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ALVEOLITES PARVUS, TABULATE CORAL FROM UPPER DEVONIAN OF IRAN

Alveolites parvus, un tabulé du Dévonien Supérieur d'Iran

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(Plates XVII and XVIII)

Abstract. — Some tabulate corals samples of the family Alveolitidae, collected in different outcrops, Frasnian in age, of Iran, and only previously mentioned, are described in this paper for the first time. The quantitative and qualitative study of their morphological features allows to assign the material to *Alveolites parvus* Lecompte. Analysis of their external morphology allows various paleoecological comments. The presence of *A. parvus* in the Frasnian of Iran is entirely consistent with palaeobiogeographical data from other faunas.

Résumé. — *Des colonies d'Alveolitidae, provenant de différentes localités frasniennes d'Iran, au préalable uniquement citées, sont ici décrites pour la première fois. L'étude quantitative et qualitative de leurs caractéristiques morphologiques permet de les rattacher à Alveolites parvus Lecompte. L'analyse de la morphologie externe de ces colonies autorise un certain nombre de remarques paléoécologiques. La présence de ce taxon dans le Frasnien d'Iran confirme les conclusions paléobiogéographiques résultant de l'étude d'autres groupes de faunes.*

Resumen. — *Corales tabulados de la familia Alvelitidae, procedentes de diversos yacimientos del Frasniense de Irán, y que con anterioridad sólo habían sido citados, son descritos por primera vez en este trabajo. El estudio cualitativo y cuantitativo de sus rasgos morfológicos ha permitido asignar este material a Alveolites parvus Lecompte. El análisis de la forma externa de las colonias ha permitido realizar diversas inferencias paleoecológicas. La presencia de este taxón en el Frasniense de Irán está de acuerdo con datos paleobiogeográficos aportados por diversas faunas.*

I. — SHORT HISTORICAL REVIEW ABOUT *ALVEOLITES* IN DEVONIAN FROM IRAN

In Iran, Devonian outcrops have been pointed out and/or described by several authors. Relatively to northern and east-central Iran, Wendt *et al.* (1997) probably gave the best restatement of the question, with maps and lithological descriptions of various sections.

Whereas some groups of fossil invertebrate, such as brachiopods, have been studied in several papers devoted to the Devonian of Iran (Brice *et al*, 1971; Brice *et al.* 1974; Djafarian & Brice, 1973; Sartenaer 1966, 1968), tabulate corals, and particularly the Alveolitids which constitute a particularly common group during the Devonian times, have not yet been studied. Up to now, they have just been mentioned.

Golshani *et al.* (1972) cited *Alveolites* sp. in a reefal limestone with abundant stromatoporoids and corals from the Upper Devonian of Bidu River section, in Kerman area.

Sharkovski *et al.* (1984) pointed out the presence of *Alveolites* sp. and *A. parvus*, in the Bahram Formation, Middle-Late Devonian in age. This is apparently the only one specific citation of an Alveolitid in the Devonian of Iran, but without any description or systematic discussion.

Dastampour (1996) cited and illustrated an *Alveolites* sp. from the Late Devonian of the Gereek section, in Kerman area.

Wendt *et al.* (1997) quoted the genus *Alveolites* in the Bahram Formation at the Gerik (= Gereek) section, with a probable Upper Middle Devonian (Givetian ?) age.

The same authors also pointed out *Alveolites* near the bottom of the Bahram Formation, at the Hodjedk section, located just 12 km South of the Gerik section, but with a probable Lower Frasnian age.

Mistiaen (1999) mentioned *Alveolites* sp. associated with the stromatoporoid *Stictostroma brylkini*, in the Ab-bid section, Kerman area, in level belonging to the Brachiopod zone 6 (Brice, 1977) Lower to Middle Frasnian.

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Mistiaen *et al.* (2000) and Mistiaen and Gholamalian (2000) cited the genus *Alveolites* in the two biostromal horizons, Frasnian in age, sampled in the Koh-e Kaftar section, Chahriseh area.

Finally, in a preliminary study, Mistiaen and Fernández-Martínez (2001) cited *Alveolites parvus* in different Devonian outcrops of Iran. The present paper describes this material.

II. — MATERIAL, LOCALITIES AND STRATIGRAPHY

The Alveolitid Tabulate corals studied in the present paper (forty samples) come from different localities situated in the three following areas (fig. 1) : the Bidu area (Kerman Province), the Chahriseh area (Esfahan Province) and the Tabas area, in the Shotori Ranges (Khorasan Province). A.F. de Lapparent in the early 1970s, and D. Brice and B. Mistiaen in December 1998 collected this material that corresponds to the samples mentioned by Mistiaen (1999), Mistiaen and Gholamalian (2000), Mistiaen *et al.* (2000) and Mistiaen and Fernández-Martínez (2001).

1) **Bidu area** (Kerman Province)

The three following sections, Ab-Bid, Bidu, and Heruz sections, provided material with Alveolitids.

a) *Ab-Bid section*

Brice *et al.* (1999) shortly described this section, according to some unpublished observations by A.F. de Lapparent in 1973. Three specimens [I-AB.BR-1/1, 1/4 and 1/5] come from this section, collected in the biozone n° 6 of Brice 1977. This biozone, characterized by *Cyphoterorhynchus koraghensis*, *C. arpaensis*, *Uchtospirifer multiplicatus minor*, corresponds to Lower to Middle Frasnian age.

b) *Bidu River section*

This section was described by Golshani *et al* (1972) and some supplementary new data, based on unpublished field notes of A. F. de Lapparent, were presented by Brice *et al.* (1999). Twenty-one specimens were collected in this section; twelve [I-BR-1d/21, /22, /23 and I-BR-3A.71/13 to I-BR-3A.71/21] also from the biozone n° 6 of Brice 1977 and nine [I-BR-2.71/33 to I-BR-2.71/38; I-BR-2.71/40; I-BR-2.71/41 and I-BR-2.71/46] from a level just below this biozone.

c) *Heruz section*

This section corresponds to the Hodjedk section described by Wendt (1997). Five specimens (three badly preserved) were also collected in this section, near Hodjedk Mine, about 5 km South of Bidu. A probable Lower Frasnian age is attributed to the beds that provided samples. Because of the poor preservation, these specimens have not been used for the statistical analysis.

2) **Chahriseh area** (Esfahan Province). One site, the Kuh-e Kaftar section n° 2, provided some Alveolitid corals.

Kuh-e Kaftar section n° 2.

In the Kuh-e Kaftar, a section was previously described by Djafarian (1972) and by Djafarian and Brice (1973). More recently, in the Kuh-e Kaftar Mountains, two sections were described by Gholamalian (1997, 1998), Yazdi *et al* (1998), Gholamalian *et al.* (2000). The second one was visited during the IGCP 421 meeting, in December 1998, and some new data published by Mistiaen *et al.* (2000). In this section, "two Frasnian biostromal horizons," are present; they are considered useful field-guide level in the considered area but, more generally, in the whole Frasnian succession in Iran (Yazdi, 1997).

Six specimens of *Alveolites* [I-CR-4/51, /54, and I-CR-4/61to /64] were collected from the second biostromal level.

3) **Tabas area**: Shotori Ranges (Khorasan Province).

Kal-e Sardar section.

