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Characteristic trace fossils from Miocene brackish-water deposits in the Niger Delta, Nigeria

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Abstract

Miocene deposits in the eastern portion of the Greater Ughelli, Central Swamp and Coastal Swamp depobelts contain well-developed brackish-water trace fossil assemblages. Twelve ichnogenera have been identified, namely: *Asterosoma*, *Bergaueria*, *Chondrites*, *Gyrolithes*, *Thalassinoides*, *Lockeia, Palaeophycus*, ?*Conichnus, Planolites*, *Siphonichnus*, *Skolithos* and *Diplocraterion*. In addition, common non-descript, passively filled burrows and fugichnia (escape structures) have also been observed. The above-mentioned ichnogenera and associated non-descript structures can be arranged into six distinct and recurring ichnoassociations within the Greater Ughelli, Central Swamp and Coastal Swamp depobelts. Each ichnoassociation is comprised of a group of trace fossils which collectively reflect specific environmental conditions during deposition of these Miocene strata. All trace fossil assemblages illustrate deposition in nearshore, restricted settings. Ichnological and sedimentological criteria which may be utilized to recognise brackish-water deposits are discussed and illustrated in pictures of the cores studied.

Key words: Ichnoassociations, ichnology, salinity, Greater Ughelli, Central Swamp, Coastal Swamp, Neogene

1. Introduction

Three geological units in the Niger Delta, i.e., the Akata, Agbada and Benin Formations, came into existence during five offlapping siliciclastic sedimentation cycles (Ezeh et al., 2016a) otherwise referred to as depositional belts or depobelts or the Northern Delta, Greater Ughelli, Central Swamp, Coastal Swamp and Offshore. Except for the last-named, which belongs to the offshore Niger Delta, all remaining depobelts are located within the onshore portion of the Niger Delta Basin. Miocene strata have remained essential in research, especially of the onshore Niger Delta, owing to their being the primary constituent the central-eastern portion of the Greater Ughelli, Central Swamp and Coastal Swamp depobelts (Fig. 1). It has been amongst the delta's most prolific play since the onset of exploration activities in the basin over fifty years ago. According to CSL 2014, the play represents 25 per cent of all exploration wells (1,300 in number) drilled in the Niger Delta and 40 per cent of onshore wells (822 in total). The average field size for the onshore Niger Delta is ~ 90 million barrels (MMbbls), with a potential future capacity of sixteen billion barrels (Bbbls) of oil equivalent (10 Bbbls for oil and 6 Bbbls for gas).

The Akata Formation represents the oldest unit, consisting of marine shales, and is overlain by the paralic Agbada Formation which represents the main reservoir unit. Most of the oil discovered in the delta is found in this particular unit which comprises intercalations of sandstone and shale sequences. The sandstones constitute an essentially

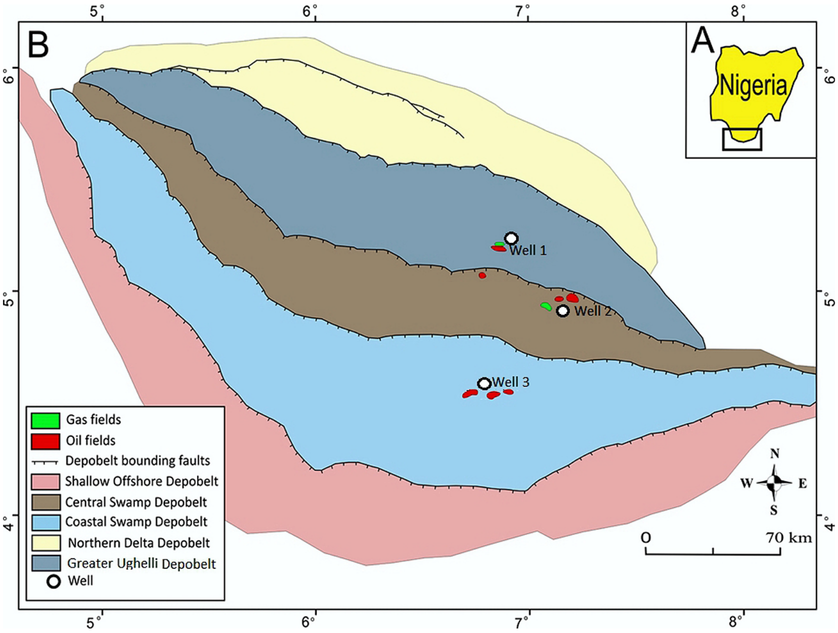

Fig. 1. Map of the study area, showing the five main depositional belts (depobelts) and the wells in the Niger Delta sedimentary basin studied.

poorly consolidated reservoir, while the shales also function as source rocks and cap rocks (Michele et al., 1999). On top of the Agbada Formation follows the Benin Formation which bears little oil and consists mainly of continental sands.

Considering the vast reserves contained within the Greater Ughelli, Central Swamp and Coastal Swamp, this is an important target for further reservoir studies. However, successful economic exploitation of these resources requires a thorough understanding of the sedimentological, stratigraphical and structural controls that have an influence on hydrocarbon distribution. Consequently, detailed and integrated facies models are an essential tool in the most efficient development of the depobelts and ichnological studies have proved to be particularly valuable in palaeoenvironmental interpretations and, by extension, in integrated facies models. Unfortunately, there are no previous detailed ichnological studies for the basin, with the exception of recent ichnological work by Ezeh et al. (2016a, b) which characterised shoreface variability, sedimentology and ichnofacies of the Coastal Swamp and shallow Offshore depobelts. Ezeh et al. (2016a) used the fully marine trace fossils recognised to characterise and interpret the deposits in the shoreface section, while Ezeh et al. (2016b) showed the usefulness of trace fossils and cores in the interpretation of reservoir facies against the conventional use of well log signatures. Although these recent papers have been very useful in our understanding of the depositional history of the area, there still is a need to document the ichnological characteristics as these relate to brackish-water deposits.

The aim of the present paper is to reconstruct the palaeoenvironment of Miocene deposits in the Niger Delta, based on trace fossil assemblages of the Greater Ughelli, Central Swamp and Coastal Swamp depobelts, which have been useful in interpretations of depositional environments and may offer valuable input to the development of integrated facies models that could be used to formulate effective developmental strategies.

2. Geological setting and stratigraphy

The Niger Delta sedimentary basin is situated in southern Nigeria, with an areal coverage of 300,000 km^2, including the geological extent of the Neogene Niger Delta (Akata-Agbada) Petroleum System (Michele et al., 1999). It is bounded in the north and northeast by the Benin flank, the Anambra Basin and the Abakaliki fold belt, in the east-south-east by the Calabar flank, while the Cameroon volcanic line lies in the east. The western axis is formed by the Dahomeyan embayment which is the easternmost West African transform-fault passive boundary (Fig. 2).

