SPECIFIC FREQUENCY AND ENVIRONMENTAL INDICATORS IN TWO HORIZONS OF THE CALCAIRE DE FERQUES (UPPER DEVONIAN), NORTHERN FRANCE

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ABSTRACT. Statistical examination of the fauna from two horizons in the Calcaire de Ferques (Frasnian) of northern France, combined with thin section studies and field observations, lead to the conclusion that while the fauna of the lowest bed of the formation suffered slight transportation, this did not disrupt the ecological associations of the fauna and a true life assemblage is represented. The fauna of the upper beds accumulated in situ in an environment with a gradually increasing argillaceous content, and shows features which may be associated with these deteriorating conditions and with the level of background radioactivity.

THE Calcaire de Ferques is a highly fossiliferous bioclastic limestone, world-famous for its rich and varied fauna, which includes topotypes of many well-known species such as *Cyrtospirifer verneuili*. It outcrops only in the Palaeozoic inlier of the Boulonnais, northern France (text-fig. 1), the geology and palaeoenvironments of which have been redescribed by Ager and Wallace (1967).

The Calcaire de Ferques has been intensively studied in the last hundred years, notably by Robinson (1920) and by Pruvost and Pringle (1924). It was given its name by de Verneuil (1838), who compared its fauna with that of the Wenlock Limestone, which it closely resembles both in faunal groupings and in mode of preservation. However, Murchison (1840) referred it to the newly erected Devonian System. It was correlated with the Calcaire de Givet, the type of the Givetian stage, by Godwin Austen (1853), but Gosselet (1860) compared it to the Calcaire de Rhisnes, which was included by d'Halloy (1862) in his newly erected Frasnian stage.

No further modifications of its stratigraphical age have been published, but it must be considered to be of Middle Frasnian age since both the underlying Schistes de Beaulieu and the overlying Schistes de Fiennes lie within this substage.

Until the end of the last war, the limestone was extensively worked in a series of small quarries strung out along the outcrop. The degree of exposure is excellent at the time of writing, but is deteriorating rapidly because many of the smaller quarries are being infilled with overburden from the more extensively worked Carboniferous Limestone nearby. The majority of the quarries terminate along the strike at one of the numerous small dextral wrench faults which dissect the area (Wallace 1968) and which are well exhibited in the largest quarry, La Parisienne at Beaulieu (text-fig. 1).

The palaeoenvironments of the main part of the Calcaire de Ferques and the palaeoecological relationships of its fauna are discussed in detail by the author elsewhere (Wallace, in press). They may be summarized as follows: a succession of environments of rapidly increasing and then gradually decreasing depth, passing from the *Zones Subturbulente* and *Turbulente* of Lecompte (1961) to deeper, quieter, open shelf conditions with the formation of brachiopod and coral-bearing calcilutites in the middle

part of the formation. The upper part of the formation shows a gradually shallowing sequence with increasing terrigenous material. No previous account, however, has attempted to discuss the environment as it changed from the hypersaline lagoons of the Schistes de Beaulieu into the biostromes of the Calcaire de Ferques, or from the latter into the subtidal mudflats of the overlying Schistes de Fiennes.

A neglected truism about quarry geology is that the most interesting features in any quarry are at the top and bottom of the working faces. This is logical, since the excavation normally ceases where the character of the rock changes. It is especially true in
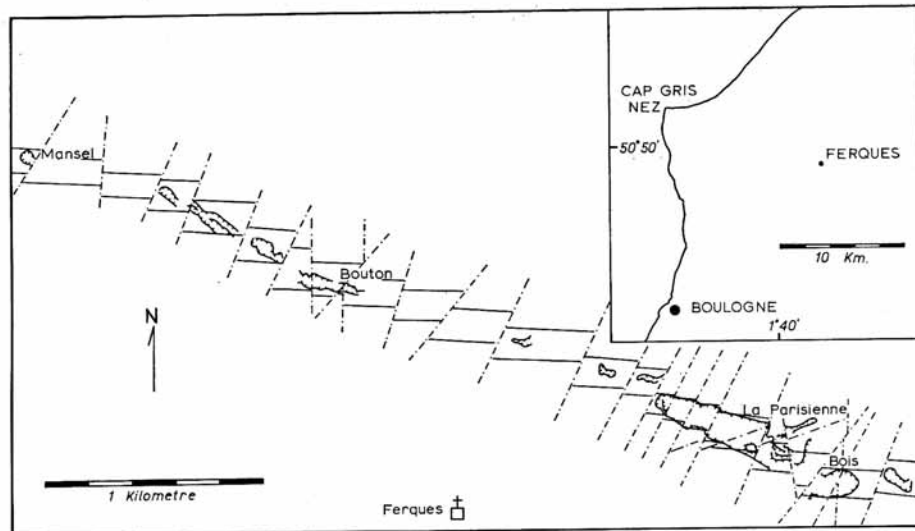
TEXT-FIG. 1. Locality map of quarries in the Calcaire de Ferques, showing the outcrop of the limestone and the position of the dextral wrench faults which displace the formation.

the numerous quarries of the Calcaire de Ferques, where only the main part of the limestone is massive. The formation dips at about 30°, and huge bedding planes of the Thin Basal Limestone are exposed in every quarry, providing the large amounts of data which are considered statistically here. Similarly, the argillaceous nature of the Upper Beds of the limestone makes them unsuitable for quarrying. They are well exposed along the southern faces of many of the quarries, where extensive collections have been made.

Although the main part of the limestone is well exposed in one or two quarries, notably Carrière du Bois, so that a general impression of the succession of environments may be obtained (Wallace, in press, text-fig. 13), only dip sections are available. That, and the more massive nature of the rock, make statistically reliable collections and observations unobtainable.

THIN BASAL LIMESTONE

The basal bed and earliest development of limestone within the Calcaire de Ferques is the Thin Basal Limestone, 2 cm. thick, resting on the dolomitic sand facies of the

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Dolomie de Fiennes and overlain by a moderately fossiliferous sandy dolomite (Ager and Wallace 1967, bottom of fig. 2). The limestone itself has a red or grey calcilutite matrix, rich in bioclastic fragments, and contains an extremely abundant and diverse fauna. Dolomitization affects both the upper and lower surfaces of the bed, but rarely alters it completely. The fauna is completely unaffected. Iron enrichment commonly accompanies the dolomitization; many of the dolomite rhombs are zoned, and the upper and lower bedding surfaces are commonly dark red.

