERTON & *al.* 1992). In the Le Portel succession this observation is confirmed. The two highly bioturbated beds represent the period of flooding to the beginning of a new gradual shallowing development. With the help of the highly bioturbated beds it was possible to define two parasequence boundaries. The order of these parasequence boundaries is unknown. It seems likely that these surfaces represent boundaries of high-frequency sequences (MITCHUM & VAN WAGONER, 1991) of fourth or higher order with only minor changes in relative sea-level.

In the second parasequence a highly diverse ichnofauna is found (Text-fig. 9), representing a time during which favourable living conditions were established and a diverse set of trace fossils was built. The majority of these trace fossils such as *Alcyonidiopsis*, *Planolites*, *Phycodes*, *Cochlichnus*, and *Gyrochorte* can be interpreted as deposit-feeder structures. A deposit-feeding mode of life suggests non shifting substrates and moderate to low hydrodynamic conditions so that food particles can settle and are not permanently kept in suspension. This succession is topped with another highly bioturbated surface (see above).

The overlying sediments belong to another shallowing-upward sequence that is very low in trace fossil diversity and shows only a low to moderate degree of bioturation, including only *Spongeliomorpha nodosa* and rare *S. suevica*. *Spongeliomoprha nodosa* indicates high energy conditions and unstable substrates and is commonly interpreted as an opportunistic trace fossil (see BROMLEY 1996), whereas *S. suevica* is built under lower energy conditions and in a cohesive sediment in which additional stabilization of the burrow wall is not necessary. The occurrence of *S. nodosa* and *S. suevica* thus gives detailed information on the colonization of the sediments.

PALAEOICHNOCOENOSES

Nine frequent palaeoichnocoenoses, plus a rare one, can be identified in the Upper Jurassic rocks of the Grès de Châtillon and Grès de la Crèche. The term 'ichnocoenosis' is understood as an equivalent of 'palaeobiocoenosis' or 'life assemblage' *sensu* BROMLEY (1996). Each palaeoichnocoenosis is characterized by a particular association of trace fossils (see Table 2) and is named after a dominant ichnogenus or ichnospecies or a group of ichnofossils.

***Diplocraterion* ichnocoenosis**

The *Diplocraterion* ichnocoenosis is dominated by domichnia/equilibrichnia of suspension-feeders such as *Diplocraterion parallelum*. *Skolithos linearis* may occur within this ichnocoenosis as an accessory trace fossil. The *Diplocraterion* ichnocoenosis is interpreted as indicator of a high energy environment (FÜRSICH 1975; HEINBERG & BIRKELUND 1984; DAM 1990). The tops of the burrows are frequently eroded. The *Diplocraterion* ichnocoenosis occurs in small- and large-scale, trough cross-bedded and swash cross-stratified sandstones (Facies J1) of the Grès de la Crèche at Cap Gris Nèz, which consists of deposits of a wave-influenced foreshore setting.

Rhizocorallium jenense type 1 ichnocoenosis

The *Rhizocorallium jenense* type 1 ichnocoenosis is characterized by domichnia/equilibrichnia of suspension-feeders such as steep, oblique specimens of *Rh. jenense* type 1 (Text-fig. 7D). As accessory trace fossils, *Skolithos linearis* or *Diplocraterion parallelum* may occur. Like the *Diplocraterion* ichnocoenosis, the *Rh. jenense* type 1 ichnocoenosis is interpreted as an indicator of a high energy environment, supported by the frequent occurrence of thick burrow linings in *Rh jenense*. The *Rh. jenense* type 1 ichnocoenosis occurs in trough cross-bedded (Facies G) and swash cross-stratified sandstones (Facies J1) of the Grès de la Crèche at Le Portel and the Grès de Châtillon at Ambleteuse. These sandstones are made up of wave-influenced shoreface to foreshore deposits. As in the *Diplocraterion* ichnocoenosis, the burrow tops are frequently eroded.