The structure of the continental boundary along the west coast of Equatorial Africa is influenced by the Cretaceous fracture zones portrayed as trenches in the deep Atlantic. These fracture zones ridges separate the boundary into different basins and, in Nigeria, develop the boundary faults of the Cretaceous Benue-Abakaliki Trough which extend into the West African shield. The trough marks the failed arm of a rift triple junction linked with the

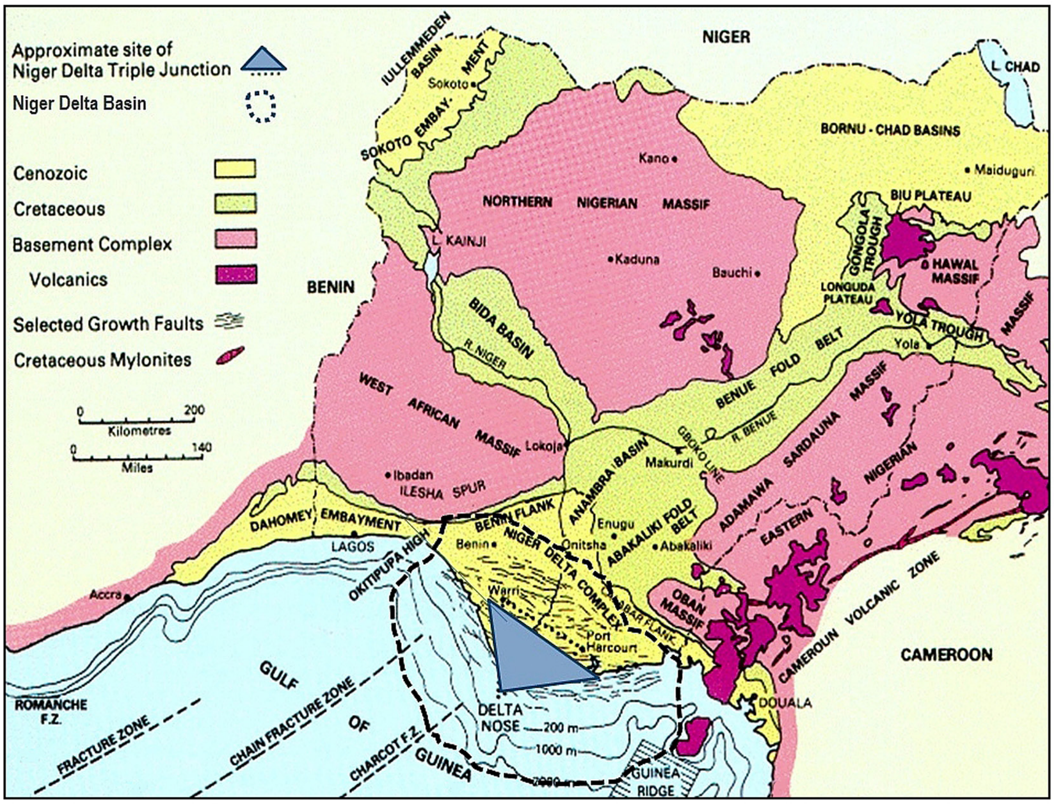

Fig. 2. Geological map of Nigeria with the main sedimentary basins, the basement complex and the prograding Niger Delta Basin (selected dotted shape) with selected growth faults (adapted after Whiteman, 1982).

opening of the South Atlantic. Lehner & De Ruiter (1977) proposed that the rifting started during the Late Jurassic and continued into the mid-Cretaceous; however, in the Niger Delta region, rifting receded entirely in the Late Cretaceous.

After rifting ceased, gravity tectonics became the primary deformational process. Mobile shale generated internal deformation and occurred in response to two processes (Kulke, 1995), i.e., shale diapirs and slope instability. Shale diapirs were formed from the loading of poorly compacted, over-pressured, prodelta and delta-slope clays (Akata Formation) by higher-density delta-front sandstone (Agbada Formation), while slope instability developed as a result of a lack of lateral, basinward, support for the under-compacted delta slope Agbada Formation (Ezeh et al., 2016a). It is believed that gravity tectonics ended prior to the development of the continental Benin Formation; this is characterised by complex structures such as shale diapirs, roll-over anticlines, collapse growth fault crests, back-to-back features and steeply dipping, spaced frank faults (Evamy et al., 1978; Xiao & Suppe, 1992).

As stated by Stacher (1995), the depobelts are 30–60 kilometres in width and prograde 250 kilometres southwestwards over oceanic crust into the Gulf of Guinea. They show synsedimentary faulting which occurred as a result of the interaction of sediment supply and subsidence (Doust & Omatsola, 1990).

The Greater Ughelli, Central Swamp and Coastal Swamp depobelts (latitude 6°62'40"–7°45'00"N; longitude 4°58'12"–5°39'10"E; see Fig. 1) are characterised by growth faults and associated roll-over anticlines. These formed contemporaneously with deposition and represent the structural trapping mechanism of petroleum in these depobelts.

As previously mentioned: the stratigraphy of the Niger Delta, and that of the study area in particular, can be divided into three major units that range in age from Eocene to Holocene (Fig. 3). The Akata Formation comprises at least 6,500 metres of marine clays with silty and sandy interbeds (Whiteman, 1982), while the Agbada Formation is characterised by paralic to marine coastal and fluvial-marine deposits, composed mainly of sandstones and shales illustrating coarsening-up offlap cycles (Weber, 1987). The Benin Formation consists of continental and fluvial sands, gravel and back swamp deposits, as is 2,500 m in thickness (Reijers, 2011). These three diachronous formations occur within growth-fault-bounded sedimentary units referred to as depobelts or depocentres that succeed each other in a south-

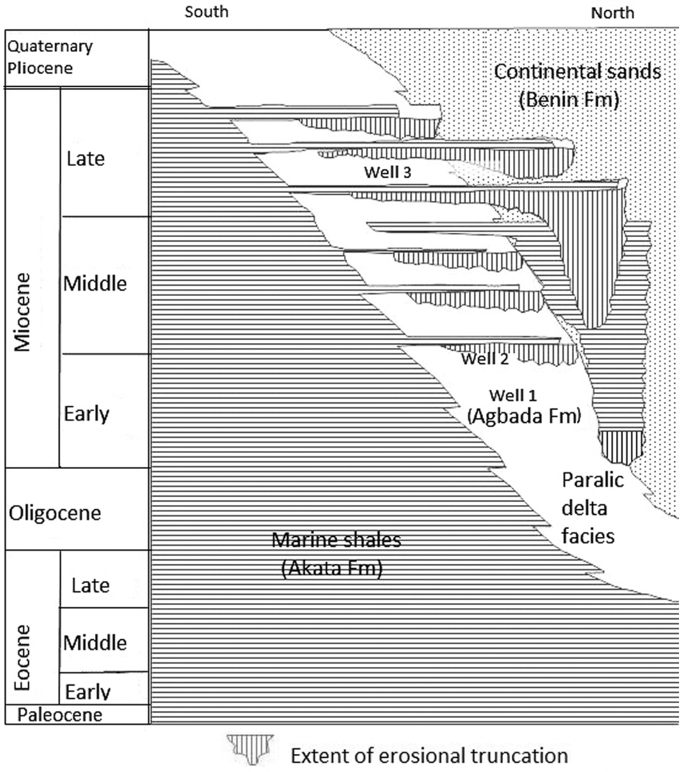

Fig. 3. Stratigraphy of the Neogene Niger Delta sedimentary basin with respective ages of the formations, facies and wells studied (adapted after Doust & Omatsola, 1990).

erly direction (Doust & Omatsola, 1990; Stacher, 1995). The sedimentation in each depobelt (Fig. 1) is a function of the rates of deposition and of subsidence with syn-sedimentary growth faults upsetting the balance (Evamy et al., 1978). The growth faults are generated by rapid sedimentation and gravitational instability during the accumulation of the Agbada deposits and continental Benin sands over mobile and under-compacted Akata prodelta shales. Lateral flowage and extrusion were also responsible for the diapiric structures on the continental slope of the Niger Delta (Reijers et al., 1997).