This section corresponds to the Niaz section, described by Wendt *et al* (1997), along the Sardar River. Five specimens of Alveolitids were collected in December 1998, in a small outcrop near the Kal-e Sardar section. Four of them [I-KS-4/21 to /24] were suitable for analysis. In this section Alveolitids are associated with some branched Tabulate corals (*Thamnopora* spp.) and with some stromatoporoids. This material is presently under study. According to the stromatoporoid fauna, this small outcrop could be uppermost Givetian in age (Mistiaen, 2001).

III. — SYSTEMATICS

Alveolites parvus Lecompte, 1933

Plates XVII and XVIII

* 1939 *Alveolites parvus* nov. sp. – Lecompte, pp. 43-44. Pl. VI, figs. 1-3

1952 *Alveolites parvus* Lecompte, 1939 – Sokolov, pp. 95-96, Pl. XXV, figs. 1-2

1958 *Alveolites parvus* Lecompte, 1939 – Stasinka, pp 212-213. Pl. XXIII, fig. 2

1984 *Alveolites parvus* Decompte (sic) – Sharkovski *et al.*, pp-29.

1993 *Alveolites parvus* Lecompte, 1939 – Fernández-Martínez, pp. 260-264. Pl. I, figs. 7, 10, Pl. 17, figs. 1-5; Pl. 18, figs. 1-4.

1) **Description**

a) *Corallum*

Most of the specimens studied correspond to fragments of colonies and many of them show erosion signs. Therefore, it is difficult to be precise about the external morphology just as the size of the samples, but the authors could deduce some data on the form and the rough size from the best-preserved colonies.

The colonies studied vary in external appearance between laminar, tabular, hemispherical (uparched, domed) or, more

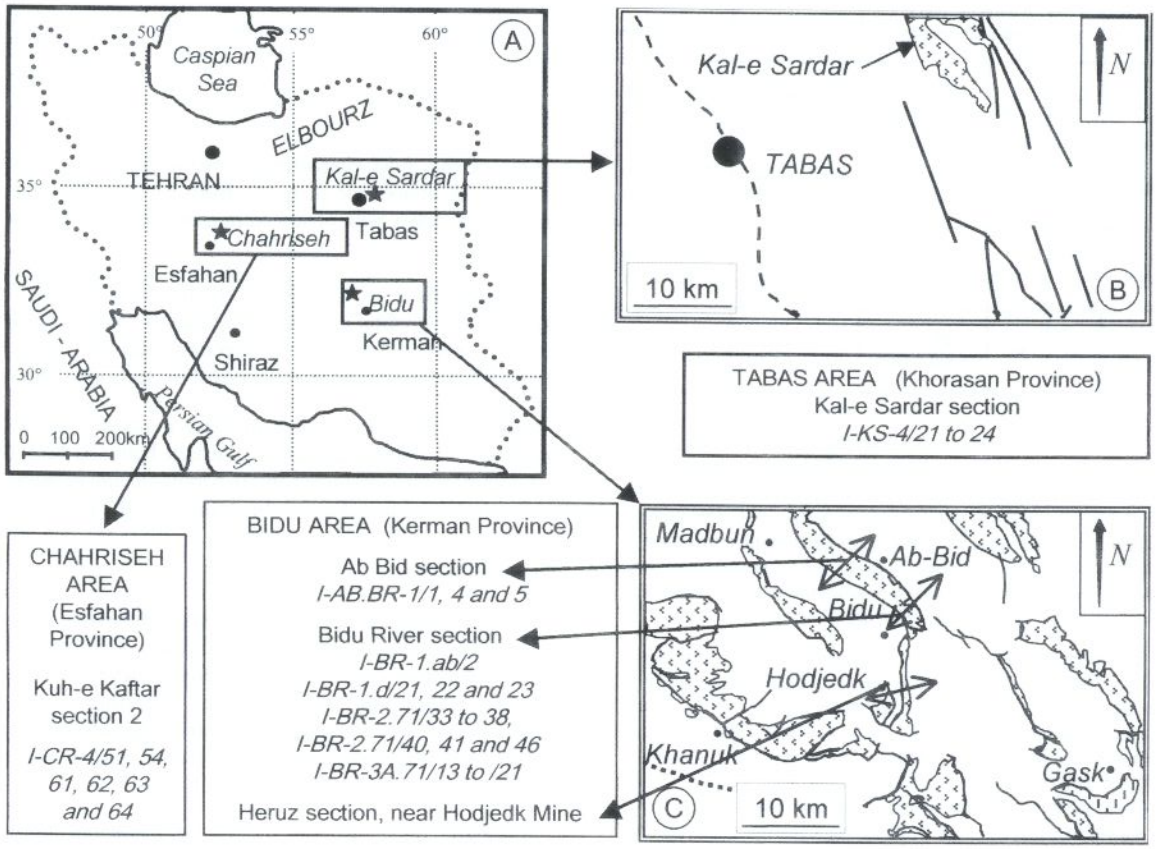

Fig. 1. — Situation map of the different outcrops providing specimens studied in the present paper. 1A: general map; 1B: detailed map of Tabas area, Khorasan Province; 1C: detailed map of Bidu area, Kerman Province.

Fig. 1. — Carte de situation des différents affleurements ayant fourni les échantillons étudiés dans ce travail. 1A: carte d'ensemble; 1B: carte de détail de la région de Tabas, province du Khorasan; 1C: carte de détail de la région de Bidu, Province de Kerman.

frequently, an intermediate form of these. In the largest samples, the thickness of the laminar forms does not exceed 0.5 cm by 5 cm in width and length. The lower surface usually shows growth ridges, and often, significant signs of necrosis can be observed.

Tabular colonies can reach several cm in height (3.5 cm in the biggest; width 8.5 cm, length 6 cm). The upper surface varies from flat to hemispherical, while the lower surface and lateral areas often display growth ridges.

The biggest colonies show nearly hemispherical morphology, although they often have strong irregularities in different areas that prevents their description as hemispherical colonies. The largest of them is 7.5 cm high by 8 cm long and over 4 cm wide. In many samples, external growth ridges are not seen but, when sectioned, one ~~it~~ can observe that skeletal layers separated by areas with necrosis form them. Once sectioned, the partial necrosis can be seen to be the principal cause of the domed and irregular morphologies that are present in numerous colonies.

The differences in morphology and size seen in the samples from each of the studied sections are analysed in the "Discussion" section.

b) *Corallites*

The cross sections of the corallites show an important variation with respect to exact orientation of the cut. In sections approximately perpendicular to the direction of corallite growth, the inner outline can be described as alveolitoid; however, many variations of minor importance can be found within this model (Pl. XVII, figs. 1-3).

Basically , there are sections with inner outlines that demonstrate a certain bilateral symmetry; the lower surface being flat, or showing slight depression while the upper surface is uparched. Regarding to the middle plate of the wall, the lower surface of each corallite is often formed by two mid-faces of the corallites placed below. Alongside these, corallites with a more flattened, rounded, kidney-shaped, or irregular outline, are present, especially when septal spines interfere significantly in wall development. Although some studied areas show uniformity of corallite outline, the majority of the cases studied do not.

The most significant data related to measurements taken (large or maximum and small or minimum internal diameter, and the relation between them) are given in Table I.