The population structure of the Thin Basal Limestone is shown in text-fig. 2. In both this histogram and the similar one for the Upper Beds (text-fig. 4) the population is expressed as percentage of sample rather than in absolute figures. Although it is realized that ideally for comparison the population should be expressed in terms of standard quadrats, this was not possible because of difficulties in the field, especially with the Upper Beds. Instead a faunal census was taken for each locality. To eliminate observation and collection bias, the accuracy of this census was checked in two ways. First, the assistance of two other people, one a geologist and the other a non-geologist in the field for the first time, was enlisted. Although the size of the collections varied, the proportions between the various species collected by the author and her two assistants remained remarkably constant. Secondly, a bulk sample from the exposed surface of the Thin Basal Limestone was analysed. Again the proportions between the species corresponded closely to those in the collections made by hand. Therefore it is considered that the faunal censuses represent a valid sample of the population.

Numerically, by far the most dominant species in the Thin Basal Limestone is *Cyrtospirifer verneuili*, which consistently forms about 40% of the sample. All growth stages are present. There is considerable size and shape variation within the species and it might be possible to erect up to a dozen nominal species for this horizon alone. All these 'species' intergrade, however, and both Gosselet (1894) and Vandercammen (1959), in statistical studies of the species from the Boulonnais and Belgium respectively, concluded that only one species was present.

Athyris concentrica is rather more common in the west of the outcrop than in the east, where its place seems to be taken by *Productella subaculeata*. This latter species, with its very delicate spines, might suggest that water conditions were rather quieter in the east than in the west, although flume experiments (Ferguson, pers. comm.) suggest that spiny productids may have been adapted to regimes with moderately strong uni-directional currents. Corals are relatively rare within the Thin Basal Limestone itself, although they occur abundantly within the dolomitic sand immediately below. Bryozoans may be more common than suggested by the histogram (text-fig. 2), but their delicate nature makes fragmentation almost inevitable, and hence counting difficult. For that reason, only their presence has been indicated and the percentages shown are not a true representation of abundance.

Even cursory examination of the histogram (text-fig. 2) shows some basic associations between species. For example, (*a*) where spiriferids and athyrids are abundant, corals are virtually absent; (*b*) there is an inverse relationship between *Cyrtospirifer* and *Athyris*; (*c*) where corals are abundant, athyrids and rhynchonellids are low, (*d*) where productellids are low there is a low specific diversity. The χ^2 test was used to test these and all other relationships in the bed. The test was applied $\sum_1^{n-1} n$ times where n = number of recognized species or species groups. Thus not only was each individually
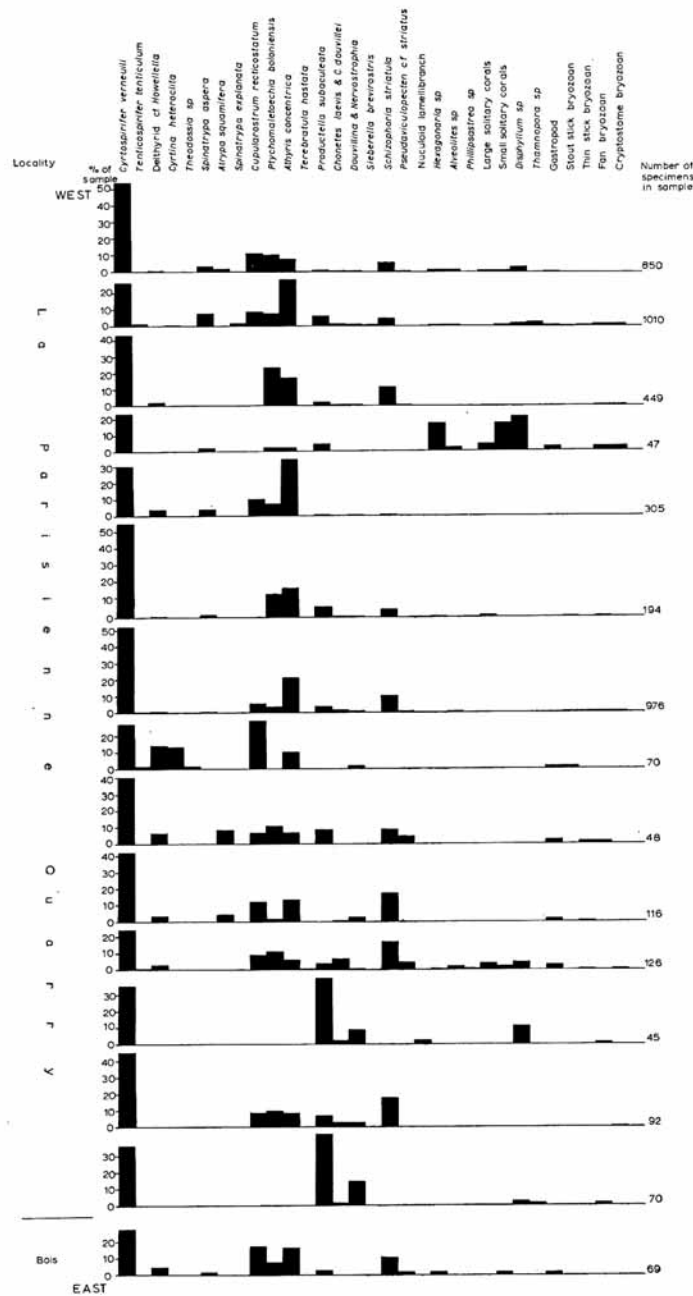
TEXT-FIG. 2. Histogram of the population structure in the Thin Basal Limestone, Calcaire de Ferques. Values are expressed as percentage of the assemblage, rather than as absolute figures, for ease of comparison. Epifaunas and minor elements omitted. Localities are in order along the strike, not in a stratigraphic succession.

listed species considered, but also certain basic groups such as spiriferids, rhynchonellids, cerioid corals, solitary corals and stick bryozoans. This brought n to 37, and hence the number of tests to nearly 600. Of these relationships, 47 were significant to a 10% level, 25 to a 5% level (the level most usually applied by modern ecologists according to Kershaw (1966) and accepted as valid by Johnson (1962)) and 3 were significant to less than 0·01%, a very high level of significance indeed. It was considered useful to include levels higher than 5% (i.e. $p = 0·05$) in both tables and figures, since this demonstrates associations and linkages which can be subjectively observed in the field both in this region and in other Devonian areas, but it should be noted that their statistical significance is small.