3. Previous research in the study area

Miocene strata assigned to the Agbada Formation represent the largest petroleum-bearing unit of the Greater Ughelli, Central Swamp and Coastal Swamp depobelts. In spite of a vast resource potential there are only very few studies of trace fossil characteristics and of the depositional environments of reservoirs by using core data. In the Coastal Swamp depobelt, Egbu et al. (2009) observed five lithofacies associations (i.e., foreshore, upper shoreface, middle shoreface and lower shoreface) using sedimentological features. While studying the stratigraphy and sedimentology of the Niger Delta, Reijers (2011) noted that shoreface sediments had formed simultaneously in the Greater Ughelli, Central Swamp and Coastal Swamp depobelts during a period of accumulation of littoral and lower coastal-plain deposits in the northern delta. In the same vein, Oyanyan et al. (2013) identified ten lithofacies from core samples in the course of determining the depositional environment of the eastern part of the Greater Ughelli. These samples aided in the reconstruction of five sub-depositional environments (i.e., lower shoreface, middle shoreface, distributary channel, tidal flat and tidal channel) in the Greater Ughelli depobelt. Similarly, Okengwu & Amajor (2014) recognised successions of well-developed shoreface deposits, illustrating the combined influence of wave and fluvial processes and sediments consisting of prograding wave-dominated shoreface with a fluvial predominance in the Greater Ughelli and Central Swamp depobelts. Prince & Minapuye (2015) identified three environments (viz., tidally influenced fluvial channel, upper shoreface and lower shoreface) in the stratigraphy of the Greater Ughelli depobelts. Of a more recent date are detailed interpretations of depositional environments on the basis of cores of onshore and shallow offshore depobelts by Ezeh et al. (2016a, b).

4. Methodology

Detailed core analysis (both sedimentologically and ichnologically) was conducted for three wells (Fig.

1) in different fields within the Greater Ughelli (well 1), Central Swamp (well 2) and Coastal Swamp (well 3) depobelts. Morphologies of both dominant and associated trace fossils aided in the classification of ichnoassociations. Trace fossils were observed and assigned to respective ichnofacies types based on Seilacher's model (1967), as modified by Pemberton et al. (2001). The degree of bioturbation is based on Droser & Bottjer's (1986) ichnofabric index, as modified by Pemberton et al. (1992). Altogether, a total length of 334 metres of core has been studied. Descriptions of sedimentary features and of characteristics of associated trace fossils were used to interpret the depositional environments. The map of the study area was developed using ArcGis Map 10.

5. Results

Twelve ichnogenera have been recognised in the Greater Ughelli, Central Swamp and Coastal Swamp depobelts, namely *Asterosoma*, *Thalassinoides*, *Bergaueria*, *Gyrolithes*, *Chondrites*, *Palaeophycus*, *Siphonichnus, Skolithos, Planolites*, *Lockeia*, *Diplocraterion* and ?*Conichnus*. In addition to distinct trace fossils, bioturbated textures, escape structures and non-descript, passively filled shafts have also been noted. Although slightly problematic, each ichnogenus can be attributed to a particular group (or groups) of organisms, to an ethological (or behavioural) category and, lastly, to a general trophic group (Table 1).

The twelve ichnogenera recognised, together with associated non-descript structures and textures, have been seen to occur in six distinct ichnoassociations. Each trace fossil association is comprised of a number of ichnogenera. Collectively, the constituent trace fossils of each ichnoassociation provide clues with respect to the nature of the depositional environment. The stratigraphical recurrence of these ichnoassociations within the Miocene deposits reflects the re-establishment of particular environmental conditions throughout deposition of the Greater Ughelli, Central Swamp and Coastal Swamp depobelts. In general, six ichnoassociations characterise the Miocene deposits within these depobelts and represent a continuum of palaeoenvironmental conditions in an overall brackish-water depositional environment. The present paper outlines ichnological and sedimentological criteria that could be integrated alongside other data so as to obtain a better interpretation of the depositional settings. In addition, it helps in gaining an appreciation of the degree of variability of the latter.

5.1. Recurring ichnoassociations

As previously noted, the overall distribution of trace fossils within the Miocene sedimentary rocks of the Greater Ughelli, Central Swamp and Coastal Swamp depobelts can be viewed in terms of six distinct, recurring ichnoassociations (Table 2). The concept of recurring ichnoassociations has seen extensive use in palaeoecological and sedimentological interpretations. The basis for this recurrence stems from the concept that trace fossils constitute the preserved record of behaviour and functional morphology and, therefore, reflect adaptations of organisms to particular ecological conditions (Frey & Pemberton, 1985; Beynon & Pemberton, 1992). Ichnoassociations characteristic of particular environmental regimes are recurrent in space and time whenever the requisite environmental conditions occurred (Frey & Seilacher, 1980; Frey & Pemberton, 1985).

Table 1. Ethological classification of brackish-water trace fossils from the Greater Ughelli, Central Swamp and Coastal Swamp depobelts

Trace fossil	Ethological classification	Trophic strategies	Probable organism
Gyrolithes	Domichnia	deposit-feeder	Annelid
Bergaueria	Domichnia/Cubichnia	suspension feeder	Anemone
Palaeophycus	Domichnia	carnivore	Annelid
Siphonichnus	Fodinichnia	suspension feeder	Annelid
Asterosoma	Fodinichnia	deposit-feeder	Annelid/Crustacean
Planolites	Fodinichnia/Pascichnia	deposit-feeder	Annelid
Lockeia	Cubichnia	deposit-feeder	Bivalve
Chondrites	Fodinichnia/Chemichnia/Agrichnia	deposit-feeder	Siphunculid/Annelid
Thalassinoides	Fodinichnia/Domichnia	deposit-feeder	Decapod/Crustacean
Conichnus	Domichnia/Cubichnia	carnivore/suspension feeder	Sea anemone
Skolithos	Domichnia	suspension feeder	Annelid
Diplocraterion	Domichnia/Equilibrichnia	suspension feeder	Crustacean

Table 2. Distribution and relative abundance of ichnogenera in recurrent brackish-water trace fossil assemblages in Miocene deposits within the cores of the Greater Ughelli, Central Swamp and Coastal Swamp depobelts.

Ichno-association	Gyrolithes-Chondrites	Planolites	Skolithos	Palaeophycus	Asterosoma	Thalassinoides
Trace fossil						
Gyrolithes	c–a	–	–	–	–	–
Bergaueria	–	–	–	–	–	o
Palaeophycus	–	r	–	o–r	c	o–r
Siphonichnus	–	–	–	c–a	–	–
Asterosoma	–	–	–	–	–	c
Planolites	c	c	–	c	c	r
Lockeia	o	–	–	–	–	–
Chondrites	c–a	r	–	–	–	–
Thalassinoides	r	r	–	–	r	a
Conichnus	–	–	–	–	–	*o–r
Skolithos	–	–	a	–	–	–
Diplocraterion	–	–	–	–	o	–
Depobelts	CS	GU & Centr.S	GU & CS	Cent.S	GU	CS

c – common, a – abundant, r – rare, o – occasional, * – opportunistic trace fossil, CS – Coastal Swamp Centr.S – Central Swamp GU – Greater Ughelli.