LOCALITY	spe	mes	D maximum	D minimum	Dmax/Dmin
BIDU	22	312	0.45 - 0.95/ 0.61/ 0.076	0.2 - 0.51/ 0.36/ 0.051	1.11 - 2.80/ 1.72/ 0.29
AB-BID	3	10	0.51 - 0.72/ 0.62/ 0.065	0.27 - 0.36/ 0.32/ 0.028	1.55 - 2.44/ 1.94/ 0.28
CHAH-RISEH	5	70	0.4 - 0.77/ 0.6/ 0.073	0.26 - 0.4/ 0.37/ 0.05	1.54 - 1.71/ 1.68/ 0.28
KAL-E-SARDAR	4	52	0.45 - 0.65/ 0.53/ 0.046	0.2 - 0.45/ 0.32/ 0.057	1.44 - 2.25/ 1.71/ 0.3

Tab. I. — Measures of the corallite size in the samples studied, arranged according to their origin (locality). *spe.*: number of specimens studied; *mes.*: number of measurements taken; *D maximum*: measurements of the large inner diameter of each corallite; *D minimum*: measurements of the small inner diameter of each corallite; *Dmax/Dmin*: relationship between the large and small inner diameters of each corallite. For each measurement, range/mean/ and standard deviation are given.

Tabl. I. — Mesures de la taille des polypiérites chez les spécimens étudiés, classés en fonction de leur origine (localité) spe: nombre d'échantillons étudiés; mes: nombre de mesures prises; D maximum: dimension du plus grand diamètre interne de chaque polypiérite ; D minimum: dimension du plus petit diamètre interne de chaque polypiérite ; Dmax/Dmin: rapport entre le plus grand et le plus petit diamètres internes de chaque polypiérit . Pour chaque mesure, on donne successivement les valeurs maximun et minumun, la moyenne et l'écart-type.

c) *Wall*

The corallite walls appear to be strongly influenced by recrystallization, thus showing diverse aspects. The median suture, which only appears locally, is usually discontinuous and presents various patterns, from black and narrow to wider, diffuse, and with a fine-grained appearance.

On both sides of this suture, the wall also shows various aspects, but the most frequent appearance is the development, especially at the edges, of neomorphic calcite rhombus that generate the typical pronounced saw-toothed structure (Pl. XVII, figs. 2, 3; Pl. XVIII, fig. 3). Various longitudinal sections demonstrate the presence of walls with shadows of fibres arranged in 'jet d'eau' (Pl. XVII, fig. 5). The correct interpretation of these structures necessitates detailed study of ultra-thin sections, but the poor preservation of the material advises against this analysis for the time being . In addition, the primary microstructure of the Alveolitids has been, up to now, poorly studied and only Lafuste (1984) has described "cupular" microlamellae on some specimens that belong to the genus *Planalveolites*.

Measured thickness of the double wall is very constant in all samples, independent of origin, and oscillates between 0.1 and 0.2 mm, with a mode around 0.15. In the initial zones of the colony, both in origin and in regenerations following necrosis, the thickness is markedly inferior, less than, or close to 0.1 mm (Pl. XVIII, figs. 1, 4).

In transverse sections of some colonies important variations in wall thickness have been observed, which do not appear to be related to phases of regeneration (Pl. XVII, fig. 4), in these cases the wall can reach thickness of up to 0.35 mm.

d) *Pores*

One of the most characteristic elements of the samples studied is the abundance of pores. Both P1 (angular) and P2 (mural) pores have been observed in cross sections (Pl. XVII, fig. 3).

In longitudinal sections (Pl. XVII, fig. 5; Pl. XVIII, figs. 1-4) a circular profile, or, more infrequently, a slight elliptic outline in the colony growth direction, can be observed. Alignment of these pores is also evident on sectioned faces.

Although infrequent, some of these pores are closed by pore-plates. Diameters are fairly constant between 0.15 (the most common measurement) and 0.2 mm. Distances between consecutive pores found in one line range 0.3-0.7 mm.

e) *Septal elements*

Septal elements show an extraordinarily variable development, both in quantity and quality. This variability can be seen not only at inter-colonial level, but also, frequently, within the same sample. Therefore, it is not unusual to find zones located in the same stage of astogenetic growth, and characterized by different septal element developments.

Basically, three different models of septal development can be distinguished: 1) absence or minimal development of septal elements (Pl. XVII, fig. 4); 2); presence of a solitary, big, septal spine ("hauptdorn") located in the very middle of the lower surface (Pl. XVII, fig. 1); and most frequently, presence of a variable number (generally between 4 and 10) of small spines arranged on both of the largest sides of the corallites (Pl. XVII, fig. 3).

In this last case, it is possible to find an alternative type of corallite with a main spine, generally on the lower surface, and various smaller spines appearing on the opposite side. Regions of a colony where one of these models is predominant appear frequently, but, in some areas of a sample, different combinations of these can also be observed. Regardless, there is no doubt that some of these septal elements have been partially or completely obliterated by recrystallization; for this reason it is not always possible to note in detail the development of these elements.

f) *Tabulae*

The tabulae are also numerous in nearly all of the colonies analysed. Although they sometimes show a very regular pattern (Pl. XVIII, fig. 3, some areas), irregular or incomplete tabulae, sometimes clearly linked to the presence of pores, can also be frequently observed (Pl. XVII, fig. 5; Pl. XVIII, fig. 3, some areas).

Distance between tabulae shows marked variation both at intra and intercolonial level (Pl II, figs. 1-3). In the same specimen, the most distanced tabulae are found in the initial zones, or in those of post necrosis colonial growth. Distances oscillate between 0.1 and 0.85 mm, the most usual being, in the majority of colonies, separations closer to the lower measurement, between 0.1 and 0.5 mm.

g) *Other observations*

In longitudinal section, owing to the morphology of the corallites, the apparent diameter of these varies according to the position of the section (parallel or perpendicular to largest diameter). Compare longitudinal sections in figures Pl. XVII, fig. 5 and Pl. XVIII, fig. 3.

In these sections, various examples of the generation of new corallites can be seen, produced by lateral increase with basal pore (Pl. XVIII, fig. 1), which can be closed by a small tabula acting as a pore-plate.

Longitudinal sections also allow the recognition of the same astogenetic model in all of the samples studied. Wherever this is visible, the origin of the colonies, and the post necrosis re-growth, is designated as dark and thin-walled corallites, lacking septal elements, and covering a hard substratum (Pl. XVIII, figs. 1, 4); thus it represents an horizontal growth, where the lines of transverse section corallites are usually visible.

For a while these corallites maintain rapid growth (thin walls, highly separated tabulae) horizontally or simply parallel to the substratum over which they grow, to later grow either at an angle to, or perpendicular to, this substratum (Pl. XVIII, figs. 1, 2 and 4). The same model is repeated posterior to, a sometimes severe, necrosis, produced by the fall of sediment on the upper surface of the colonies.

2) Discussion

Massive cerioid colonies with corallites possessing alveolitoid profile, thin walls in the origin of colonial growth, septal elements consisting basically of spines, single row pores, and lateral increase - such as those described above - are assigned to the genus *Alveolites* Lamarck

For specific assignation, a three stage process was followed: 1) selection of features of systematic importance; 2) comparison of colonies from different locations (intrapopulational variation); and 3) comparison with species of the genus *Alveolites* Lamarck described in the literature.

a) *Selection of features of systematic importance.*

Owing to the reduced number of quantifiable features displayed by tabulate corals in general, and alveolitids in particular, all present features are usually used to identify species. However, some of these features are strongly influenced by environmental conditions, and others can be fairly similar even in species that are not close.