The results of the χ^2 test are summarized in Table 1. They show a close correlation between all types of coral, especially *Hexagonaria* and the solitary corals. Corals are also fairly strongly associated with other species; for example *Spinatrypa aspera* and (less strongly) *Ptychomaletoechia boloniensis* with the cerioid forms; and gastropods, *Tenticospirifer tenticulum* and *S. aspera* with the solitary forms. *Cyrtospirifer* shows a negative correlation with both cerioid and solitary forms when it is present in proportions greater that 30%, which was observed from casual inspection of the histogram, but the converse association, that of high (>30%) *Athyris concentrica* with corals is not justified statistically, although the inverse relationship between *Athyris* and *Cyrtospirifer* is significant to $p = 0·07$.

Some of the associations, such as *Chonetes* with *Douvillina* and *Nervostrophia*, might have been expected since the forms concerned were probably adapted to rather similar environments. Close associations also appear to exist between other brachiopods, such as the rhynchonellids (both *Ptychomaletoechia* and *Cupularostrum*), *Athyris*, delthyrids, *Schizophoria*, and *Spinatrypa*, and these are also associated with gastropods and *Pseudaviculopecten*. Since *Cyrtospirifer* occurs in every collection, it is difficult to prove a statistically valid association between it and the other brachiopods, but logically this association (which may be only a tolerance of similar conditions) can be seen to exist.

Negative associations, from which one might possibly deduce some antipathy or intolerance of similar conditions, occur between *Cyrtospirifer* (when present in very high proportions) and gastropods, and between strophomenids and gastropods. A general negative correlation also occurs between the spiriferid group and the coral group; it is exhibited by *Cyrtospirifer*/*Hexagonaria*, *Cyrtospirifer*/massive corals, *Cyrtospirifer*/solitary corals, *Tenticospirifer*/*Alveolites* and delthyrids/*Disphyllum*.

Text-fig. 3 is a constellation diagram of the positive associations in the Thin Basal Limestone. The strongest associations are between the two major coral groups, the solitary and the massive corals, with a weak association with phaceloid forms. This plexus is linked more loosely with the *Cyrtospirifer*/*Athyris* association of brachiopods and with gastropods. Very loose links occur with the remainder of the brachiopods, the pectinids and the stick bryozoans, which form a separate plexus centred round a strong association of *Ptychomaletoechia* with *Schizophoria*. A strong link exists between *Chonetes* and the strophomenids, but the strophomenids are negatively associated with several other members of both plexuses, and this association, although positive in itself, is probably not related to the main constellation.

The only major species which shows no statistically significant association with any

TABLE 1

Significant associations in the Thin Basal Limestone, as proved by the χ^2 test.

Sign	P	Association	Sign	P	Association
+ve	0·001	Hexagonaria/solitary corals	−ve	0·08	Delthyrid/Disphyllum
+ve	0·001	Massive corals/solitary corals	+ve	0·08	Cupularostrum/Ptychomaletoechia
+ve	0·001	Hexagonaria/small solitary corals	+ve	0·09	Hexagonaria/Disphyllum
+ve	0·002	Ptychomaletoechia/Schizophoria	−ve	0·09	Schizophoria/Disphyllum
+ve	0·005	Hexagonaria/large solitary corals	+ve	0·10	Tenticospirifer/Cupularostrum
+ve	0·005	Spinatrypa aspera/massive corals	−ve	0·10	Rhynchonellids/Disphyllum
+ve	0·006	Chonetes/strophomenids	+ve	0·10	Rhynchonellids/gastropod
+ve	0·007	Alveolites/small solitary corals	−ve	0·10	Strophomenids/solitary corals
+ve	0·01	Cyrtospirifer < 30%/gastropod	+ve	0·10	Hexagonaria/gastropod
+ve	0·01	Small solitary corals/gastropod	+ve	0·10	Large solitary corals/Disphyllum
+ve	0·01	Rhynchonellids/Schizophoria	+ve	0·11	Solitary corals/Disphyllum
−ve	0·015	Tenticospirifer/stick bryozoans	−ve	0·11	Productella/stick bryozoans
+ve	0·02	Tenticospirifer/solitary corals	+ve	0·12	Cyrtospirifer > 30%/Chonetes
+ve	0·02	Cyrtospirifer < 30%/Hexagonaria	−ve	0·12	Cyrtospirifer > 30%/Alveolites
+ve	0·03	Alveolites/Disphyllum	−ve	0·13	Spinatrypa/Chonetes
+ve	0·03	Athyris > 10%/Schizophoria	−ve	0·13	Atrypa squamifera/Athyris < 10%
+ve	0·03	Hexagonaria/Alveolites	+ve	0·15	Alveolites/gastropod
+ve	0·03	Alveolites/large solitary corals	−ve	0·15	Chonetes/gastropod
+ve	0·03	Delthyrid/Pseudaviculopecten	+ve	0·15	Cupularostrum/stick bryozoans
+ve	0·03	Delthyrid/Schizophoria	+ve	0·15	Rhynchonellids/stick bryozoans
+ve	0·03	Delthyrid/rhynchonellids	+ve	0·15	Delthyrid/Athyris > 10%
+ve	0·03	Cyrtospirifer < 30%/solitary corals	−ve	0·15	Delthyrid/Atrypa squamifera
−ve	0·03	Tenticospirifer/Alveolites	−ve	0·15	Delthyrid/Cupularostrum
+ve	0·04	Large solitary corals/small solitary corals	+ve	0·16	Spinatrypa/Productella
+ve	0·06	Cupularostrum/Schizophoria	+ve	0·17	Rhynchonellids/Athyris > 10%
+ve	0·06	Delthyrids/stick bryozoans	+ve	0·17	Cyrtospirifer > 30%/strophomenids
+ve	0·07	Cupularostrum/gastropod	+ve	0·18	Delthyrid/Ptychomaletoechia
−ve	0·07	Ptychomaletoechia/Athyris > 10%	−ve	0·18	Productella/gastropod
+ve	0·07	Ptychomaletoechia/massive corals	+ve	0·18	Rhynchonellids/massive corals
−ve	0·07	Strophomenids/gastropod	+ve	0·19	Massive corals/gastropod
+ve	0·07	Schizophoria/Pseudaviculopecten	+ve	0·19	Atrypa squamifera/Cupularostrum
+ve	0·07	Spinatrypa/Ptychomaletoechia	+ve	0·20	Athyris > 10%/massive corals
+ve	0·07	Spinatrypa/solitary corals	−ve	0·20	Athyris > 10%/gastropod
+ve	0·07	Atrypa squamifera/gastropod	+ve	0·20	Solitary corals/gastropod
+ve	0·07	Cyrtospirifer < 30%/Athyris > 30%	+ve	0·20	Atrypids/rhynchonellids
+ve	0·08	Cyrtospirifer < 30%/massive corals			
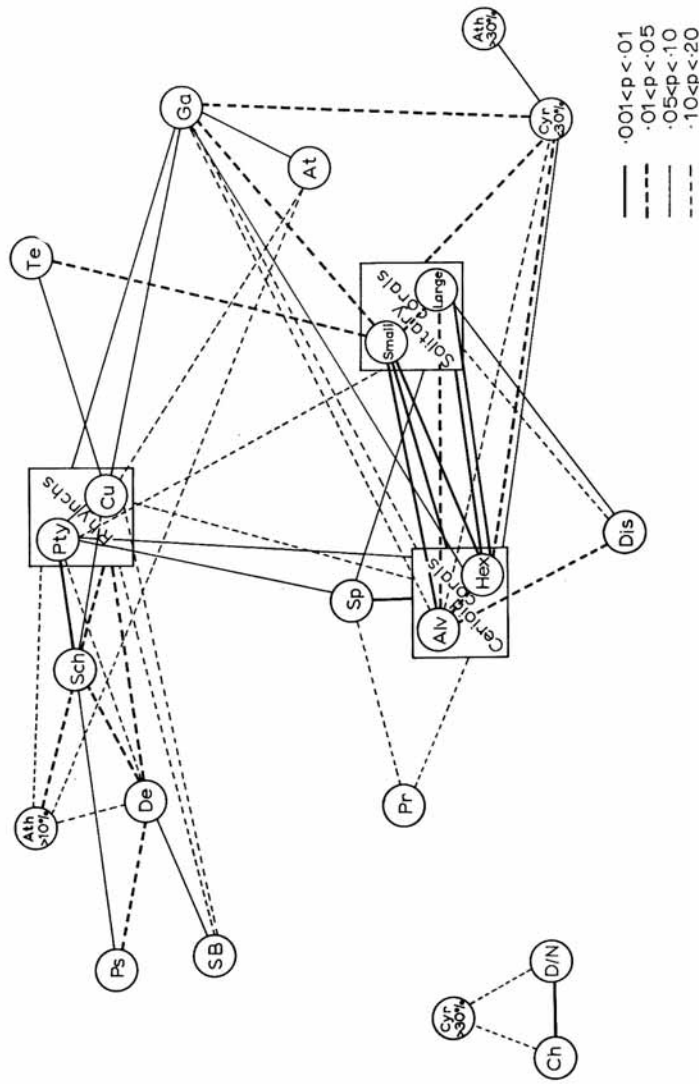
TEXT-FIG. 3. Constellation diagram of positive associations in the Thin Basal Limestone, Calcaire de Ferques. Data drawn from Table 1. Levels of *p* above 0·05 are of little statistical significance, but are included here to indicate the grouping of associations. There is no significance other than draughting convenience in the relative distances of the various elements. Alv, *Alveolites*; At, *Atrypa*; Ath, *Athyris*; Ch, *Chonetes*; Cu, *Cupularostrum*; Cyr, *Cyrtospirifer*; De, Delthyrid; Dis, *Disphyllum*; D/N, *Douvillina/Nervostrophia*; Ga, Gastropod; Hex, *Hexagonaria*; Pr, *Productella*; Ps, *Pseudaviculopecten*; Pty, *Ptychomaletoechia*; Sch, *Schizophoria*; Sp, *Spinatrypa*; SB, Stick Bryozoans; Te, *Tenticospirifer*.