5.1.1. *Gyrolithes-Chondrites* ichnoassociation

This association is characterised by a low-diversity ichnoassemblage which is dominated by *Gyrolithes* and *Chondrites* (Fig. 4). Associated ichnofossil taxa and structures may include *Lockeia*, syneresis cracks and load structures. For the most part, this ichnoassociation is restricted to inclined heterolithic, cross-stratified sediments and mudstones which are abundant in the middle portions (4,051–4,054 m depth) of well 3 in the Coastal Swamp depobelt. Bioturbation intensity is generally low, but a unique feature of this ichnoassociation is the occurrence of horizons which are pervasively bioturbated by these trace fossils. The low-diversity nature of this ichnoassociation may reflect extremely stressful environmental conditions such as brackish-water

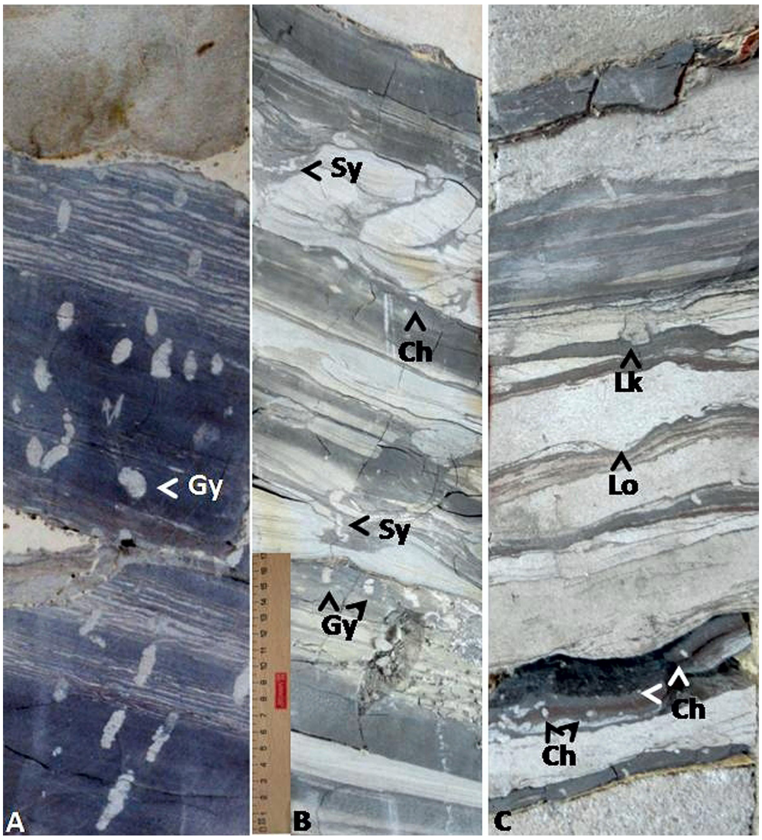

Fig. 4. *Gyrolithes-Chondrites* ichnoassociation (well 3; depth 3,950 m). **A** – *Gyrolithes* (Gy) within a dark brownish grey mudstone-heterolithic deposit; **B** – *Gyrolithes* (Gy), *Chondrites* (Ch) and syneresis cracks (Sy) on an inclined heterolithic, cross-stratified (IHCS) bed; **C** – *Lockeia* (Lk), *Chondrites* (Ch) and load structure on an IHCS bed (well 3; depth 3,950.5 m). Scale bar in centimetres.

and/or other ecological conditions. The morphology of *Gyrolithes* is interpreted to reflect a burrowing adaptation to escape from extreme salinity fluctuations at the sediment-water interface (Gernant, 1972; Powell, 1977; Netto et al., 2007). Gernant (1972) suggested that the *Gyrolithes* trace-making organism was restricted to marginal marine strata and therefore *Gyrolithes* might be utilized as a brackish-water indicator. Although palaeoenvironmental interpretations constructed on the basis of only a single sedimentary structure should be avoided, it is interesting to note that other lines of sedimentological evidence such as syneresis cracks and current beddings (Fig. 4) are indicative of a brackish-water depositional environment, suggesting this assumption may have some validity in this particular case.

5.1.2. *Planolites* ichnoassociation

This ichnoassociation is mostly restricted to carbonaceous and laminated mudstones, but locally is found within interlaminated mudstones. The relative degree of bioturbation is extremely low, being represented by a low-density, monospecific assemblage of *Planolites* (Fig. 5). Accessory features include abundant carbonaceous debris, both as laminae and as disseminated matter as well as siderite concretions. The relatively low intensity of bioturbation suggests that bottom waters were not sufficiently oxygenated to support a diverse, oxygen-dependent benthic community. Oxygenation of the water column is important to all benthic organisms; however, some taxa can tolerate and may even preferentially inhabit low oxygen or oxygen-depleted ecological niches (Ekdale, 1988). The