Of the features given in the description, the external morphology, the distance between consecutive tabulae, and the septal element development haves a clear external influence. The wall thickness (in the absence of intensive recrystallizations) and the diameter of the pores remains fairly constant in the forms studied, but both features have similar dimensions in many *Alveolites* species. Therefore , only measurements that are related to the diameter of the corallites were used in statistical analysis.

b) *Comparison between colonies originating in different localities.*

Two different statistical studies were applied in this comparison. Firstly, two cluster analyses were carried out, using both the large (maximum) and small (minimum) diameter. In both cases, similar results were obtained. The clusters thus defined (between 5 and 2 groups) did not coincide in any way with groups of different origin and the sample collected in the section of Bidu (the most numerous) showed high levels of instability.

In the second analysis, box diagrams were made showing all the analysed samples according to diameter sizes (large and small). The results are given in fig. 2.

Regression analysis enabled the authors to confirm that the relation between both diameters was 0.51. For this reason, we can say that both measurements give similar statistical information. However, the large diameter shows a more normal distribution than that showns by the small diameter (compare fig. 2 a vs. b), which represents a greater dispersion in their values. The best confiability of large diameter leads us to select it as the most satisfactory measure to the specific classification of these samples.

As can be seen in the diagrams, there is a undeniable variability in the values of the data collected. However, except in a few concrete cases (particularly in the samples coming from Kal-e Sardar, which have corallite diameters slightly smaller than those of colonies from other localities, see Table I and fig. 3), the range of this data remains within well-defined limits. Thus, all the colonies studied can be considered co-specific (fig. 3).

c) *Specific determination*

Alveolites is a very common genus in the Devonian reefal facies worldwide. This fact, in combination with the difficulties mentioned above of their classification, has multiplied, no doubt artificially, the number of species assigned to the genus.

One of the most cited is the type species *Alveolites suborbicularis* Lamarck which shares with the Iranian colonies all the qualitative features, the wall thickness and the pore diameter. However, *A. suborbicularis* has bigger corallites (large diameter between 0.6 and 1 mm; small diameter between 0.4 and 0.6 mm).

Many species close to *A. suborbicularis* have been described. Among them, Lecompte (1939) defined *Alveolites parvus* with material from the Frasnian of the Dinant Basin. This species is quite close to *A. suborbicularis* but the corallites are smaller (large diameter between 0.5 and 0.6 mm and small diameter between 0.35 and 0.4 mm), than the corallites of this species.

At the same time, the *Alveolites parvus* corallites are similar in size to the measurements obtained from the Iranian material. The main difference between *A. parvus* and the Iranian material is that the corallites described in this paper are sometimes slightly bigger. In the opinion of the authors, this slight variation is not of sufficient significance to assign the Iranian samples to a different species.

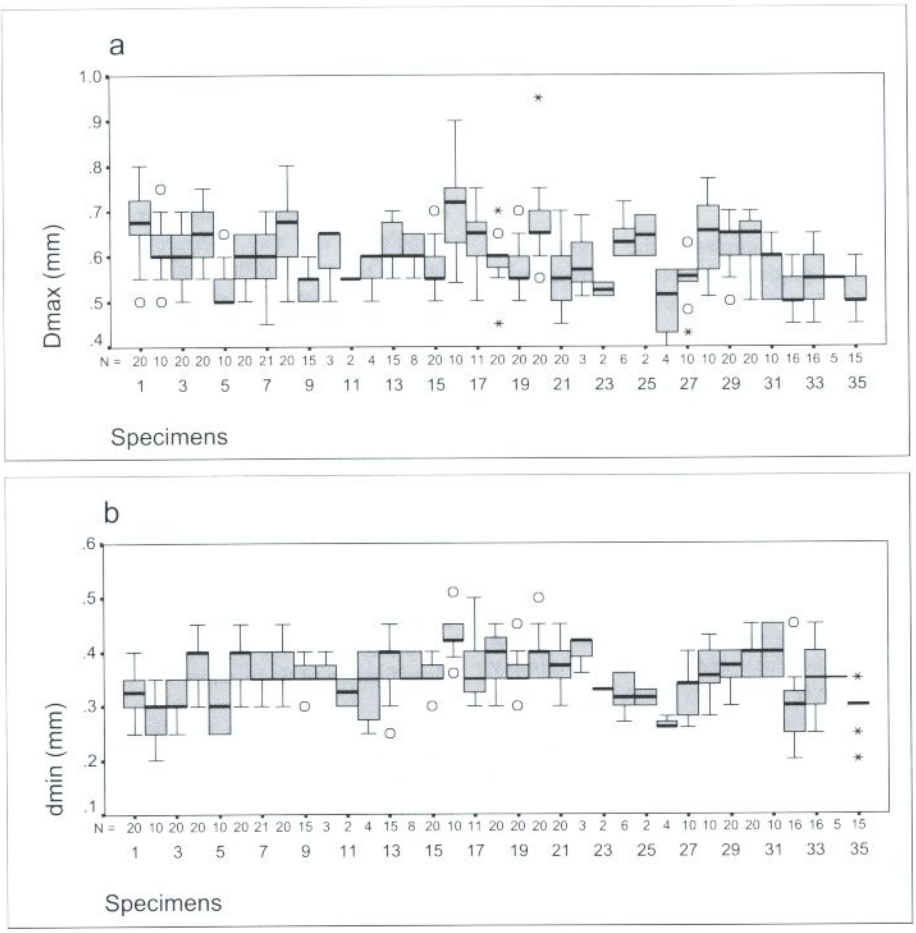

Fig. 2. — Box and whisker displays representing the dimensions (in mm, Y axis) of the measured corallites in the specimens studied. Box: interquartil range or IQR. Line into the box: median. Lines out of the box (whiskers): 1.5 x IQR. ° and * (outliers): remote and extreme values. On the X axis measured specimens: Bidu River section (1 to 22); Ab Bid section (23 to 25); Kuh-e Kaftar section (26 to 31) and Kal-e Sardar section (32 to 35). N = number of measures taken in each sample.
a) Box and whisker displays representing the dimensions of the large inner diameter (D maximum = maximum inner diameter)
b) Box and whisker displays representing the dimensions of the small inner diameter (D minimum = minimum inner diameter)

*Fig. 2. — Diagramme de type boite à moustaches représentant les dimensions (en mm, ordonnée) des polypiérites mesurés parmi les exemplaires étudiés. Boite: intervalle interquartile ou IQR. Ligne dans la boite: médiane. Lignes hors de la boite (moustaches): 1.5 x IQR. ° et * (outliers): valeurs éloignés et extrêmes. Horizontalement, spécimens mesurés: Coupe de Bidu River (1 to 22);coupe d'Ab Bid (23 to 25); coupe de Kuh-e Kaftar (26 to 31) et coupe de Kal-e Sardar (32 to 35). N = nombre de mesures prises sur chaque échantillon.*
a) Diagramme de type boite à moustaches représentant les dimensions du grand diamètre interne (D maximum = diamètre maximum).
b) Diagramme de type boite à moustaches représentant les dimensions du petit diamètre interne (D minimum = diamètre minimum).