other is *Productella subaculeata*. Its strongest association is with *S. aspera* (positive with $p = 0.16$). The general trend of its associations shows that it would form part of the coral plexus, linked more loosely to the massive forms than to the solitary forms.

Epifaunal encrustation is moderately common at this horizon, the brachiopods particularly being affected. About 10% of individuals of *Cyrtospirifer verneuili* and a rather smaller proportion of *A. concentrica* are affected. The most common organism, and often apparently the first to arrive, was *Spirorbis*. *Aulopora* frequently encrusts the fold of the brachial valve of the spiriferids, though it also occurs on the wings. Other epifaunal elements, such as the encrusting bryozoans *Hederella* and *Paleschara*, are rarer. These encrustations are similar to those observed by Ager (1961) on *Spinocyrtia* from the Devonian of Iowa.

Thin-section studies permit close examination of matrix relationships, especially those of the broken shells and bioclastic fragments (Pl. 70, fig. 2; text-fig. 5). Separated brachiopod valves fell concave downwards in the biocalcarenitic matrix, often leaving an 'umbrella structure' of space beneath them. These spaces were colonized by *Girvanella*-like algae, which also acted as a cement for the matrix. The overturned shells and shelly sand provided a protected environment for the algal colonies and would also have shielded them from excessive light. Seneš (1967) has found that most Recent algae in the Mediterranean (although not directly comparable to *Girvanella*, whose affinities are uncertain) cannot tolerate more than 70% luminosity and many prefer much less, often living beneath overhanging ledges or amongst rocks and sand-grade sediment. After the growth of the algae beneath the shells, burial and lithification, drusy growth of calcite filled the remainder of the cavity. Subsequently dolomitising fluids attacked both the upper and lower surfaces of the bed.

The highly broken nature of much of the shell debris suggests forceful comminution, either by waves or by scavenging organisms, but the algae show that once deposited, the bed remained undisturbed until lithification. It is thus possible that the bed was formed in rather deeper water than suggested by the comminution of the shell debris, perhaps by the action of a single storm, dumping shell debris and whole shells in an alien environment,

The size frequency histograms of the main species of brachiopods (text-fig. 6) mainly show a normal bell-shaped distribution, which according to Boucot (1953) suggests post-mortem transport and sorting of the assemblages. Other features which suggest transported assemblages are the absence of juvenile rhynchonellids, and the remarkable correlation of endpoints of three of the species, and of the main size peak in all four species at 1·1 or 1·2 cm. length. It is most unlikely that all four species would achieve mature shell sizes to within 1 mm. of each other, but size sorting of this kind might be expected in a transported assemblage. The frequency of all species tails off at 1·5–1·7 cm., again a remarkable correlation, though it should be noted that the spiriferids show a small peak of larger individuals.