Ichnospecies	Ethology	Feeding behaviour	Possible producer
Traces			
Lockeia siliquaria	Cubichnia	?	infaunal bivalves
Skolithos linearis	Domichnia	suspension-feeder	annelids or phoronids
Alcyonidiopsis longobardiae	Pascichnia	deposit-feeder	polychaetes
Palaeophycus striatus	Domichnia/?Fodinichnia	deposit-, suspension-feeder, predator	?polychaetes
Palaeophycus tubularis	Domichnia/?Fodinichnia	deposit-, suspension-feeder, predator	?polychaetes
Planolites beverleyensis	Fodinichnia/Pascichnia	deposit-feeder	various vermiform animals
Planolites isp.	Fodinichnia/Pascichnia	deposit-feeder	various vermiform animals
Arenicolites statheri	Domichnia	suspension-feeder	polychaetes
Chondrites intricatus	Chemichnia/Fodinichnia	chemosymbiont, deposit-feeder	bivalves, sipunculids, polychaetes, arthropods, pennatulaceans
Treptichnus aequalternus	Agrichnia/Fodinichnia	farmer, trapper, ?deposit-feeder	vermiform animals
Treptichnus bifurcus	Agrichnia/Fodinichnia	farmer, trapper, ?deposit-feeder	vermiform animals
Asterosoma ludwigae	Fodinichnia	deposit-feeder	crustaceans
Asterosoma isp.	Fodinichnia	deposit-feeder	crustaceans
Spongeliomorpha cf. *borneensis*	Domichnia/Fodinichnia	deposit-, suspension-feeder, scavanger, predator	crustaceans
Spongeliomorpha irregulaire variation *densa*	Domichnia/Fodinichnia	dito	crustaceans
Spongeliomorpha nodosa	Domichnia/Fodinichnia	dito	crustaceans
Spongeliomorpha suevica	Domichnia/Fodinichnia	dito	crustaceans
Phycodes isp. A	Fodinichnia	deposit-feeder	annelids
Phycodes isp. B	Fodinichnia	deposit-feeder	annelids
Asterichnus lawrencensis	Fodinichnia	deposit-feeder	?, possibly crustaceans
Diplocraterion parallelum	Domichnia/Equilibrichnia	suspension-feeder	annelids, crustaceans, ?
Rhizocorallium irregulare	Fodinichnia	deposit-feeder	?, possibly crustaceans
Rhizocorallium jenense	Domichnia/Fodinichnia/ Equilibrichnia	deposit-, suspension-feeder	?, possibly crustaceans
Zoophycos isp.	Fodinichnia	deposit-feeder	polychaetes, arthropods, hemicordates
Teichichnus patens	Fodinichnia	deposit-feeder	annelids, arthropods, ?
Teichichnus rectus	Fodinichnia	deposit-feeder	annelids, arthropods, ?
Rosselia socialis	Domichnia/?Fodinichnia	detritus-, ?deposit-, suspension-feeder	terebellids, sea anemones, annelids, ?
'concentrically laminated burrows'	Domichnia/Fodinichnia/ Equilibrichnia	detritus -, ?deposit-, suspension -feeder	?, possibly annelids
Cochlichnus anguineus	Pascichnia/Repichnia	deposit-feeder	annelids, insect larvae, nematodes, cyclostomatid Agnatha, leeches
Gyrochorte comosa	Fodinichnia/Pascichnia	deposit-feeder	arthropods
Bolonia lata	Pascichnia/Repichnia	?, detritus-feeder, scavenger	polychaetes, gastropods, ?
Beaconites coronus	Pascichnia/Repichnia	deposit-feeder	arthropods
Taenidium barretti	Pascichnia	deposit-feeder	worm-like animals
Taenidium serpentinum	Pascichnia	deposit-feeder	worm-like animals
Nereites missouriensis	Pascichnia	deposit-feeder	worm-like animals, ?phoronids
Borings			
Teredolites clavatus	Fodinichnia/Domichnia	wood-, suspension-feeder	bivalves

Table 2. Ethology, feeding behaviour, and possible producers of trace fossils from the Upper Jurassic of the Boulonnais