Alveolites lindensis Iven 1980, from the lower Givetian of the Bergisches land (Rheinisches Schiefergebirge) is a little known form, poorly differentiated from other species of the *suborbicularis* group. It is fairly close in size to the Iranian samples, and thus, to *Alveolites parvus* although having thinner walls.

Finally, *Alveolites intermixtus minimus* (Iven, 1980), from the Eifelian of the Bergisches land (Rheinisches Schiefergebirge), has similar dimensions to that of the Iranian material, but the species has traditionally been characterized by the full development of the main septal spines ("hauptdorn"), which are only occasionally present in the Iranian samples. Nevertheless, in our specimens and in most of the Alveolitid species, the septal spines density is shown to be very variable.

Thus, the authors believe that the colonies described in this paper can be assigned to the species *Alveolites parvus* Lecompte, which is quite close to, (if not co-especific with) *A. lindensis* Iven and to *A. intermixtus minumus* (Iven). *A. parvus* has been found in the Frasnian of the Dinant Basin (Lecompte, 1939) and of the Russian Platform (Sokolov, 1952); also in the Givetian of the Holy Cross Mountains in Poland (Stasinska, 1958) and of the Cantabrian Mountains of Northern Spain (Fernández-Martínez, 1993).

IV. — PALAEOECOLOGICAL CONSIDERATIONS

External morphology of the alveolitid colonies shows a broad phenotypic plasticity related to environmental changes occurring during the astogenetic development of these

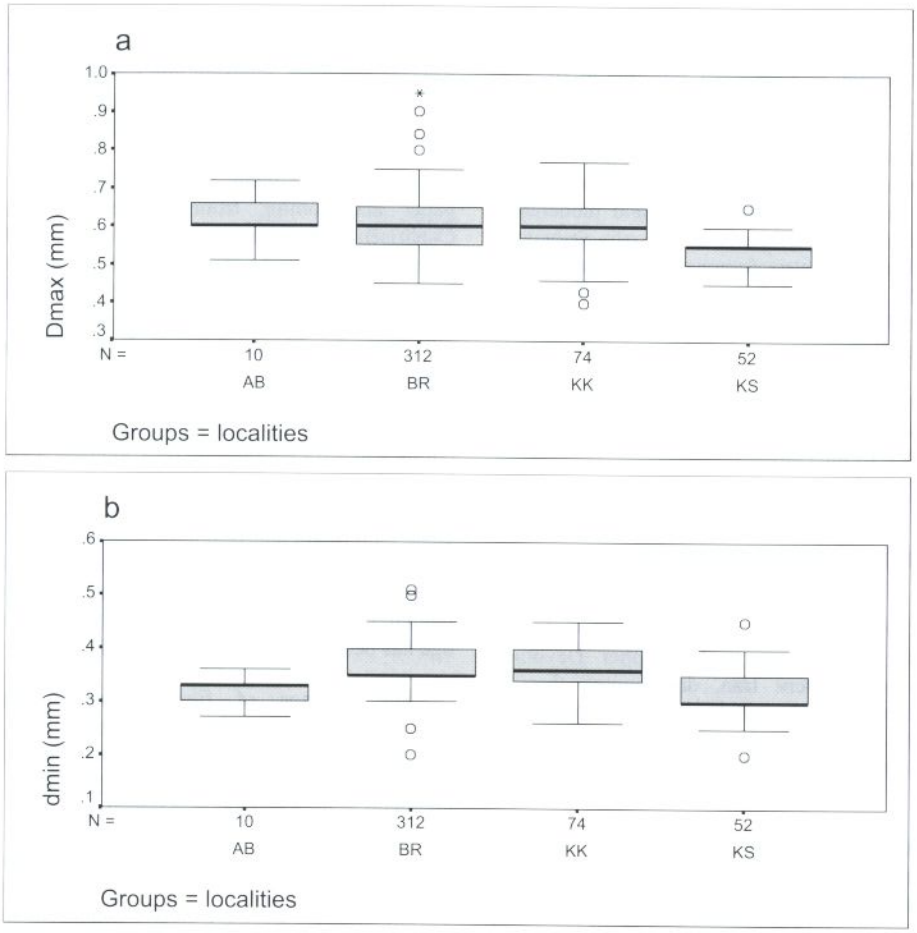

Fig. 3. — Box and whisker displays representing the dimensions (in mm, Y axis) of the measured corallites in the specimens studied sorted by origin (X axis). AB = Ab-Bid section; BR = Bidu River section; KK = Kuf-e Kaftar section and KS = Sal-e Sardar section. Same caption of fig. 2.

a) Box and whisker displays representing the dimensions of the large inner diameter (D maximum = maximum inner diameter)

b) Box and whisker displays representing the dimensions of the small inner diameter (D minimum = minimum inner diameter)

Fig. 3. — Diagramme de type boite à moustaches représentant les dimensions (en mm, ordonnée) des polypiérites mesurés parmi les exemplaires étudiés regroupés selon la section d'origine (axe X). AB = section Ab-Bid; BR = section Bidu River; KK = section Kuf-e Kaftar et KS = section Sal-e Sardar. Même légende que pour fig. 2.

a) Diagramme de type boite à moustaches représentant les dimensions du grand diamètre interne (D maximum = diamètre maximum).

b) Diagramme de type boite à moustaches représentant les dimensions du petit diamètre interne (D minimum = diamètre minimum).

modular animals. The morphology of the specimens studied can be placed at some point on a continuum that ranges from laminar to tabular and to hemispherical forms. All of them, especially the latter ones, can show different degrees of irregularity. Basically, these colonies seem to be laminar at the start of growth, later showing a clear tendency to be tabular and domed. Final morphology is mainly dictated by rate of growth, plus frequency and location of necrosis. Frequent and regular necroses usually cause an erratic morphology and, within the hemispherical forms, fairly thick sediment layers are often seen.

Basically, whilst staying within the continuum described above, all colonies from the four sections studied show slightly different morphologies.

Colonies from Kuh-e Kaftar section n° 2 (Chahriseh area) are laminar and tabular, showing numerous necroses, the latter being obvious from the layers – sometimes significant – of argillaceous matrix, and often having small gastropods attached to the lower surface, whilst on the upper surface, small bryozoan colonies frequently established post-mortem.

The colonies collected in the locality of Kal-e-Sardar (Tabas area) are also mostly laminar and are associated with stromatoporoids and some massive rugose corals.

The three specimens coming from Ab-Bid (Bidu area) show laminar morphologies and they are related to stromatoporoids.

The alveolitid corals from the Bidu section are very diverse in form, but can be divided into two groups. Samples from Biozone 6 (after Brice, 1977) are tabular, hemispherical and irregular, medium to big in size, with numerous signs of necrosis of little significance, rapidly repaired. Several of the samples collected in this locality were found to have grown on stromatoporoids –usually thin- which in turn had grown on

rugose corals. On the other hand, samples collected from immediately beneath this layer, and three examples of unknown origin (collected by Lapparent, possibly in 1972; I-BR-1ab/2, I-BR-1c/5 y I-BR-1c/6), are laminar.