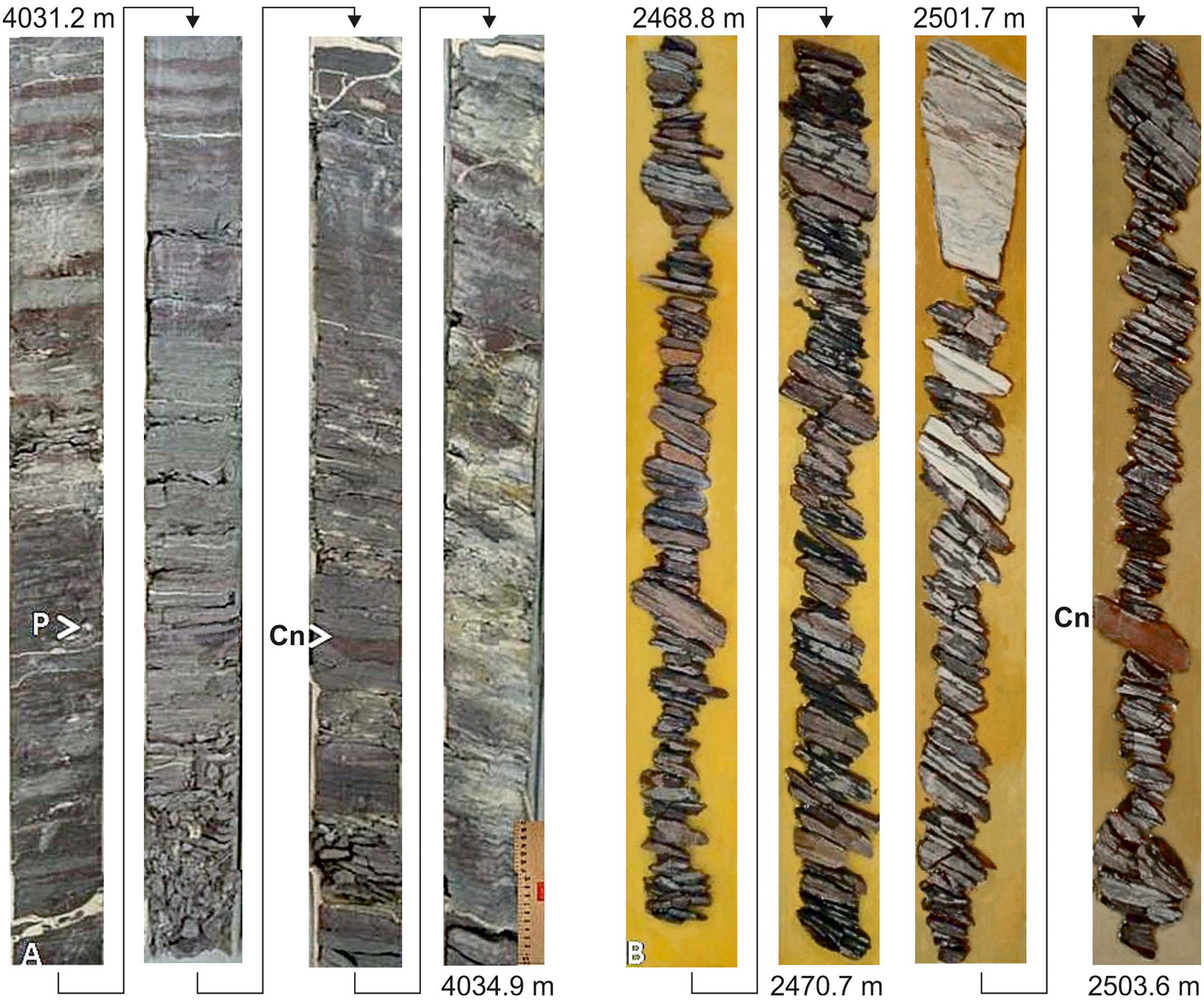

Fig. 5. *Planolites* ichnoassociation. **A –** Section through an estuarine dark brown-grey laminated and carbonaceous mudstone with abundant concretions (Cn) and *Planolites* (well 1; depth 4,031.2–4,034.9 m); **B –** Laminated mudstone with concretions (Cn). Note the monospecific nature of trace fossils and their low density. Scale bar in centimetres; each core box is 0.91 m in length.

inferred nature of the *Planolites* trace-making organism (i.e., endostratal deposit-feeding) suggests that, although sediments may have been organic rich, the interstitial environment was not completely devoid of oxygen. Thinly laminated zones devoid of biogenic structures imply that periodically, anoxic conditions may have been established. Prolonged periods during which the interstitial environment and/or the overlying water column were oxygen depleted would have been lethal to benthic organisms (Ekdale, 1985; Beynon & Pemberton, 1992).

The distinct lack of biogenic structures created by suspension-feeding organisms implies that the physical and ecological conditions were not conducive to the development of a suspension-feeding community. In low-oxygen environments, sediments commonly contain high concentrations of unoxidised organic matter which may support dense deposit-feeding communities. Such environments are typically stagnant and devoid of currents of sufficient strength to suspend nutrients in the water column. As a result, low-oxygen environments are typified by a predominance of deposit-feeding organisms and a general absence of suspension-feeding organisms (Tognoli & Netto, 2003). Therefore, oxygen-depleted deposits characteristically contain low-density, low-diversity trace fossil assemblages that are dominated by deposit-feeding structures. Alternatively, other environmental factors such as variable and low salinities may also have imposed severe physiological stresses on benthic organisms and have resulted in the preferential exclusion of suspension-feeding organisms. Burrowing, especially deep burrowing, is an adaptation which lends benthic organisms the capability of withstanding salinity fluctuations due to the buffering capacity of sediments (Wightman et al., 1987). Sanders et al. (1965) investigated salinity fluctuations in the water and sediments of the Pocasset River Estuary from 2.3 ppm to 29.3 ppm during a single tidal cycle and found that the interstitial environment (depth = 5–20 cm) remained relatively constant at 20.5 ppm. Therefore, even shallowly burrowing organisms are significantly removed from the harsh physical and chemical environment of the sediment-water interface and overlying water column. Thus, because of the ability of deposit-feeding organisms to flourish within the interstitial environment, they may have been able either to escape from or tolerate harsh ecological conditions and may have preferentially inhabited a stressful ecological niche because of low levels of interspecific competition (Ekdale et al., 1984).

The abundance of siderite concretions complements the interpretation of anoxic or reducing conditions. The formation of siderite is enhanced when interstitial pore waters are depleted with respect to free oxygen and dissolved sulphur. Thus, the presence of siderite may be suggestive of rapid accumulation and decomposition of organic matter in a restricted, anoxic or oxygen-limited environment (Gauthier, 1982). However, the low diversity and density of biogenic structures, abundance of siderite and the carbonaceous nature of the sediments suggest that the interstitial waters were not well oxygenated.

In turn, this suggests that both salinity and oxygenation may have been limiting factors in the distribution of benthic organisms. It is difficult to discern whether or not these factors independently or dependently influenced the distribution of benthic organisms. Regardless of which was the dominant factor, the low-density, monospecific assemblages indicate that only a limited number of benthic organisms could flourish in this unstable or unpredictable setting (Beynon & Pemberton, 1992). Organisms which inhabit unstable settings, such as estuaries and other marginal marine environments, naturally have broad environmental tolerances and can adapt to environmental disturbances. Such organisms, because they are subjected to high levels of physiological stress, tend to display opportunistic or r-selected population dynamics (Ekdale, 1985). In contrast, benthic organisms which inhabit stable or predictable settings are more severely affected by physical or biological stresses such as variable salinity or oxygenation levels. Conditions of abundant organic matter, fluctuating salinity and low concentrations of dissolved oxygen are common in estuarine and delta plain environments in which large volumes of organic-rich mud are laid down in restricted settings.

5.1.3. *Skolithos* ichnoassociation

This association occurs in fine-grained, cross-stratified and planar-laminated sandstones, being characterised by *Skolithos* in moderate density and low diversity (Fig. 6). This consists predominantly of vertical dwelling and feeding structures such as *Skolithos*, *Siphonichnus* and *Planolites* created by suspension-feeding organisms. The predominance of biogenic structures created by suspension-feeding organisms is suggestive of nutrient-rich and well-oxygenated bottom waters. Currents were of sufficient magnitude to suspend nutrients within the water column, but were moderate enough to allow organic detritus to settle from suspension, offering nutrient resources to shallow suspension-feeding organisms. The characteristics of this ichnoassociation, i.e., the predominance of vertical dwelling structures, generally low diversity and