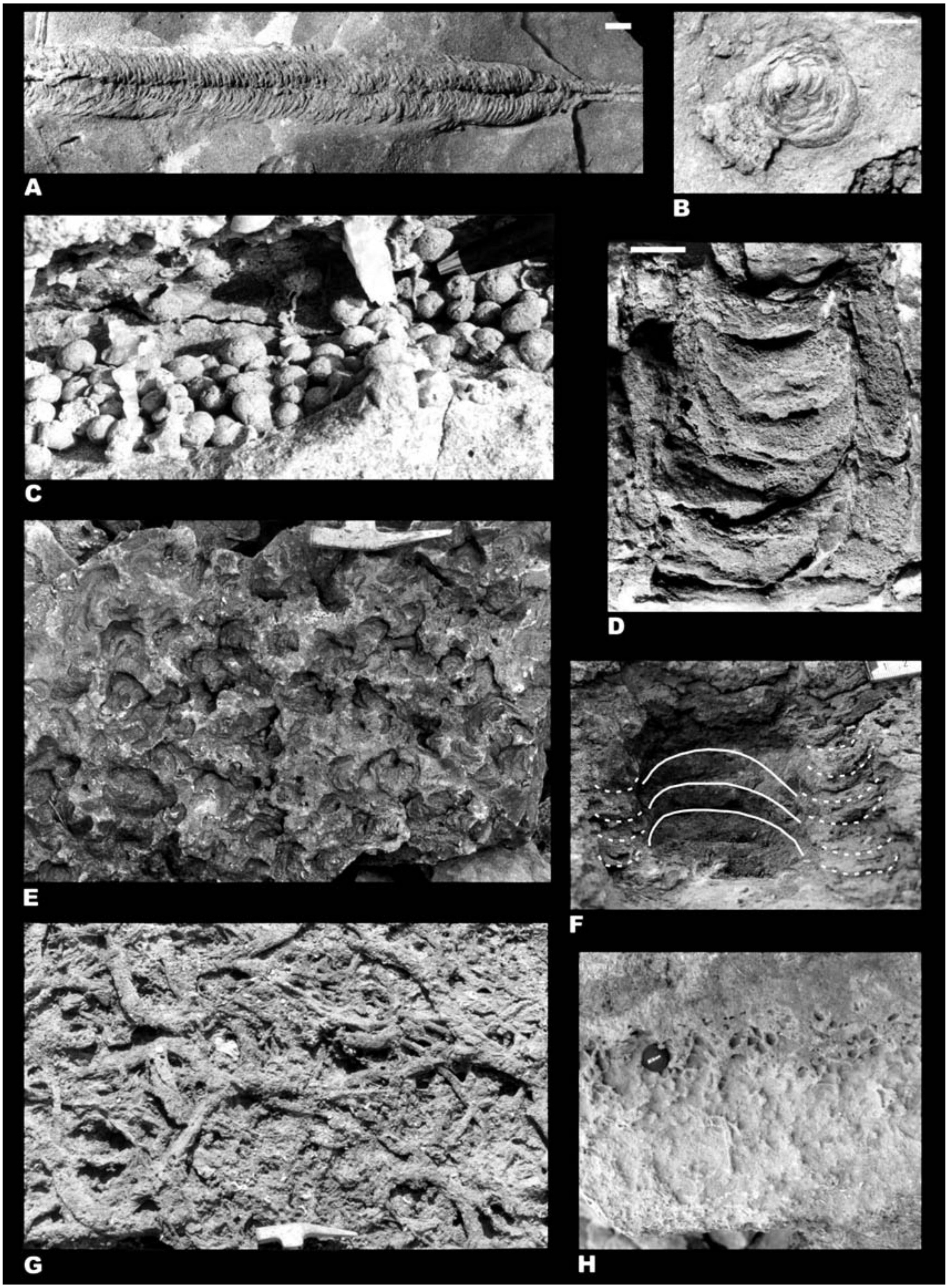

Fig. 7. A – *Bolonia lata*, top view, full relief. Grès de la Crèche at Le Portel. Scale bar: 1 cm; B – Concentrically laminated burrow of uncertain taxonomic position, top view, full relief. Grès de Châtillon at Ambleteuse. Scale bar: 1 cm; C – *Teredolites clavatus* in completely weathered piece of driftwood, full relief. Grès de la Crèche at Le Portel. Roller-pen head for scale; D – *Rhizocorallium jenense* type 1 with pelletal fill in spreiten, side view, full relief. Grès de Châtillon at Ambleteuse. Scale bar: 1 cm; E – *Rhizocorallium jenense* type 2, top view, full relief. Grès de la Crèche at Le Portel. Hammer head for scale; F – *Rhizocorallium jenense* type 2, side view, full relief; white dashed lines indicate retrosive spreiten of side limbs, white continuous lines indicate spreiten of U-turn of the limbs. Spreiten between limbs are completely weathered out. Grès de la Crèche at Le Portel. Ruler for scale; G – *Spongeliomorpha suevica* maze form, top view, full relief. Grès de Châtillon at Pointe de la Crèche. Hammer head for scale; H – *Spongeliomorpha suevica* boxwork form, side view, full relief. Grès de Châtillon at Pointe de la Crèche. Lens cap for scale: 5.2 cm in diameter