UPPER BEDS

The Upper Beds of the Calcaire de Ferques, varying in thickness from c. 8–10 m. are noticeably richer in argillaceous material than the underlying bulk of the limestone, and pass gradually into the shales of the overlying Schistes de Fiennes. The fossils, although of species similar to or identical with those in the main part of the limestone,

are markedly bigger, especially those species of brachiopod presumably attached by a pedicle during life.

The first large individuals to occur are preserved in a matrix of grey bioclastic calcilutite very similar to that of the main part of the formation, but the argillaceous content of this calcilutite increases rapidly upwards. The fauna within the calcilutite is very well preserved; for example, atrypids still have their spires and very delicate fringe of lamellose growth lines undamaged (Pl. 70, fig. 1; text-fig. 4).

Some incipient dolomitisation is present; the proportion increases towards the top of the formation. Limonitic zoning within the rhombs is frequent, but there is little iron staining within the rock as a whole, and no iron sulphide is present. The uppermost limestones are greenish-grey (5 GY 6/1) in colour and frequently have a sandy appearance because of the numerous rhombs of dolomite on their surfaces. They are interbedded with greenish-grey shales.

Although the fossils are the largest within the formation, the fauna is the least diverse, and epifaunal encrustation similar in species and position to that in the Thin Basal Limestone is common.

Pathologically deformed specimens of both spiriferids and atrypids form a surprisingly large proportion of the assemblages, often up to 10%. Deformation usually took place at a growth-line, and consists either of invagination of both valves or, in the case of the spiriferids, of a marked branching of the ribs on the wings.

The population structure of the Upper Beds is shown in text-fig. 7. As with the Thin Basal Limestone, visual inspection indicates an inverse relationship between *Cyrtospirifer* and *Athyris*. Where *C. verneuili* forms a dominant (i.e. >30%) part of the sample, and especially where this is supported by the presence of other spiriferids, the proportion of *Athyris concentrica* is markedly lower. It can be seen from Table 2 that the number of significant associations in the Upper Beds is considerably lower than in the Thin Basal Limestone, largely as a result of the greatly diminished diversity of the former. Many of the most important members of the assemblage still remain, and this diminished diversity has been achieved at the expense of elements such as bryozoa and some of the less-abundant brachiopods. The constellation diagram (text-fig. 8) shows rather different groupings from those of the Thin Basal Limestone, with a plexus based on a strong

TEXT-FIG. 4. Diagram of the main features of the photomicrograph shown in Plate 70, fig. 1. An atrypid brachiopod is in presumed position of life. The shell structure can be clearly seen, and the position of the frills and small pieces broken from them show that the shell has been undisturbed since death, and was probably killed by burial. Geopetal sedimentation within the shell indicates the horizontal: it can be seen that more sediment entered through the anterior commissure and piled up against the first spire. The spires have moved from their position during life, possibly owing to internal decay of the soft parts. They are surrounded by an oval shadow which may represent the final position of some of the soft parts. Drusy crystalline calcite fills the upper part of the shell.

TEXT-FIG. 5. Diagram of the main features of the photomicrograph shown in Plate 70, fig. 2. Separated valves of brachiopods, convex up, in a bioclastic, calcarenitic matrix, have left umbrella-shaped sheltered spaces beneath. The large shell covers a gastropod with an open umbilicus. *Girvanella*-type algae grew in the enclosed spaces, carpeting the sheltered bottom and filling the body-chamber of the gastropod. The remaining space beneath the shell was subsequently filled with drusy crystalline calcite. Dolomitisation attacked the upper and lower surfaces of the bed: the iron-enriched rhombs form dark patches on the photomicrograph. Large-zoned rhombs grew in the inner chambers of the gastropod. The shell structure of the brachiopod shells (probably atrypids) is clearly visible.
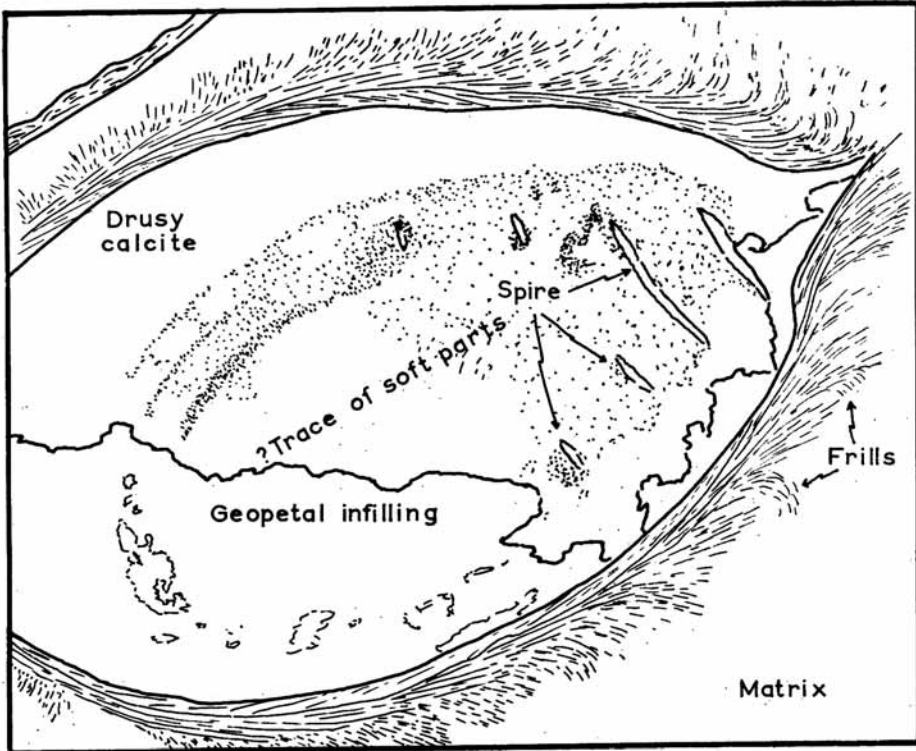
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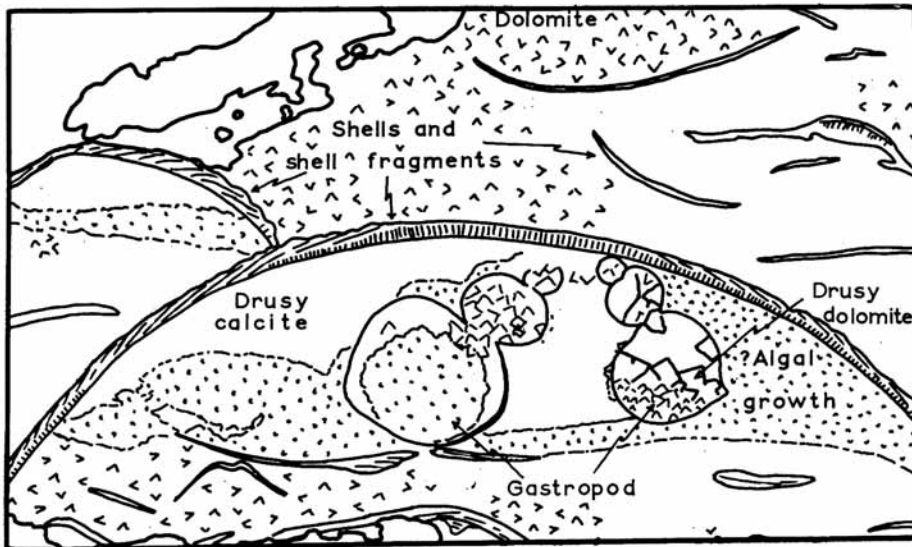
TEXT-FIG. 5