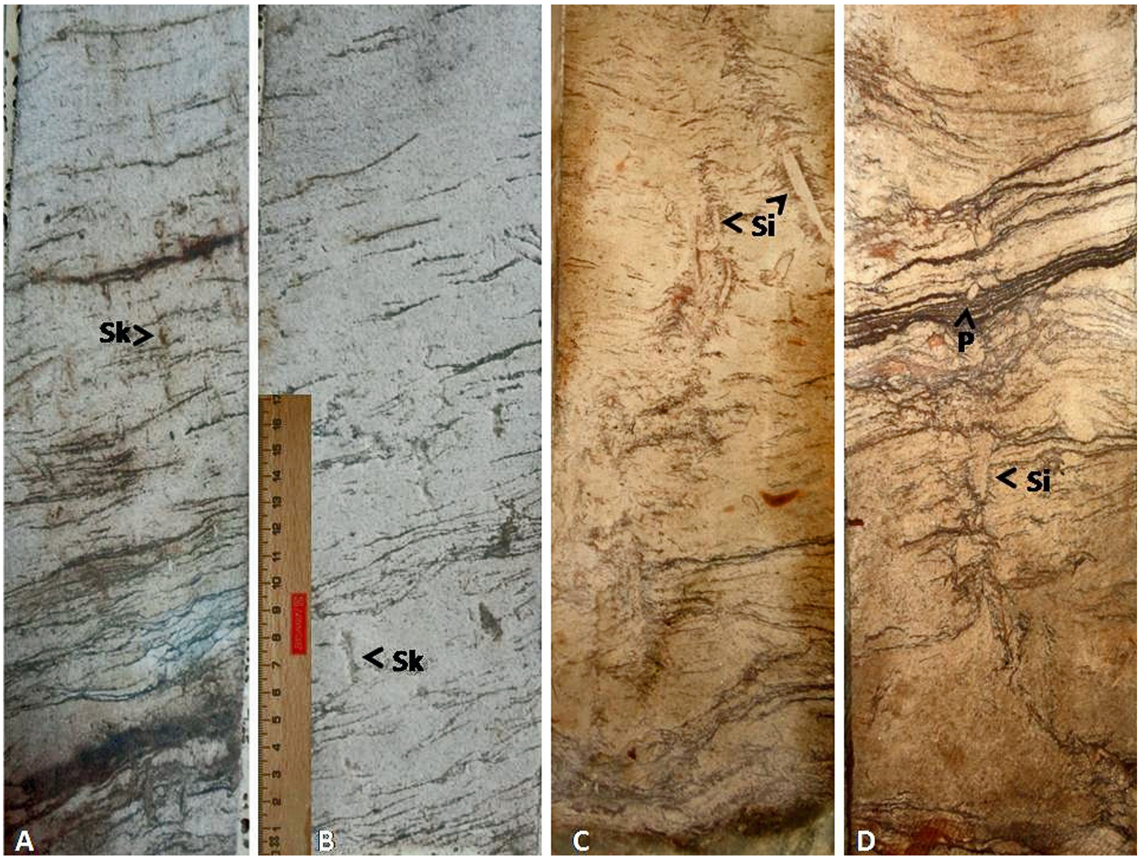

Fig. 6. *Skolithos* ichnoassociation. **A, B –** *Skolithos-* (Sk) dominated, laminated-cross-stratified sandstone bed (well 3; depth 2,974 m). Note the moderate density and monospecific characteristics of the ichnoassociation; **C, D –** *Siphonichnus* (Si) and *Planolites* (P) on moderately bioturbated, sandy heteroliths. Similarly, note low diversity, moderate density and associated mud couplets.

moderate burrow density are, for the most part, indicative of the *Skolithos* ichnofacies (Beynon & Pemberton, 1992; Pemberton et al., 2001).

Units characterised by this ichnoassociation typically consist of alternating bioturbated and laminated or cross-stratified beds. The bioturbated beds contain a low-diversity, *Skolithos*-dominated assemblage. Laminated zones reflect energetic periods in which shear stress in the benthic boundary layer could not be tolerated by the benthic community. Bioturbated beds record periods in which current velocities were sufficiently reduced, permitting organisms to rework the substrate.

5.1.4. *Palaeophycus* ichnoassociation

This association is typical of laminated to bioturbated mudstones and heteroliths and is represented by low-diversity, low-density assemblages comprising *Palaeophycus*. Other associated ichnofossils include *Diplocraterion*, *Planolites* and ?*Conichnus* (Fig. 7). In addition, numerous beds are characterised by a bioturbated texture, in which very few discrete trace fossils can be identified; this could have been above storm wave base and possibly fairweather wave base. Emplacement of these beds does not represent sudden shallowing events, but rather a temporary lowering of wave base in response to coastal upwelling associated with meteorological disturbances. The occurrence of these dwelling structures may represent the displacement of the resident benthic community by high physiological stress, associated with the deposition of sandstone beds (flood event). With the return to normal, fairweather conditions the resident deposit-feeding community was re-established and the opportunistic, suspension-feeding community was eventually displaced. Similar event-related examples of ichnological dynamics have been documented from ancient shallow-marine deposits (compare Frey & Seilacher, 1980; Pemberton & Frey, 1984; Vossler & Pemberton, 1988; Beynon & Pemberton, 1992; Pemberton et al., 2001).

The overall increase in ichnotaxonomic diversity of this trace fossil association relative to that of the *Planolites* ichnoassociation reflects a fundamental change in a number of environmental parameters such as nutrient supply, sediment consistency, de-

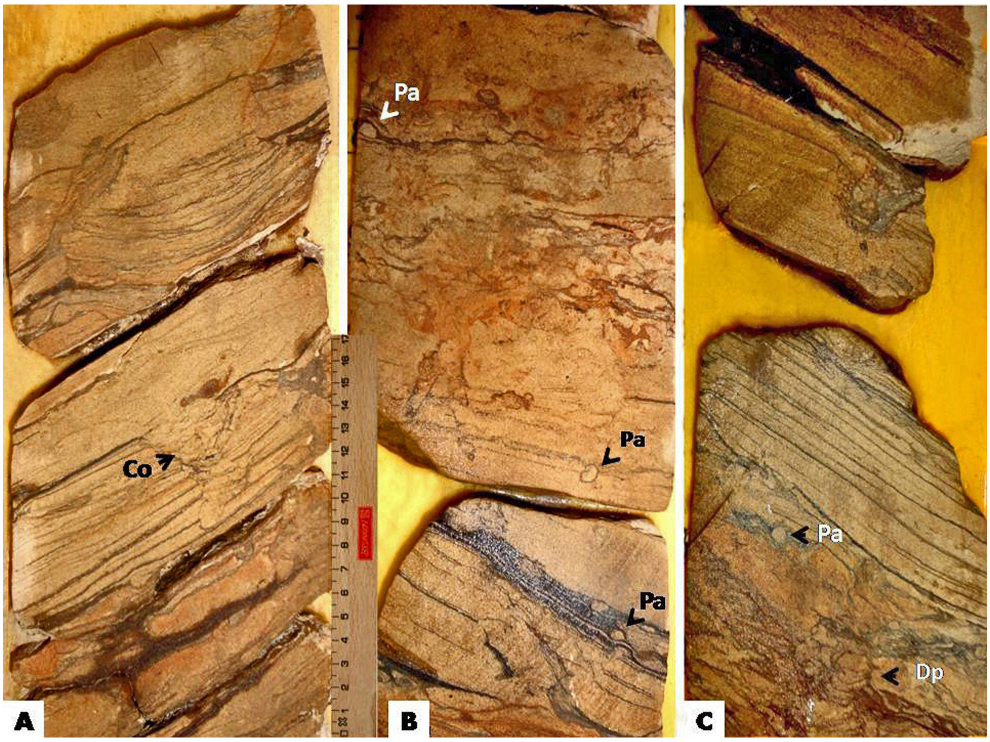

Fig. 7. *Palaeophycus* ichnoassociation (well 2; depth 2,496 m). **A, B –** ?*Conichnus* (Co) and *Palaeophycus* (Pa) within sandy heterolithic facies. Note low diversity and low density of the association; **C –** *Palaeophycus* (Pa) and *Diplocraterion* (Dp) on heterolithic facies (well 2; depth 2,497 m).