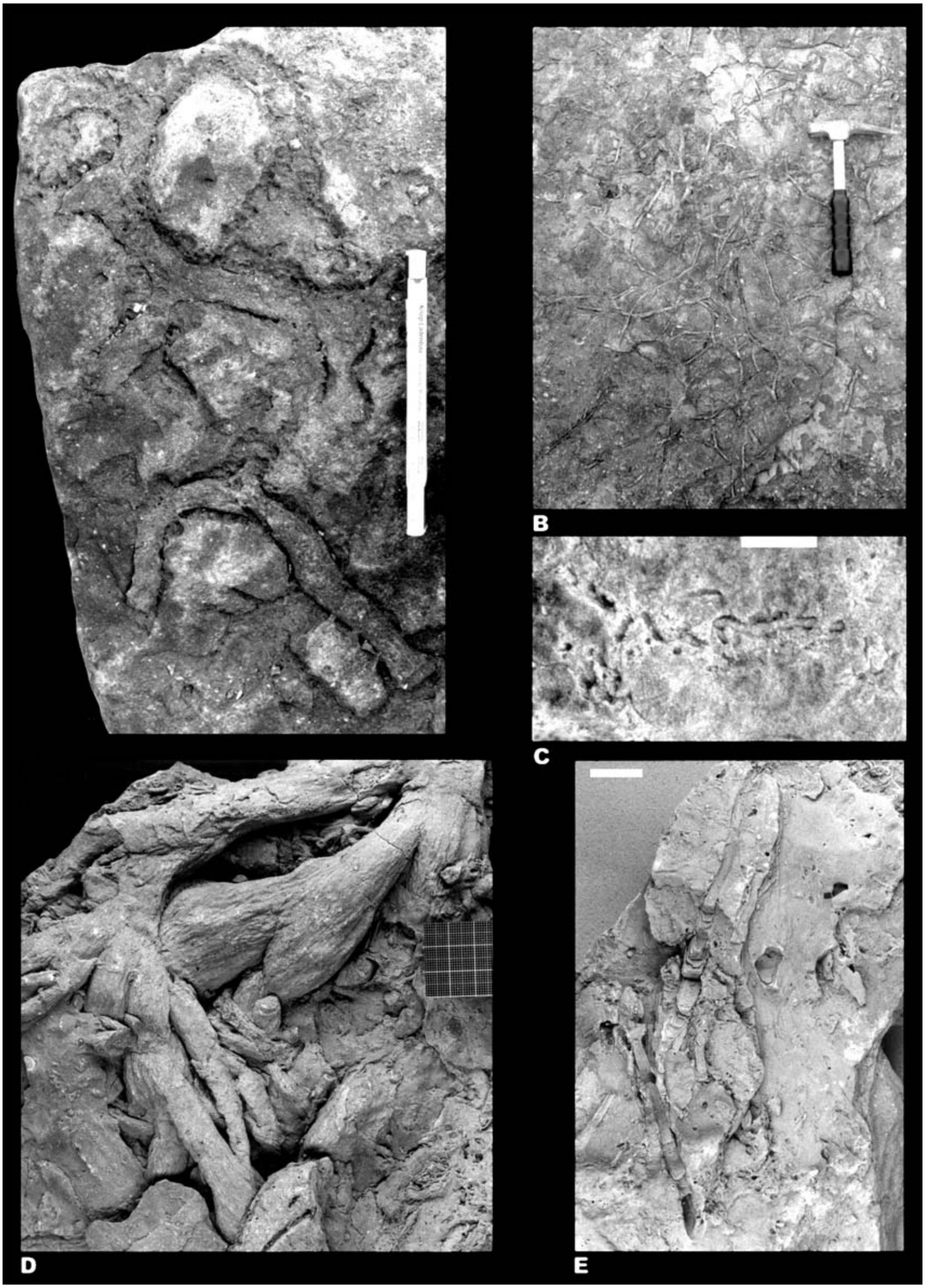

Fig. 8. A – *Spongeliomorpha nodosa* type C, forming more-or-less hexagonal networks, top view, positive epirelief. Grès de Châtillon at Ambleteuse. Ruler for scale; B – *Spongeliomorpha nodosa* type B, forming irregular networks, top view, full relief. Grès de la Crèche at Le Portel. Hammer for scale; C – *Spongeliomorpha nodosa* type A, rarely branching and smallest form of occurring *Spongeliomorpha*, side view, full relief. Grès de Châtillon at Pointe de la Crèche. Scale bar = 1.4 cm; D – *Asterosoma ludwigae*, full relief, basal view Grès de Châtillon at Ambleteuse. Millimetre grid for scale; E – *Teichichnus patens*, full relief, top view, Grès de Châtillon at Ambleteuse; Scale bar: 5 cm

Spongeliomorpha nodosa type B ichnocoenosis

This monospecific ichnocoenosis consists of *Spongeliomorpha nodosa* type B of SCHLIRF 2000 (Text-fig. 8B). It occurs in large- to small-scale trough cross-bedded sandstones (Facies G) of a shoreface setting of the Grès de la Crèche at Le Portel. The ichnocoenosis corresponds to the *Ophiomorpha* ichnocoenosis of HEINBERG & BIRKELUND (1984) and DAM (1990) and is interpreted as an indicator of high energy conditions and shifting substrates, which favour opportunistic behaviour (DAM 1990).

Spongeliomorpha suevica ichnocoenosis

This ichnocoenosis can be divided into two sub-ichnocoenoses: 1) the maze sub-coenosis (Text-fig. 7G), and the 2) the boxwork sub-coenosis (Text-fig. 7H). Both sub-coenoses consist of the domichnia and/or fodinichnia of crustaceans that followed various modes of feeding. The maze sub-coenosis, consisting of the *Spongeliomorpha suevica* maze form, occurs in large-scale trough (Facies G) or planar cross-bedded sandstones (Facies J1) of the Grès de la Crèche at Cap Gris Nèz. Occasionally *Planolites* isp. may be found in association with *S. suevica* maze form. The boxwork sub-coenosis includes *S. suevica* boxwork form, sometimes associated with *Planolites* ispp., which occurs in calcareous, large-scale trough (Facies G) or planar cross-bedded sandstones (Facies J1) of the Grès de la Crèche at Pointe de la Crèche. The ichnocoenosis is interpreted as an indicator of physically unstable conditions like those of the *Ophiomorpha* ichnocoenosis of HEINBERG & BIRKELUND (1984) and DAM (1990). However, since there is no evidence of a need to stabilize the burrow wall, the sediment consistency must have been higher than that described by HEINBERG & BIRKELUND (1984) and DAM (1990).

Asterosoma-Teichichnus ichnocoenosis

This ichnocoenosis is dominated by pascichnia/fodinichnia of deposit-feeders such as *Asterosoma ludwigae*, *Teichichnus patens*, *Cochlichnus anguineus*, *Taenidium serpentinum*, *T. baretti*, and *Rhizocorallium irregulare*. In addition, *Chondrites intricatus*, *Spongeliomorpha nodosa*, *Palaeophycus striatus*, ‘concentrically laminated burrows’ (Text-fig. 7B), *Planolites* ispp., and *Arenicolites statheri* can be found. This ichnocoenosis corresponds to the ‘*Teichichnus* association’ of FÜRSICH (1975) and is interpreted as an indicator of a low energy regime with comparatively low rates of deposition and a fairly stable substrate that allowed intensive bioturbation. Nevertheless, the sediments such as thin to moderately thick bedded, oscillation rippled medium sandstones (Facies D) in which the *Asterosoma-Teichichnus* ichnocoenosis occurs are interpreted as wave-dominated, high energy deposits, which indicate that the ichnocoenosis was not contemporaneous. This leads to the conclusion that the environment was occasionally dominated by high sedimentation rates in combination with high energy conditions that alternated with times of more-or-less quiet conditions during which the burrowers were active. The intensity of bioturbation changes within a section may indicate changes in the environmental conditions or rates of erosion, or both. The occurrence of both *S. nodosa* (indicating a soft, unstable sediment) and *A. ludwigae* (indicating firm, stable sediment) at first appears to be contradictory. However, close examination and cross-cutting relationships suggests that the maker of *S. nodosa* was a pioneer, a member of the first colonization relatively shortly after the sediment had been deposited. At that time the sediment still had a high water content and, thus, was unstable. By contrast, *A. ludwigae* represents a later stage of colonization during which the sediment cohesiveness was higher (Text-fig. 8D shows that *Asterosoma* is only cross-cut by other *Asterosoma*, this indicates that they were build last). Since the ichnocoenosis was studied on loose blocks, colonization surfaces could not be observed. The *Asterosoma-Teichichnus* ichnocoenosis exclusively occurs in the Grès de Châtillon at Ambleteuse.