inverse link between *Cyrtospirifer* and *Athyris* very loosely linked to a coral/rhynchonel-lid/*Schizophoria*/strophomenid plexus. These links are considerably less strong than those of the Thin Basal Limestone, but the relationships between species are similarly oriented, i.e. a species does not change the nature of its relationship with another species from bed to bed, but only the strength of the relationship.

Other associations and occurrences may be noted from the histogram, such as the presence of fan bryozoans at the eastern end of the outcrop only, and of stick bryozoans only in the west. It may be noted that gastropods are more important than they were in the Thin Basal Limestone.

ECOLOGICAL DEDUCTIONS

The environments in which the earliest and latest beds of the Calcaire de Ferques were laid down were clearly very different, although both fall within the broad classification of 'shelf biostrome'.

The Thin Basal Limestone consists of an assemblage of very well-preserved whole fossils in a coarsely bioclastic matrix. It may well be that much of the comminution of the shell debris was achieved by scavengers turning over the sediment in their search for food, rather than by current or wave action. All the fauna (with the possible exception of the nuculoid lamellibranch found at one locality only) is epibiontic, most are suspension feeders and many are attached forms, which may suggest that this was a firm bottom fauna. The author considers it more probable, however, that the original sea floor was covered by a layer of bioclastic debris, since in all species where one may see an attachment area (such as both solitary and cerioid corals, and exceptionally *Schuchertella*), the attachment areas show moulds of shell ornament, either spiriferid, strophomenid, or schizophorid, or show evidence of attachment to other bioclastic debris, such as crinoid ossicles. No evidence is found of forms attached to a substrate such as a rocky sea floor.

Although the bell-shaped curves of the size frequency diagrams suggest a transported fauna, the fact that χ^2 tests show significant associations between species argues against extensive transportation, as does the unabraded nature of all members of the assemblage The presence of *in situ* algae beneath overturned shells suggests very little reworking of the bed. There are three possible solutions of this apparent incompatability:

(*a*) The curves may not be truly bell-shaped;
(*b*) The curves are bell-shaped, but true life associations are still represented;
(*c*) The associations proved by the χ^2 test may be mechanical rather than ecological.

Thus if the faunal associations are significant ecological associations, it must be concluded that bell-shaped curves may occur in biocoenoses as well as in thanato-coenoses, as suggested by Hallam (1967). Moreover, it may be deduced from the work
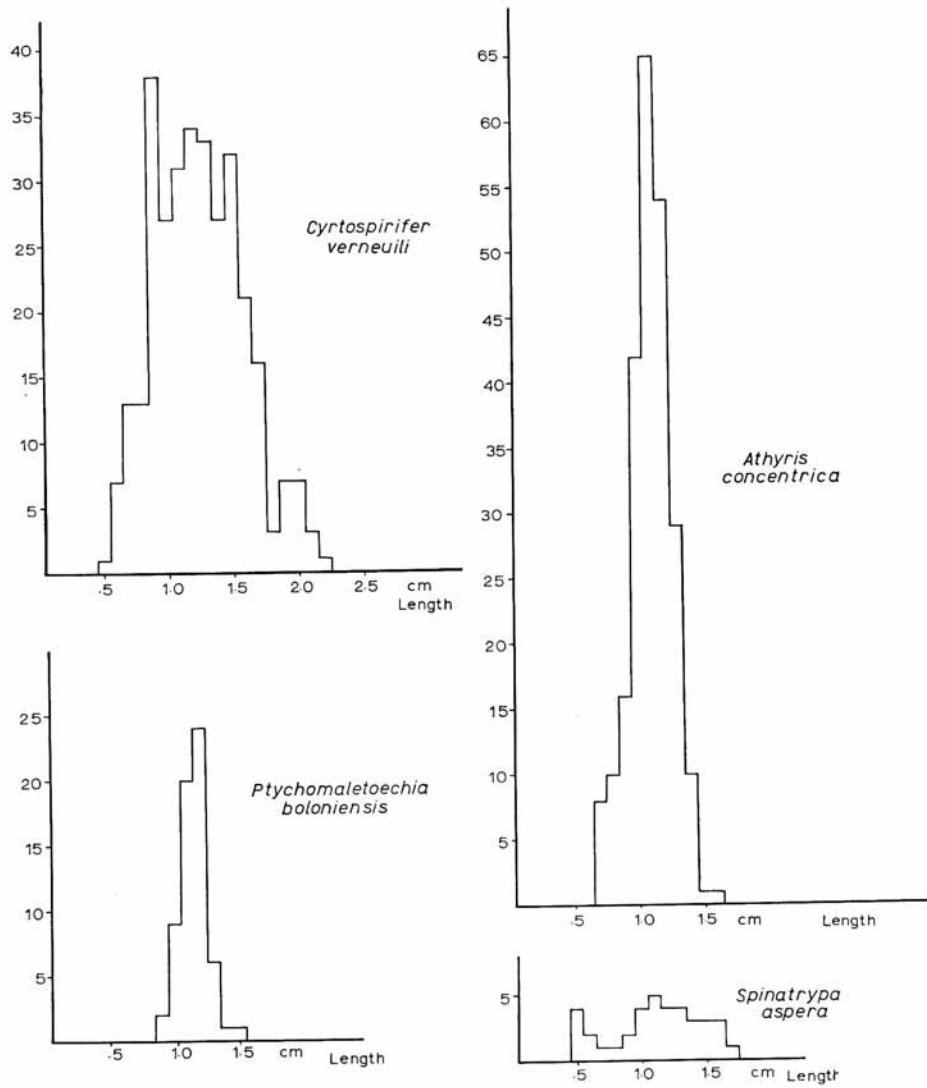
EXPLANATION OF PLATE 70

Fig. 1. Photomicrograph of a vertical section through the Upper Beds, Calcaire de Ferques; ×10, (see text-fig. 4).