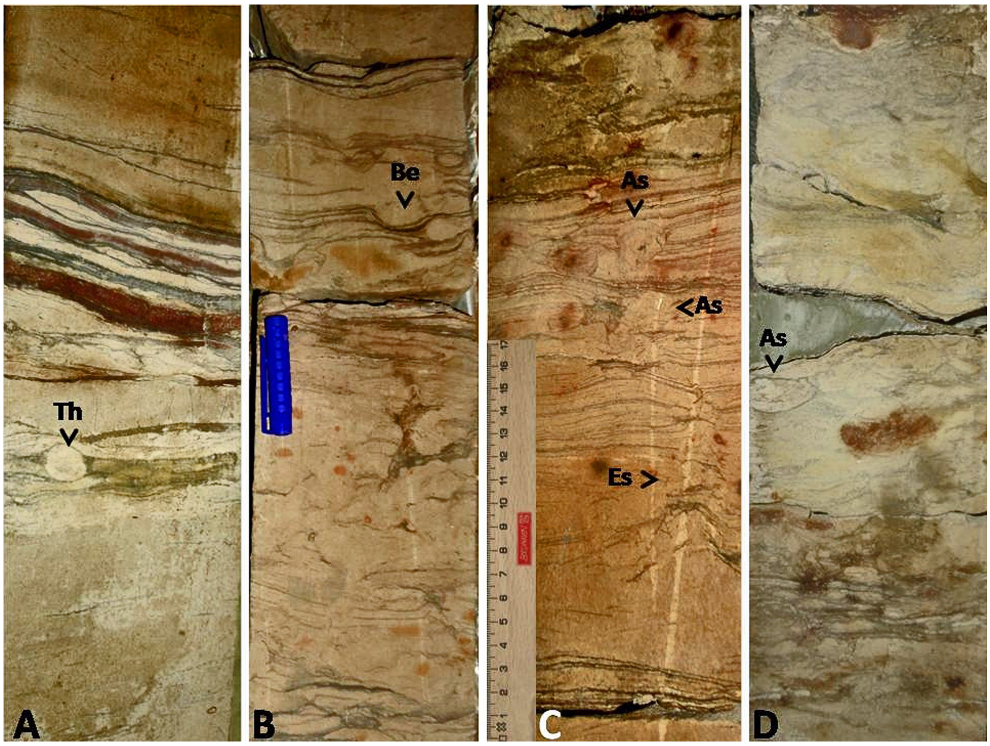

Fig. 8. *Asterosoma* ichnoassociation (well 1; depth 2,954 m). **A, B –** *Thalassinoides* (Th) and *Bergaueria* (Be) within sandy heterolithic facies which consists of *Asterosoma* (As); **C** (well 1; depth 2,965 m) and **D** (well 1; depth 2,955 m) illustrate *Asterosoma* (As) and escape structure (Es) on sandy heterolithic facies. Scale bar in centimetres.

gree of oxygenation and salinity. The end effect was the establishment of physical and biological conditions that were more conducive to benthic colonisation.

5.1.5. *Asterosoma* ichnoassociation

Interlaminated mudstones and heteroliths are typified by low-diversity trace fossil assemblages dominated by reduced forms of *Asterosoma* (Fig. 8). Associated trace fossil genera include *Planolites*, *Thalassinoides* and *Bergaueria*. This ichnoassociation is characterised by a predominance of horizontal deposit-feeding structures. Although diversity is low, individuals, particularly *Asterosoma*, attain very high densities, being commonly represented by a wispy, bioturbated texture in which distinct, other burrow elements are not always readily apparent. The ichnogenus *Asterosoma* is regarded as typical of the transition between the lower shoreface and offshore (Ezeh et al., 2016a), but the low degree of bioturbation, low diversity and sediment characteristics suggest an environment influenced by salinity fluctuation, probably a tidally influenced delta. This is consistent with the interpretation of the palaeoenvironment of the Sorthat Formation on Bornholm (Denmark) by Bromley & Uchman (2003). In addition, ichnofaunal assemblages of this kind have been interpreted as characterised by a mixed *Cruziana* and *Skolithos* ichnofacies (Howard & Frey, 1973, 1975, 1985; Dorjes, 1977; Ekdale et al., 1984, Frey & Pemberton, 1985; Wightman et al., 1987; Beynon & Pemberton, 1992; Tognoli & Netto, 2003).

5.1.6. *Thalassinoides* ichnoassociation

This ichnoassociation is monospecific in nature, consisting of *Thalassinoides* (Fig. 9). The illustrated examples show thin laminae or lenses of sands in a matrix of brown mudstones. The mudstones are preserved in between coarse-grained estuarine channel sand bodies. These mudstones may represent stable cohesive sediments that were laid down in a protected, low-energy setting that came into existence when the estuarine channel was abandoned. The trace fossil characteristic of this ichnoassociation has considerable implications; despite the low diversity and monotypical nature, which is indicative of a brackish-water environment, the palaeoenvironment had normal salinity.

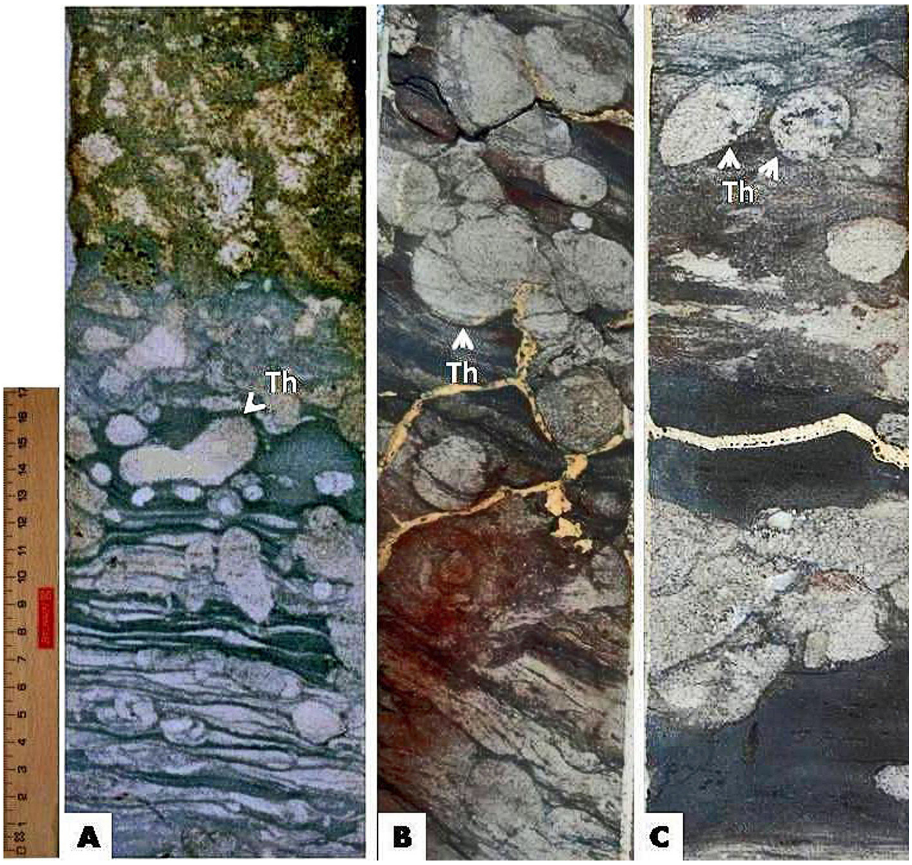

Fig. 9. *Thalassinoides* ichnoassociation (well 3; depth 4,097 m). **A –** *Thalassinoides* (Th); **B, C –** *Thalassinoides* (Th) on a brownish mudstone deposit; infill comprises pebbly grained sandstone matrix probably formed during surface exposure or originating from the overlying sandstone deposit.