Palaeophycus-Treptichnus ichnocoenosis

This ichnocoenosis is dominated by agrichnia, fodinichnia, and domichnia of farming, trapping, carnivorous, deposit-, detritus-, and/or suspension-feeding organisms. It consists of *Palaeophycus tubularis*, *Treptichnus bifurcus*, *Rosselia socialis*, ‘concentrically laminated burrows’, *Spongeliomorpha nodosa* type A (of SCHLIRF 2000; see Text-fig. 8C), *Beaconites coronus*, and *Arenicolites statheri*. *Palaeophycus*, *Treptichnus*, and *S. nodosa* type A are interpreted as pioneer colonizers of this ichnocoenosis since they can be observed exclusively within beds in which the *Palaeophycus-Treptichnus* ichnocoenosis occurs. In beds where all the trace fossils of this ichnocoenosis occur together, *Palaeophycus*, *Treptichnus*, and *S. nodosa* are usually cut or crossed by the others. This indicates that *Palaeophycus*, *Treptichnus*, and *S. nodosa* were built at an early stage of colonization. The sediments that bear the *Palaeophycus-Treptichnus* ichnocoenosis include current- and or oscillatory-rippled, partly flat-topped, medium to coarse sandstones (Facies F), with shell-

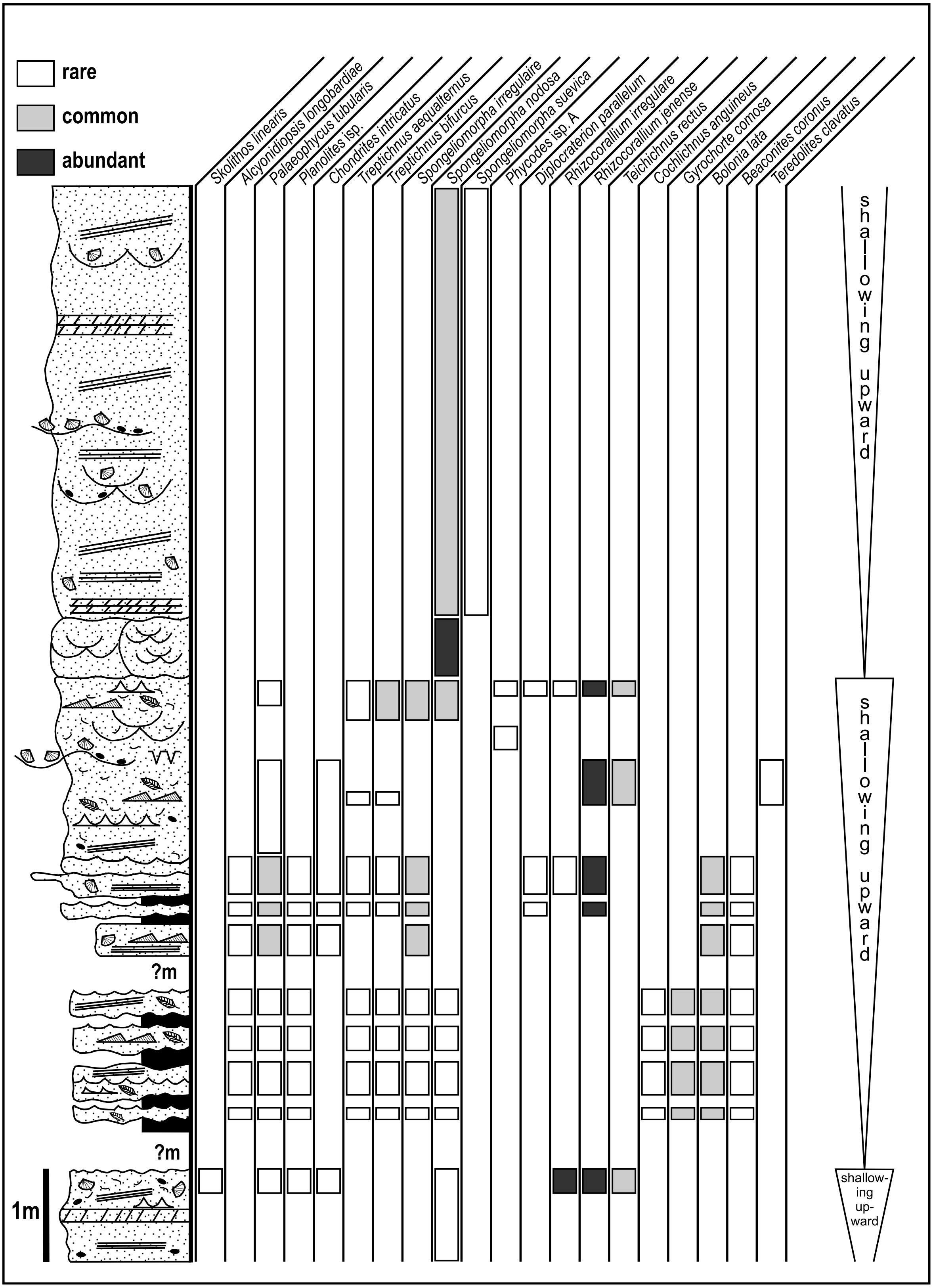

Fig. 9. Graphic log with position of ichnofossils in the Grès de la Crèche at Le Portel and a sequence stratigraphic interpretation; see Text-fig. 3 for legend

beds and conglomerates, trough (Facies G) and planar cross-bedded sandstones (Facies H) and rare intercalations of silty clays. Occasionally synaeresis cracks can be found. These deposits are interpreted as storm and tidally influenced upper shoreface to foreshore deposits of the Grès de la Crèche. The ichnocoenosis predominantly occurs at Le Portel and Pointe de la Crèche and is interpreted as an indicator of low to intermediate energy conditions since suspension-feeders are only sparsely represented. Again, this ichnocoenosis formed during quieter conditions within a generally high energy environment.