It has been traditional to interpret stromatoporoids and alveolitid corals with laminar morphologies in coexistence as colonizers of soft substrates, in both quiet and moderately energetic environments. The existence of necrosis associated with layers of argillaceous matrix demonstrates a periodic fall of sediments. In the case of the Biozone 6 layer, the muddy supply is occasionally significant and would seem to recur with undeterminated frequency.

In these sometimes muddy waters, the alveolitids' capacity for regeneration would have been a very important factor for the survival of the colonies.

V. — PALAEOBIOGEOGRAPHIC REMARKS

Brice *et al.* (1999) achieved an approximation to the palaeobiogeographic connections in the Upper Devonian faunas of central and eastern Iran, documented through rugose corals, stromatoporoids and brachiopods studies. In this paper, the data obtained by the systematic study of the alveolitids in the scheme proposed by these authors will be added.

At the generic level, Frasnian tabulate corals are cosmopolitan, being the faunas dominated by Alveolitidae and species of Thamnoporidae. Some genera of second family as well as *Alveolites* appeared conspicuously in all the reefal facies of the Middle and Upper Devonian. They are also the main representatives of the tabulate faunas in the reefal levels of the Frasnian studied in different sections of Iran. Another recognised taxa in these outcrops, despite being less abundant than the above mentioned, is *Scoliopora* sp. (Mistiaen and Gholamalian, 2000), a very common branched alveolitid, which is found with *Alveolites* in the Givetian and Frasnian reefs of Eurasia.

Other genera mentioned in the literature (*Favosites* sp., *Heliolites* sp., *Michelinia* sp. and *Cladochonus* sp., see Mistiaen and Gholamalian, 2000), have not been found in the studied material for this paper, probably due to biostratigraphic and facial reasons; nevertheless, all cases are cosmopolitan.

At the subgeneric level, two species of tabulate coral have been reported from Iran. *Thecostegites bouchardi* (Michelin) has been described by Mistiaen and Gholamalian (2000); it is a fairly uncommon but broadly distributed species, which has been reported from the Frasnian of Belgium, France, Poland, Russian Platform, Pakistan and China. Also, from the Upper Givetian of the Cantabrian Mountains and from the Upper Givetian or ? Lower Frasnian of Afghanistan.

On the other hand, the Alveolitid corals studied in this paper and coming from different sections in Kerman, Chahriseh and Tabas areas, are represented by *Alveolites parvus* Lecompte. As mentioned above, *Alveolites parvus* has been described from the Holy Cross Mountains in Poland (Givetian), the Cantabrian Mountains in Spain (Upper Givetian), the Dinant Basin in Belgium (Frasnian) and the Russian Platform (Frasnian).

As Brice *et al.* (1999) established, brachiopods, rugose corals and stromatoporoids data indicate a close relationship between central and east regions from Iran and Russian Platform and Poland (level III from these authors) and even close with Spain and Belgium. In Spain, as well as in Poland, *Alveolites parvus* has been mentioned in the Givetian and not in the Frasnian; although no systematic detailed study of the tabulates which are presented in the reefal sediments of this age has been done, to date, in either region.

The absence of frasnian reefal sediments and/or systematic published data also hinders the comparison of tabulate faunas from Iran with those from other proximal regions. But the species under investigation could well be abundant in the Frasnian of Afghanistan.

In conclusion, the authors wish to indicate that although *Alveolites parvus* has not been mentioned in several areas in Europe or Asia, these are clearly connected with those where *Alveolites parvus* has been cited. Note that in these same areas, *Alveolites suborbicularis* and other species related to faunas from Iran have been mentioned.

Therefore, the presence of *Alveolites parvus* Lecompte in the reefal outcrops from the Upper Devonian of Iran supports the relationship found in this region and other areas from the northern margin of Gondwana, as well as the important increase in cosmopolitanism of the benthic marine invertebrate during the Frasnian.

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PLATES XVII

Fig. 1. —Specimen I-BR-2-71/33 [GFCL 3959]. Transverse section showing the variation of the alveolitoid corallites outline and the occasional presence of solitary, big spines ("hauptdorn" type). x15.

Fig. 1. — Spécimen I-BR-2-71/33 [GFCL 3959]. Coupe transversale montrant les variations du contour des polypiérites alveolitoides et la présence occasionnelle de grosses épines isolées (type « hauptdorn ») x 15.

Fig. 2. — Specimen I-BR-3A-71/21 [GFCL 3960]. Transverse section showing the outline of the corallites and the development of the septal elements. x15.

Fig. 2. —Spécimen I-BR-3A-71/21 [GFCL 3960]. Coupe transverse montrant le contour des polypiérites et le développement d'éléments septaux. x 15.

Fig. 3. — Same specimen as Fig. 2. Detail of a transverse section showing the corallites' outline and some mural pores, mostly situated on the lateral faces of the corallites. Note the septal elements which are basically composed of numerous, small spines developed on all sides of the corallites. x37.5

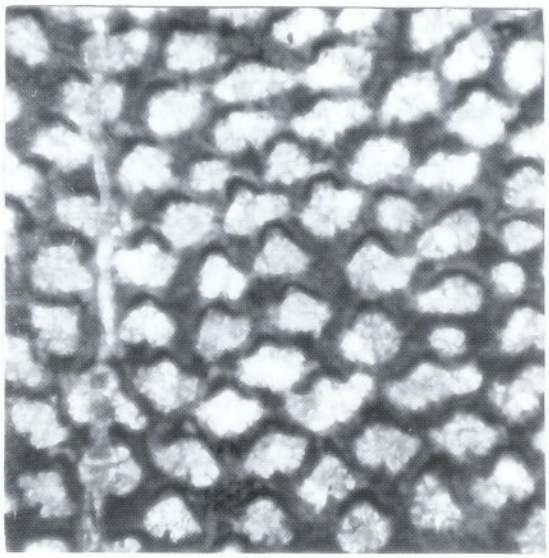
Fig. 3. — Même spécimen que la figure 2. Détail d'une coupe transversale montrant le contour des polypiérites et quelques pores muraux, surtout situés sur les faces latérales des polypiérites. A remarquer les éléments septaux qui sont fondamentalement composés de nombreuses petites épines développées sur tous les cotés des polypiérites. x 37,5.

Fig. 4. — Specimen I-BR-1ab/2 [GFCL 3961]. Transverse section, slightly oblique. Note the important intracolonial variation in the thickness and appearance of the wall. x15.

Fig. 4. — Spécimen I-BR-1ab/2 [GFCL 3961]. Coupe transversale, légèrement oblique. A remarquer l'importance de la variation intracoloniale de l'épaisseur et de l'aspect des murailles. x 15.

Fig. 5. — Specimen I-BR-1d/22 [GFCL 3962]. Longitudinal section showing the appearance of the wall (with local presence of "jet d'eau" type structures: white arrow), some pores and the tabulae pattern. x15.

Fig. 5. — Spécimen I-BR-1d/22. (GFCL 3962). Coupe longitudinale montrant l'aspect de la muraille (avec la présence locale d'une structure « en jet d'eau », flèche blanche), quelques pores et l'allure des planchers ; x 15.