5.2. Palaeoenvironmental implications

Even though the recurring ichnofaunal assemblages have significant palaeoenvironmental implications, the overall trace fossil suite is characterised by: (1) a predominance of morphologically simple, vertical and horizontal structures; (2) a generally low to very low diversity; (3) reduced size, compared to marine counterparts; (4) an association of siderite concretions and (5) an admixture of elements which are common to both the *Cruziana* and *Skolithos* ichnofacies. The overall low ichnotaxonomic diversity which typifies the majority of the recurring ichnoassociations differentiated in the Greater Ughelli, Central Swamp and Coastal Swamp depobelts parallels diversity trends documented from modern brackish-water environments. Ichnoassemblages in such settings typically are reduced with respect to species diversity in comparison to freshwater and fully marine counterparts (Beynon & Pemberton, 1992; Tognoli & Netto, 2003). This is evident in trace fossil assemblages here assigned to the *Gyrolithes-Chondrites*, *Skolithos* and *Asterosoma* ichnoassociations. This low diversity is a reflection of the limited number of benthic species which evolved physiological specialisations needed to inhabit brackish-water environments (Barnes, 1984). Very few freshwater species are capable of withstanding salinities in excess of 35 ppm; similarly, very few marine species can tolerate salinities lower than 18 ppm. These species are known as euryhaline organisms; good examples are the green crab (*Carcinus maenas*) and the green sea urchin (*Strongylocentrotus droebachiensis*).

The non-marine and normal marine faunas denote stable end-members at opposite ends of a salinity gradient. With even a slight increase in salinity, the diversity of the non-marine faunal component declines rapidly. On the other hand, with decreasing salinity the diversity of the normal marine component declines at a more gradual rate. Thus, the brackish-water faunal assemblage more appropriately represents an impoverished marine assemblage rather than a true mixture of non-marine and normal marine components (Ekdale et al., 1984; Wightman et al., 1987). This is illustrated very well in the *Palaeophycus* ichnoassociation. Such diversity trends in the distribution of modern benthic organisms are reflected to some extent in the ancient sedimentary record by the occurrence of low-diversity to monospecific ichnofossil assemblages, depicted by the *Planolites* and *Thalassinoides* ichnoassociations. Various authors have pointed out that such characteristically low levels of ichnotaxonomic diversity reflect harsh ecological parameters and may potentially be utilized as a palaeo-indicator of brackish-water conditions (compare Frey & Howard, 1975, 1980, 1985; Ekdale et al., 1984; Wightman et al., 1987; Tognoli & Netto, 2003).

In addition to a decrease in species diversity, benthic organisms which inhabit brackish-water environments typically display a reduction in size relative to their normal marine counterparts. For instance, this is seen in the *Asterosoma* ichnoassociation (Fig. 8) where the nominate ichnogenus is smaller in form in comparison to the fully marine counterparts recognised by Ezeh et al. (2016a) in the same basin. Similarly, *Thalassinoides* (Fig. 8) associated in the *Asterosoma* ichnoassociation is typically reduced when compared to larger forms of *Thalassinoides* within the *Thalassinoides* ichnoassociation which is indicative of fuller marine conditions (Fig. 9). This trend is not apparent in non-marine species (Barnes, 1984) which have the ability to adapt to low-salinity conditions (Remane & Schlieper, 1971). The relative reduction in size is an adaptive, morphological response evolved by predominantly marine organisms in order to tolerate the high, salinity-induced physical and chemical stresses which the inhabited brackish-water settings impose upon such organisms. And, to buttress this point, Remane & Schlieper (1971) argued that reduced salinity affected the size of benthic organisms in a number of ways, including decreased metabolism, retarded growth and development, promotion of an early onset of sexual maturity, among others, and that the rigours of such waters impose an increased demand for oxygen on benthic organisms. By decreasing their effective surface area these organisms can decrease their total oxygen consumption and therefore function more efficiently. This reduction in size also serves as an adaptation to facilitate the osmo-regulation of internal body chemistry due to salinity fluctuations.

The relative morphological simplicity of the trace fossils such as the ones illustrated in Figures 4 to 9 reflects the non-specialised feeding strategies employed by the trace-making community. Such organisms are opportunistic in nature and display r-selected strategies in population dynamics. Opportunistic organisms flourish in areas of high physiological stress, such as brackish-water settings, where animal communities are not resource limited (Levington, 1970; Grassle & Grassle, 1974). Opportunistic or r-selected organisms are characterised by rapid reproduction and growth rates, small body size, short life cycles, broad environmental tolerances and non-specialised feeding strategies (Levington, 1970; Jones, 1981; Ekdale, 1985). Such organisms are particularly well adapted to high stress and/or low-resource environments (Ekdale, 1985).

6. Conclusions

Miocene deposits within the Greater Ughelli, Central Swamp and Coastal Swamp depobelts are characterised by several well-developed, recurring brackish-water ichnoassociations that occur in a monotonous and systematic manner. Many of these ichnoassociations are typified by a mixture of simple, horizontal and vertical structures common to both the *Skolithos* and *Cruziana* ichnofacies. This manifestation has been described from intertidal deposits from the Lower Palaeozoic onwards.

Twelve ichnogenera (*Asterosoma*, *Bergaueria*, *Chondrites*, *Gyrolithes*, *Thalassinoides*, *Lockeia*, *Palaeophycus*, ?*Conichnus, Planolites*, *Siphonichnus*, *Skolithos* and *Diplocraterion*) have been recognised along with bioturbated textures, escape structures and non-descript, passively filled shafts. These ichnogenera were grouped in six distinct ichnoassociations: (1) *Gyrolithes-Chondrites*, (2) *Planolites*, (3) *Skolithos*, (4) *Palaeophycus*, (5) *Asterosoma* and (6) *Thalassinoides*.

Within the Greater Ughelli depobelt (well 1) the following ichnoassociations have been noted: *Planolites*, *Skolithos* and *Asterosoma*. In the Central Swamp depobelt (well 2) the *Planolites* and *Palaeophycus* ichnoassociations have been identified, while the Coastal Swamp depobelt (well 3) is characterised by the *Gyrolithes-Chondrites*, *Skolithos* and *Thalassinoides* ichnoassociations.

In addition to the *Thalassinoides* and *Palaeophycus* ichnoassociations, which are more fully marine, all other ichnoassociations typify brackish-marine settings.

The overall degree of bioturbation and trace fossil diversity are low.

Although many ichnogenera present have been recognised in lower shoreface and offshore settings, the low diversity (and in some cases monospecific nature), the occurrence of sideritic concretion or stains and the low degree of bioturbation indicate a nearshore, restricted environment. The presence of carbonaceous debris within the facies supports this interpretation.

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