Fig. 2. Photomicrograph of a vertical section through the Thin Basal Limestone, Calcaire de Ferques; ×7·5, (see text-fig. 5).
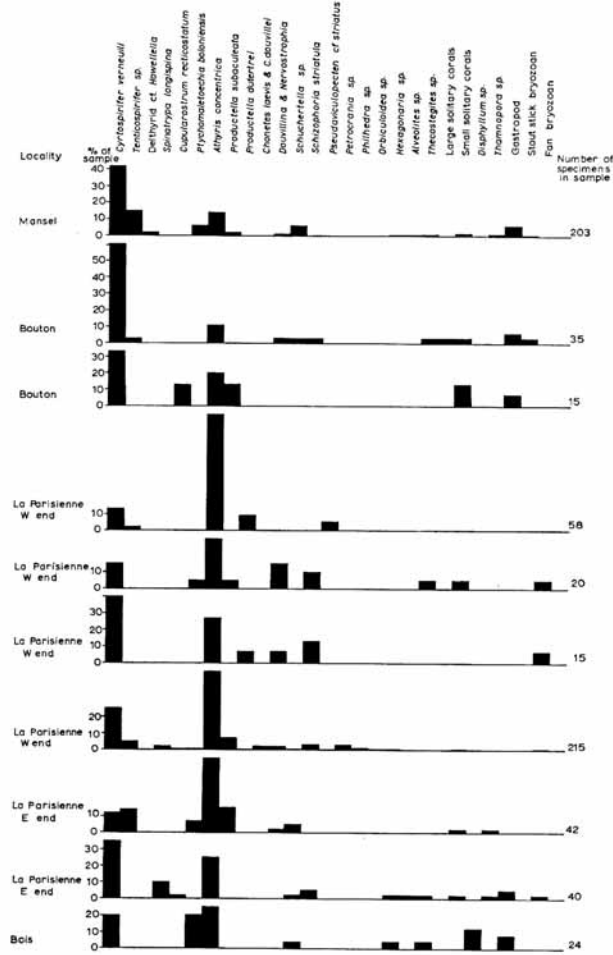
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TEXT-FIG. 6. Size-frequency histograms of the main brachiopod species from a single locality in the Thin Basal Limestone at Carrière de La Parisienne.

TEXT-FIG. 7. Histogram of the population structure of the Upper Beds of the
Calcaire de Ferques. Values expressed as in text-fig. 2.

of Middlemiss (1962) that extensive transportation would cause almost complete
destruction of brachiopod shells. This is confirmed by many workers on Recent faunas,
especially on molluscs (Schäfer 1962, Holme 1961, and Johnson 1965). Thus it may be
concluded that if the assemblage has been transported, it was only over a very short
distance and had little disruptive effect on associations. Hence the fauna is still representa-
tive of a life assemblage.

It is suggested that the fauna lived and accumulated in water of shallow to moderate
depth (i.e. below wave base but not greater than 10 fathoms). A catastrophic event such

as a storm subsequently transported both fauna and matrix to its present position where it was not subject to currents and was quickly cemented, first by algae and then by crystalline calcite. This interpretation is supported by the field relationships of the bed. It is thin and developed only relatively locally, being confined to the eastern end of the outcrop. It immediately overlies a formation whose environment of deposition has been interpreted as lagoonal (Wallace, in press), the uppermost beds of which are a black and yellow sandy dolomite containing branching stromatoporoids, a facies interpreted by Lecompte (personal communication) as 'sub-lagoonal'. This facies in fact occurs

TABLE 2.

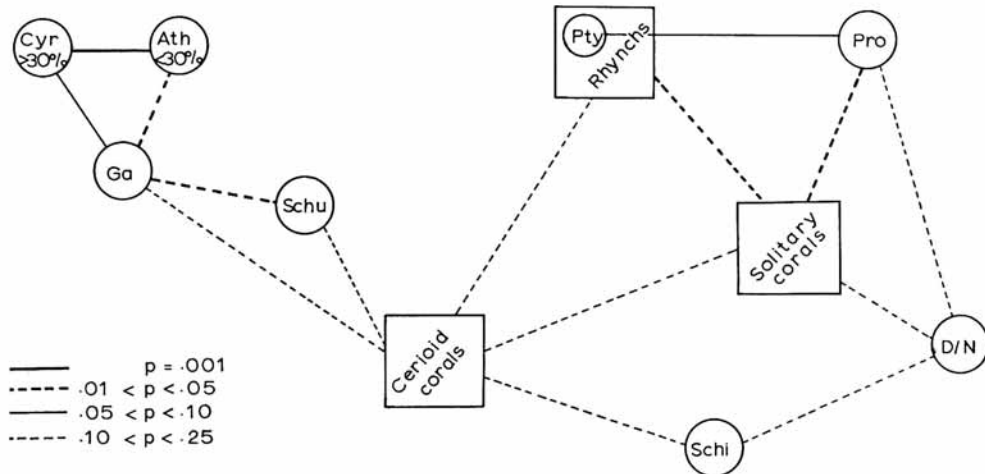Significant associations in the Upper Beds, as proved by the χ^2 test.

p		
0·001	+ve	*Cyrtospirifer* > 30%/*Athyris* < 30%
0·01	+ve	Gastropod/*Athyris* < 30%
0·01	+ve	*Schizophoria*/fan bryozoan
0·015	+ve	Rhynchonellids/solitary corals
0·04	+ve	Solitary corals/*Productella subaculeata*
0·05	+ve	*Schuchertella*/gastropod
0·06	+ve	Gastropod/*Cyrtospirifer* > 30%
0·06	+ve	*Ptychomaletoechia*/*Productella subaculeata*
0·10	−ve	*Schuchertella*/*Schizophoria*
0·20	+ve	*Tenticospirifer*/strophomenids
0·20	+ve	*Productella subaculeata*/strophomenids
0·20	+ve	*Schizophoria*/strophomenids
0·20	+ve	*Schuchertella*/massive corals
0·20	+ve	*Schizophoria*/massive corals
0·20	−ve	Productids/gastropods

both below and immediately above the bed, leaving the anomalous situation of a thin limestone with a good marine fauna sandwiched between lagoonal, possibly strongly saline, dolomites. It would seem likely that the Thin Basal Limestone thus represents a marine association washed, perhaps by a sudden storm, into lagoons, which in a short time were themselves swamped by a sudden marine transgression which laid down the limestones of the main part of the Calcaire de Ferques.