Rhizocorallium jenense **type 2 ichnocoenosis**

This ichnocoenosis is characterized by *Rhizocorallium jenense* type 2 (Text-figs 7E-F), *Teichichnus rectus, Planolites* ispp., *Rh. irregulare*, and *Spongeliomorpha nodosa* type B. The beds that bear this ichnocoenosis generally show a high degree of bioturbation. The uppermost 25 cm of a bed may be completely bioturbated with *S. nodosa* reaching the deepest tier with a depth of up to 75 cm. The *Rh. jenense* type 2 ichnocoenosis occurs in very low angle to planar cross-bedded sandstones with a relatively high content of shell debris, predominantly the oyster *Nanogyra* and an occasional occurrence of quartz pebbles (Facies J2). This ichnocoenosis is interpreted as an indicator of medium to low energy levels although the sediments that bear this ichnocoenosis indicate a high energy environment of a wave influenced foreshore setting. However, the occurrence of deposit-feeder structures, such as *Teichichnus*, *Planolites*, *Rh. irregulare* and possibly *Rh. jenense* type 2, indicate quiet conditions. As for the *Asterosoma-Teichichnus* ichnocoenosis, the traces were formed during quiet conditions within a generally high energy environment. The *Rh. jenense* type 2 ichnocoenosis occurs exclusively in the Grès de la Crèche at Le Portel (*see* also above, sequence stratigraphic interpretation of the Grès de la Crèche at Le Portel).

Gyrochorte-Bolonia **ichnocoenosis**

This ichnocoenosis is characterized by pascichnia of deposit-feeders, such as *Gyrochorte comosa* and *Bolonia lata* (recently re-validated by SCHLIRF 2002). *Alcyonidiopsis longobardiae*, *Planolites* isp., *Palaeophycus tubularis*, and rarely *Arenicolites statheri* may also occur. This ichnocoenosis is dominated by burrows of deposit-feeders. However, some suspension-feeder burrows occur and indicate that enough energy was present to keep detritus in suspension. The *Gyrochorte-Bolonia* ichnocoenosis is interpreted as an indicator of an intermediate to low energy environment and occurs predominantly in isolated, oscillatory-rippled fine to medium sandstone interbeds in silty clays (Facies C) of the Grès de la Crèche at Le Portel. These sediments are interpreted as deposits of the transitional zone between a low energy, offshore environment and a wave and storm influenced shoreface environment. The ichnocoenosis can also be found in rippled sandstone beds that alternate with silty, organic-rich fine sandstone beds (Facies C) of the Grès de Châtillon at Ambleteuse. These sediments are also interpreted as deposits of the transitional zone but with a more 'proximal' terrigenous influence than the first one, indicated by the high plant remains content.

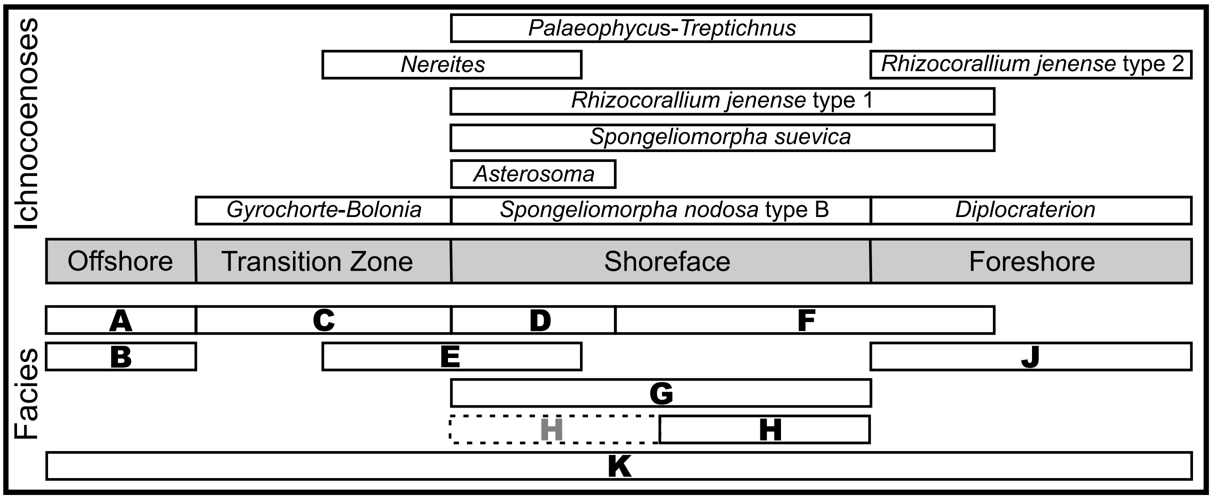

Fig. 10. Environmental distribution of facies and ichnocoenoses; Letters A to K refer to the facies described in the text. Trace fossil names refer to the ichnocoenoses described in the text

Nereites ichnocoenosis

This ichnocoenosis is dominated by *Nereites missouriensis*, pascichnia of deposit-feeders. Other traces, such as *Palaeophycus tubularis* and *Planolites* isp. are rarely associated with *N. missouriensis.* In some cases *Arenicolites*, *Chondrites*, and *Teichichnus* have been observed, but always crossing and/or interpenetrating *Nereites* and are thus interpreted as later than the members of this ichnocoenosis. The sediments in which the ichnocoenosis occurs are made up of large-scale trough or planar cross-bedded sandstones (Facies E) of the Grès de Châtillon at Ambleteuse, representing deposits of a wave influenved lower shoreface to transition zone. The trace fossil *N. missouriensis* indicates a low energy environment, and contrasts the interpretation of the host sediment. Similar observations with the occurrence of *Zoophycos* (also indicating low energy environments) in high energy sandstones in the Upper Cretaceous Carlile Shale were made by BASAN & SCOTT (1980). Only the mudstone fill of the *Zoophycos* structures within sandstones unveiled that there were times of low energy conditions within a generally high energy environment.