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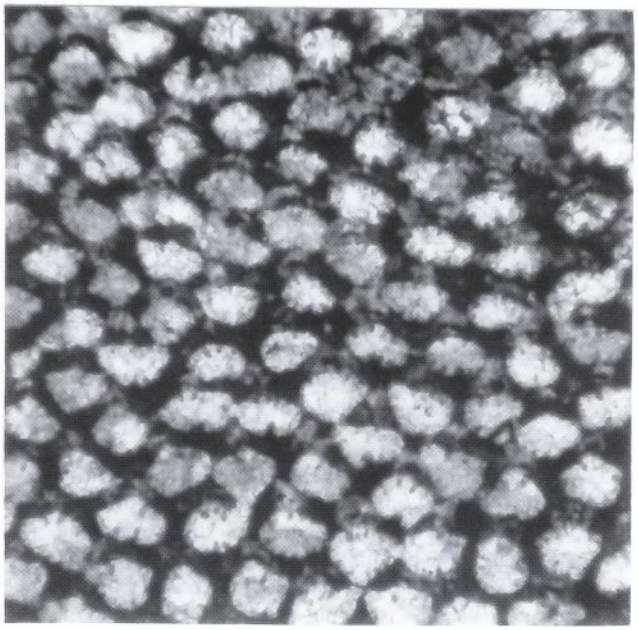

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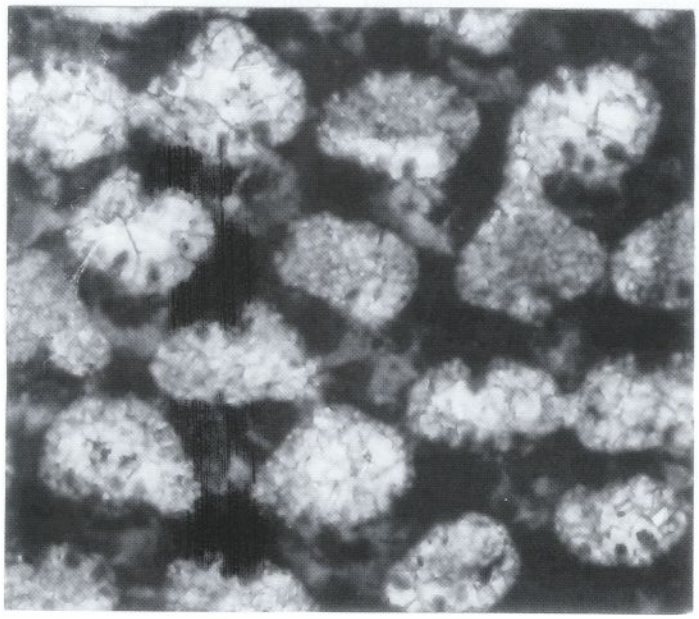

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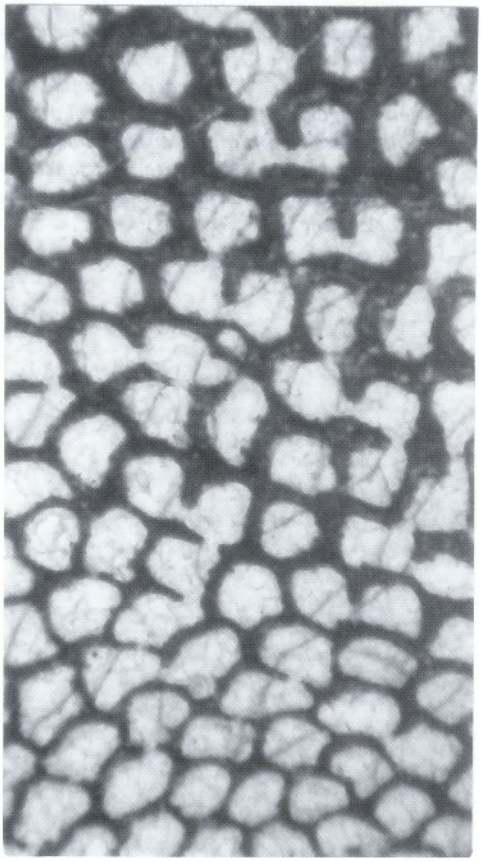

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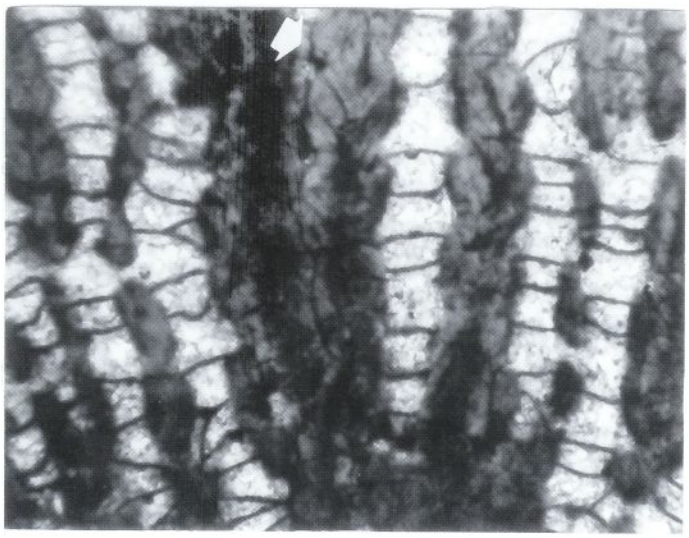

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PLATES XVIII

Fig. 1. — Specimen I-BR-1ab/2 [GFCL 3961] (same as in Plate I, fig. 4) exactly where colonial growth (placed on the right of the figure) starts. Note the path taken by the corallites and the reduced thickness of the wall in this area of the colony. x15.

Fig. 1. — Spécimen I-BR-1ab/2 [GFCL 3961] (même spécimen que la planche I, fig. 4) exactement là où la croissance de la colonie (à droite sur la figure) commence. A remarquer le parcours suivi par les polypiérites et l'épaisseur réduite le la muraille dans cette partie de la colonie. x 15.

Fig. 2. — Specimen I-BR-3A-71/21 [GFCL 3960] (same as in Plate I, figs. 2 and 3). Longitudinal section at the precise point where the corallites start to become vertical, at the beginning of a regeneration. Note the slender wall and the alignment of the pores. Observe also the tabulae, showing a rather regular pattern, more distanced at the beginning of the upright than during the normal horizontal growth of the corallites. x15.