The higher argillaceous content and lower bioclastic content of the Upper Beds of the limestone at once suggest a quieter, possibly deeper, environment of deposition than that of the main part of the limestone, but this initial impression may be erroneous since they pass up to shales and sandstones interpreted as the products of an intertidal (and just subtidal) environment (Wallace, in press). The excellent preservation of much of the fauna and especially that of the atrypid frills, however, indicates that little or no reworking of the sediment, either by currents or by burrowing organisms, took place, and that the environment was extremely quiet.

The increase in size of many of the species is most marked in those brachiopods which presumably were attached by a pedicle during life, and may be a response to the increased argillaceous content of the sediment. It is noticeable, however, that the size increase does not coincide exactly with the increase in clay content, but is first observed some metres below; thus the two may not be connected. These large brachiopods do not show the crowding of growth-lines near the anterior commissure usually considered as indicative of adulthood, a feature which is seen in smaller specimens from other parts

of this formation and from other formations in the area. Ager (1963, p. 142) has suggested that in exceptional circumstances 'gigantism' in fossils may be a result of delayed sexual maturity. This effect has also been observed in several living vertebrates, largely by inhibition of the action of the thyroid (Comfort 1965, pp. 85–6). It is interesting,

TEXT-FIG. 8. Constellation diagram of positive associations in the Upper Beds of the Calcaire de Ferques. Symbols as in text-fig. 3. Ath, *Athyris*; Cyr, *Cyrtospirifer*; D/N, *Douvillina/Nervostrophia*; Ga, Gastropod; Pro, *Productella subaculeata*; Pty, *Ptychomaletoechia*; Schi, *Schizophoria*; Schu, *Schuchertella*

therefore, that this gigantism occurs most markedly in those species which have a high proportion of pathologically deformed individuals. The two phenomena may be connected, possibly through an external influence such as increased background radio-activity affecting the genetic balance of certain species.

REFERENCES

AGER, D. V. 1961. The epifauna of a Devonian spiriferid. *Q. Jl geol. Soc. Lond.* **117**, 1–10.

—— 1963. *Principles of Paleoecology.* 371 pp. McGraw-Hill, New York.

—— and WALLACE, P. 1967. The environmental history of the Boulonnais, France. *Proc. Geol. Ass.* **77** (for 1966), 385–417.

BOUCOT, A. J. 1953. Life and death assemblages among fossils. *Am. J. Sci.* **251**, 25–40.

COMFORT, A. 1965. *The Process of Ageing.* 152 pp. Weidenfeld and Nicolson, London.

GODWIN-AUSTEN, R. A. 1853. On the series of Upper Palaeozoic groups in the Boulonnais. *Q. Jl geol. Soc. Lond.* **9**, 231–45.

GOSSELET, J. A. A. 1860. *Mémoire sur les terrains primaires de la Belgique des environs d'Avesnes et du Boulonnais.* 164 pp. Martinet, Paris.

—— 1894. Étude sur les variations du *Spirifer Verneuili. Mém. Soc. géol. N.* **4** (1), 61 pp., **7** pl.

HALLAM, A. 1967. The interpretation of size-frequency distributions in molluscan death assemblages. *Palaeontology,* **10**, 25–42.

HALLOY, D'O, D'. 1862. *Abrégé de géologie.* 7th edn.

HOLME, N. A. 1961. The bottom fauna of the English Channel. *J. mar. biol. Ass.* **41**, 397–461.

JOHNSON, R. G. 1962. Interspecific associations in Pennsylvanian fossil assemblages. *J. Geol.* **70**, 32–55.

—— 1965. Pelecypod death assemblages in Tomales Bay, California. *J. Paleont.* **39**, 32–55.

KERSHAW, K. A. 1966. *Quantitative and Dynamic Ecology.* 2nd edn., 183 pp. Edward Arnold, London.

LECOMPTE, M. 1961. Faciès marins et stratigraphie dans le Dévonien de la Belgique. *Annls Soc. géol. Belg.* **85**, B17–57.

MIDDLEMISS, F. A. 1962. Brachiopod ecology and Lower Greensand palaeogeography. *Palaeontology,* **5**, 253–67.

MURCHISON, R. I. 1840. Sur les roches dévoniennes du Boulonnais et des pays limitrophes. *Bull. Soc. géol. Fr.,* 1re sér., **11**, 229–57.

PRUVOST, P. and PRINGLE, J. 1924. A synopsis of the geology of the Boulonnais including a correlation of the Mesozoic rocks with those of England, with report of excursion. *Proc. Geol. Ass.* **35**, 29–67.

ROBINSON, J. W. D. 1920. The Devonian of Ferques (Lower Boulonnais). *Q. Jl geol. Soc. Lond.* **76**, 228–36.

SCHÄFER, W. 1962. *Actuo-Paläontologie nach Studien in der Nordsee.* 666 pp. W. Kramer, Frankfurt.

SENEŠ, J. 1967. Répartition bathymétrique des algues fossilisables en méditerranée. *Geol. Sb., Bratisl.,* **18**, 141–50.

VANDERCAMMEN, A. 1959. Essai d'étude statistique des *Cyrtospirifer* du Frasnien de la Belgique. *Mém. Inst. r. Sci. nat. Belg.* **145**, 1–175.

VERNEUIL, E. de. 1838. Note sur les terrains anciens du Bas-Boulonnais. *Bull. Soc. géol. Fr.,* 1re sér., **9**, 388–96.

WALLACE, P. 1968. The sub-Mesozoic palaeogeology and palaeogeography of northeast France and the Straits of Dover. *Palaeogeog., Palaeoclimatol., Palaeoecol.* **4**, 241–55.

—— (in press). The sedimentology and palaeoecology of the Devonian of the Ferques inlier, northern France. *Q. Jl geol. Soc. Lond.*

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