Nereites is now usually interpreted as a deep tier, single layer colonizer and is commonly found in flysch deposits (UCHMAN 1995).

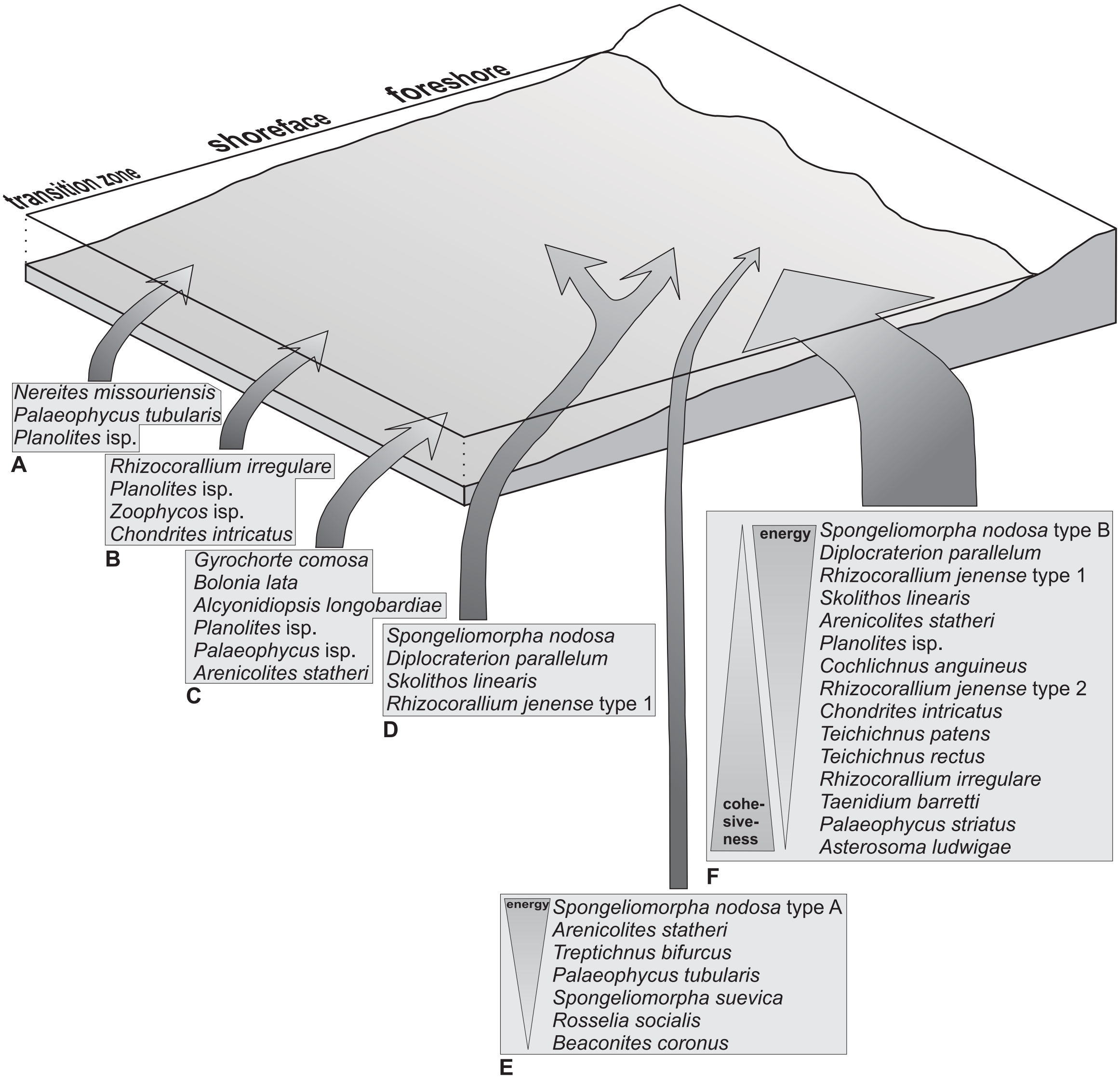

Fig. 11. Environmental distribution of the trace fossils in the Upper Jurassic of the Boulonnais. Letters below light-grey boxes refer to trace fossil assemblages described in the text. Triangles with 'energy' indicate decreasing hydrodynamic energy on the sea-floor from top to bottom and corresponding increase in sediment cohesiveness indicated by a 'cohesiveness' triangle

Teredolites ichnocoenosis

This ichnocoenosis consists exclusively of *Teredolites clavatus* (Text-fig. 7C), a trace of wood-boring bivalves. The ichnocoenosis was observed in a completely weathered piece of wood where no remains of the former plant material are left. This ichnocoenosis could only be found once in the Grès de la Crèche at Le Portel.