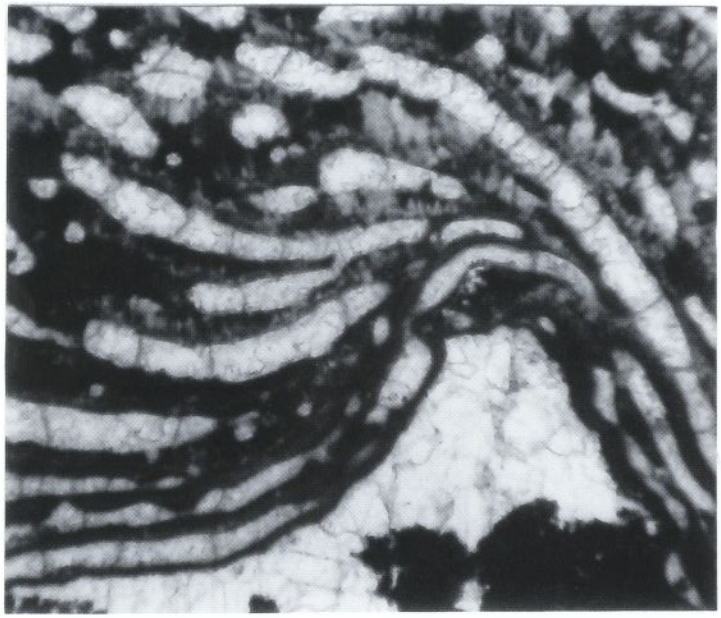
Fig. 2. — Spécimen I-BR-3A-71/21 [GFCL 3961] (même spécimen que la planche I, fig. 2 et 3). Coupe longitudinale à l'endroit précis où les polypiérites commencent à devenir verticaux, au début d'une régénération. A remarquer la finesse des murailles et l'alignement des pores. A remarquer aussi les planchers montrant une distribution assez régulière, plus écartés au début de la croissance verticale des polypiérites que pendant leur croissance normale horizontale. x 15.

Fig. 3. — Specimen I-BR-1d/22 [GFCL 3962] (same sample as in Plate I, fig. 5). Longitudinal section. Observe the alignment of the pores, arranged in the middle part of a face. Note also the tabulae design, locally rather irregular. x15.

Fig. 3. — Spécimen I-BR-1d/22 [GFCL 3962] (le même que planche I, fig. 5). Coupe longitudinale. A remarquer l'alignement des pores, situés sur la partie moyenne des faces. A noter aussi l'allure des planchers, localement assez irréguliers. x 15.

Fig. 4. — Specimen I-BR-1d/23 [GFCL 3963]. Longitudinal section in a region showing a post necrosis regeneration. Note the reduced thickness of the wall and the fairly lying disposition of the corallites. x15.

Fig. 4. — Spécimen I-BR-1d/23 [GFCL 3963]. Coupe longitudinale dans une région montrant une régénérescence post-nécrose. A remarquer l'épaisseur réduite des murailles et la disposition assez couchée des polypiérites. x 15.



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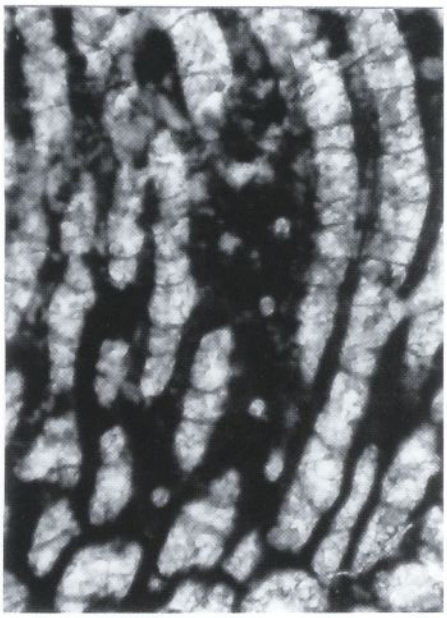

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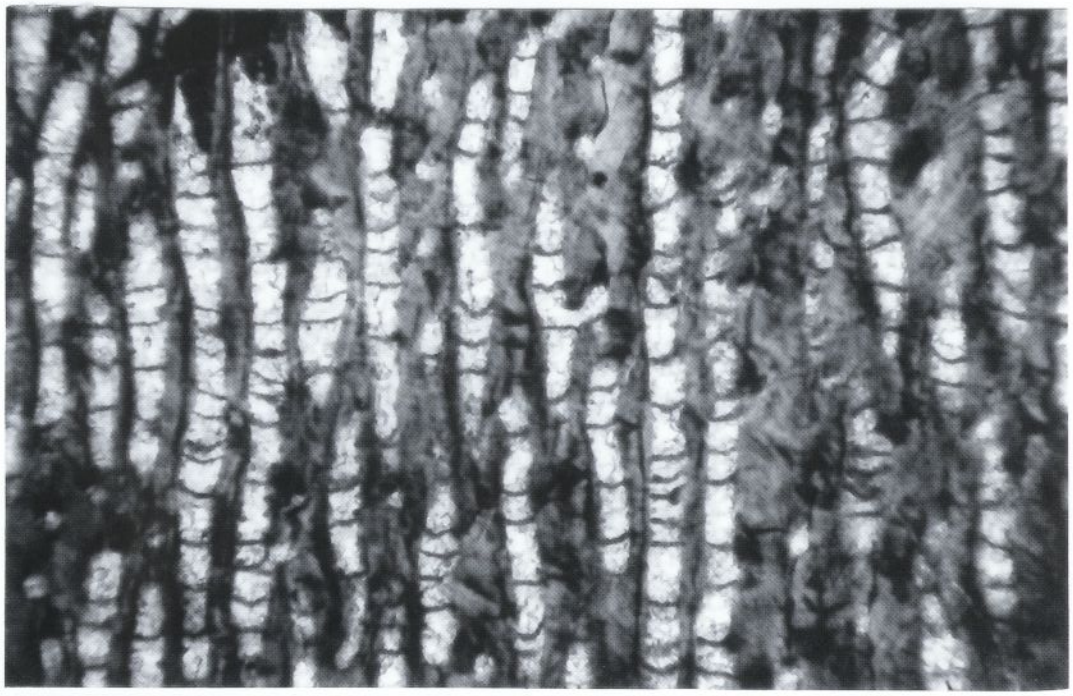

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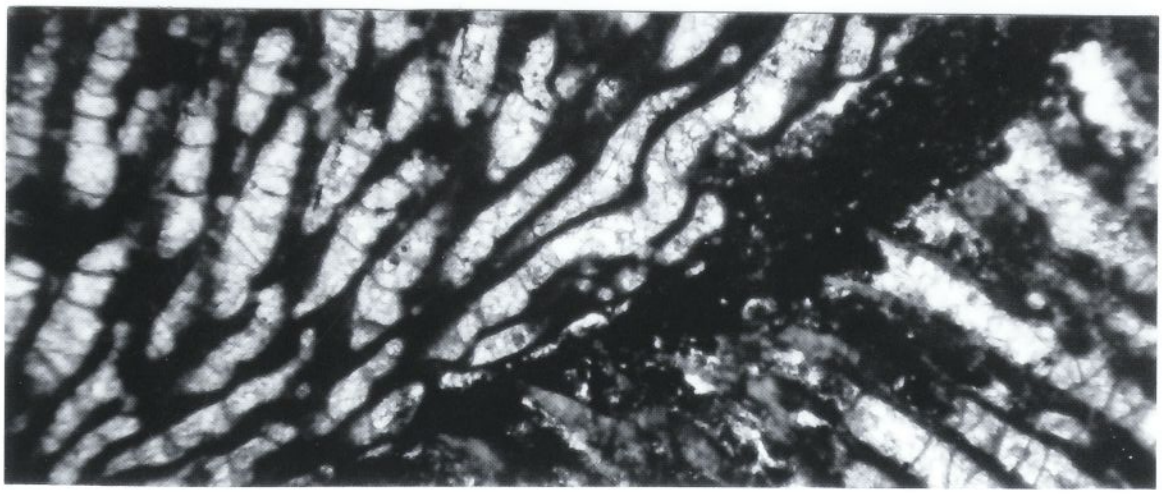

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