Depositional environments and their trace fossil content

Although single ichnotaxa are only rarely of use for environmental reconstructions, recurrent trace fossil assemblages can be used for this purpose. The entire set of trace fossils in the Upper Jurassic of the Boulonnais can well be compared with other Jurassic/Lower Cretaceous trace fossil assemblages (e.g., FÜRSICH 1975, 1998; HEINBERG & BIRKELUND 1984; DAM 1990) that show similar environmental distributions. Besides the above described ichnocoenoses (contemporaneous) one can also distinguish assemblages (non-contemporaneous) of trace fossils that are characteristic of certain environments (Text-fig. 10). The assemblages described below all represent non-contemporaneous, spatially separated assemblages. In contrast to the ichnocoenoses, which reflect more-or-less contemporaneous trace fossils, the ichnoassemblages include all occurring trace fossils in a particular sedimentary facies with only minor interest concerning their chronological relationship. Three assemblages are characteristic for the storm influenced transition zone to lower shoreface environment (Text-fig. 11). They include A) *Nereites missouriensis*, *Palaeophycus tubularis*, *Planolites* isp., *Chondrites intricatus*; B) *Rhizocorallium irregulare*, *Planolites* isp., *Zoophycos* isp., *Chondrites intricatus*; C) *Gyrochorte comosa*, *Bolonia lata*, *Alcyonidiopsis longobardiae*, *Planolites* isp., *Palaeophycus* isp., *Arenicolites statheri*. The wave influenced shoreface to lower foreshore settings including submarine shoals are dominated by: D) *Spongeliomorpha nodosa*, *Diplocraterion parallelum*, *Skolithos linearis*, *Rhizocorallium jenense* type 1. The tide influenced shoreface to foreshore is inhabited by the producers of: E) *Spongeliomorpha nodosa*, *Arenicolites statheri*, *Treptichnus bifurcus*, *Palaeophycus tubularis*, *Rosselia socialis*, *Beaconites coronus*; and F) *Spongeliomorpha nodosa*, *Diplocraterion parallelum*, *Rhizocorallium jenense* type 1, *Skolithos linearis*, *Arenicolites statheri*, *Planolites* isp. *Cochlichnus anguineus*, *Rhizocorallium jenense* type 2, *Teichichnus patens*, *Teichichnus rectus*, *Palaeophycus tubularis*, *Asterosoma ludwigae*.

The two assemblages that occur in the shoreface to foreshore environment differ in their trace fossil composition. Assemblage E is interpreted as diagnostic of moderately high energy conditions. Within this assemblage a decrease in hydrodynamic energy is inferred, with dominance shifting from *Spongeliomorpha nodosa* to *Arenicolites statheri* to *Treptichnus bifurcus* to *Palaeophycus tubularis* to *Rosselia socialis* to *Beaconites coronus* (Text-fig. 11). This indicates a water energy gradient from high-energy conditions where dominated by *Spongeliomorpha nodosa* to low-energy quiet conditions where dominated by *Beaconites coronus*. The same is true for the assemblage F composed of *Spongeliomorpha nodosa*, *Diplocraterion parallelum*, *Rhizocorallium jenense* type 1, *Skolithos linearis*, *Arenicolites statheri*, *Planolites* isp. *Cochlichnus anguineus*, *Rhizocorallium jenense* type 2, *Teichichnus patens*, *Teichichnus rectus*, *Palaeophycus tubularis*, *Asterosoma ludwigae*. A decrease in water energy is again postulated by a dominance of the first mentioned taxon (*S. nodosa*) in this series over *A. ludwigae*. In addition, an increase in sediment cohesiveness in the opposite direction can be observed with a high sediment cohesiveness indicated by *A. ludwigae* and unstable substrate conditions indicated by *S. nodosa* (Text-fig. 11). In this case it seems likely that the first taxon in the series represents pioneers and the last ones elite trace fossils.

CONCLUSIONS

The Upper Jurassic rocks studied herein show a great variety of very well preserved trace fossils. A study of their occurrence in the various sections results in grouping the trace fossils in nine frequent palaeoichnocoenoses and one exceptional palaeoichnocoenosis. Two palaeoichnocoenoses (*Diplocraterion* and *Spongeliomorpha nodosa* type B) are monospecific and are characteristic of a high energy, foreshore environment. The *Palaeophycus-Treptichnus* ichnocoenosis indicates moderate energy levels in a shoreface environment. For the shoreface to foreshore, the *Asterosoma-Teichichnus* and the *Rhizocorallium jenense* type 2 ichnocoenosis are indicative of moderate to low energy conditions. The *Rhizocorallium jenense* type 1 ichnocoenosis represents high energy conditions within a shoreface to lower foreshore environment. The *Spongeliomorpha suevica* ichnocoenosis is characterized by low to intermediate energy levels in a shoreface to lower foreshore position. The *Gyrochorte-Bolonia* and *Nereites*-ichnocoenosis are indicative of a low energy environment in the transition zone between offshore and shoreface. The exceptional *Teredolites* ichnocoenosis indicates a woodground. This study shows that the integrated analysis of trace fossils and sedimentology proved to be the most successful approach for plaeoenvironmental reconstructions.

Single, even name giving trace fossils of ichnofacies such as *Nereites* are not indicative of particular bathymetries but tell a lot about hydrodynamic conditions. As recently shown again by SCHLIRF & *al*. (2001) a detailed study of the occurrence of trace fossil assemblages may offer a detailed picture of palaeoenvironmental conditions that is much more precise than sedimentologic studies alone. Additionally, a detailed sedimentologic study of a succession can be a very helpful tool in interpreting the ethology of certain trace fossils, as has been shown in the case of *Rhizocorallium jenense* type 2. Furthermore, also in sequence stratigraphic interpretations trace fossils once more showed their potential value in order to determine parasequence boundaries.

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