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Revision of *Orionastraea* SMITH, 1917 (Rugosa) from the Lower Carboniferous (uppermost Viséan) of the Moscow Basin, and comments on patterns of variability, evolution and range of the genus in Eastern Europe and in the British Isles

Revisión de los Orionastraea *SMITH, 1917 (Rugosa) del Carbonífero Inferior (Viseense terminal) de la Cuenca de Moscú, con comentarios sobre los patrones de variabilidad, la evolución y el rango del género en Europa del Este y las Islas Británicas*

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Abstract: Studies of variability of *Orionastraea* from the Moscow Syneclise formerly (DOBROLYUVOBA, 1958) attributed to four species allow to prove the synonymy of three specific names. The genus is confined to the upper part of the Aleksin horizon (uppermost Viséan) and includes two species, *O. kurakovensis* DOBROLYUVOBA, 1958 restricted to the southern part of the Moscow Syneclise and *O. rareseptata* DOBROLYUVOBA, 1958 restricted to its north-western part.
The range and synonymy of the genus are discussed. Patterns of variability based on examination of *Orionastraea* specimens from the Coelenterate Collections of the Natural History Museum, London are outlined. Three stages of evolution of the genus are discerned. Both Russian species appeared during the first stage.
Key words: *Orionastraea*, variability, evolution, uppermost Viséan, Moscow Basin, Britain.

Resumen: El estudio de la variabilidad en las especies del género *Orionastraea* de la Sineclisa de Moscú, que previamente incluía cuatro especies (DOBROLYUVOBA, 1958), ha mostrado la sinonimia de tres de ellas. La distribución del género está limitada a la parte superior del horizonte Aleksin (Viseense terminal), e incluye dos especies: *O. kurakovensis* DOBROLYUVOBA, 1958 restringida a la región sur de la Sinclisa de Moscú, y *O. rareseptata* DOBROLYUVOBA, 1958, restringida a la región noroccidental de la misma.
Se discuten el rango y las sinonimias del género. Se exponen los patrones de variabilidad deducidos a partir de la revisión de los ejemplares de *Orionastraea* de las colecciones del Museo de Historia Natural de Londres. Se reconocen tres estados en la evolución del género, reconociéndose el primero de ellos como el estado en el que se desarrollaron las dos especies de Rusia.
Palabras clave: *Orionastraea*, variabilidad, evolución, Viseense terminal, Cuenca de Moscú, Gran Bretaña.

INTRODUCTION

The rugose coral genus *Orionastraea* was erected by SMITH (1916, 1917) for the British Lower Carboniferous colonial species related to the genus *Lithostrotion* FLEMING, 1828. SMITH chose *Sarcinula phillipsi* MCCOY, 1849 as the type species, considered it as the senior synonym of *S. tuberosa* MCCOY, 1849, and attributed to the genus two more species, *S. placenta* MCCOY, 1849 and *Lithostrotion ensifer* MILNE-EDWARDS & HAIME, 1851. Therefore, the genus *Orionastraea* as established by SMITH included species with pseudoastraeoid (cerioid-astraeoid) and thamnasterioid colonies, well developed septa of both orders, columella present or lacking. It was mainly confined to the interval of the Brigantian which is now considered as the equivalent of the rugose coral fauna I of MITCHELL (1989) of the Bristol area, North

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Five new species and four new varieties have been referred to *Orionastraea* by HUDSON (1926, 1929), most of them coming from northern England (North Yorkshire and Cumbria). *O. ensifer* var. *matura* is here removed from *Orionastraea*. Other representatives of the genus described by HUDSON are astraeoid, thamnasterioid and aphroid, typically have smaller tabularia and less septa than the species attributed to the genus by SMITH and are confined to the interval equating with the upper part of the fauna I through fauna J of MITCHELL (1989). In the interval of the Brigantian succession of northern England corresponding to the Tyne Bottom through the Single Post limestones and their equivalents, HUDSON (1929) recognized the *Orionastraea* zone subdivided into two subzones (Fig. 1).

The genus *Orionastraea* has since been broadly interpreted, reported from various areas in Europe, Asia and even in Australia, and considered as ranging from the Lower Carboniferous through the Permian (for major revisions of the genus see HILL, 1940; DOBROLYUBOVA, 1958; KATO & MITCHELL, 1970). HILL (1981) restricted the stratigraphic range of *Orionastraea* to the Viséan, but the geographic distribution still remained very wide: Great Britain, Urals, Novaya Zemlya, Russian Platform, Donets Basin, Asia (Japan, Hansu) and Australia (Queensland, New South Wales). As already mentioned by KATO & MITCHELL (1970), the record of the genus from Central Japan by MINATO (1955) is doubtful and the form most probably belongs to *Pseudopavonia* YABE, SUGIUAMA & EGUCHI, 1943. *Orionastraea columellaris* PICKETT, 1966 reported from eastern Australia (PICKETT, 1966; JULL, 1974; WEBB, 1990) differs from true *Orionastraea* in having a very stout columella composed of a medial lamella with radiating septal lamellae, heavy skeletal dilation and in some other characteristics. WEBB (*ibid.*) conditionally referred it to *Orionastraea* together with a few Viséan pseudocerioid to aphroid Australian species formerly assigned to *Lithostrotion* before a new genus for this group is established. Few uppermost Viséan and Serpukhovian astraeoid (sometimes with vestigial corallite walls), thamnasterioid and aphroid species resembling *Orionastraea* are reported from Central, South, Northwest and Northeast China. They are attributed either to *Orionastraea* (LUO & ZHAO, 1962, JIA *et al.*, 1977, DENG *et al.*, 1979, GUO, 1980, LIAO & RODRIGUEZ, 1999) or to *Orionastraea, Paraorionastraea* LIN, 1966 and *Vesiorionastraea* YÜ, LIN, SHI, HUANG & YU, 1983 (YÜ *et al.,* 1983). Most probably, they belong to an undescribed genus closely related to *Heterostrotion* POTY & XU, 1996. These Chineese *Orionastraea*-like corals as well as thamnasterioid *O. carinata* SHCHUKINA, 1970 reported from the Serpukhovian of Tian-Chan (SHCHUKINA, 1970) resemble *Heterostrotion* in highly variable axial structures represented by impersistent columella and/or aulos, in septa being carinate, and major septa - pinnately connected.

I am not aware of any records of *Orionastraea* from the former USSR other than those in the uppermost Viséan (lower Brigantian) of the Moscow Syneclise and Donets Basin. The presence of the genus in the Aleksin horizon of the Moscow Syneclise was recognized by DOBROLYUVOBA (1958) based on six specimens, five of which came from the north-western part of the syneclise, and one - from the southern part. No more specimens have been obtained since. In the north-western part of the syneclise, *Orionastraea* is reported from the Msta River. It is confined to the 2.9 m thick Limestone a_2 representing one of the eight laterally persistent limestone units in the uppermost Viséan sequence of the area which is to considerable extent composed of sands and clays (HECKER, R.,1938). The interval of this sequence comprising the Limestone a_2 and the Limestone a_3 developed higher in the succession approximates to the Parsukovo subsuite of the southern part of the syneclise in the sense of MAKHLINA *et al.* (1993), i.e. to the upper part of the Aleksin horizon. In the southern part of the syneclise, *Orionastraea* also most probably also occurs high in the Aleksin.

As a short ranging and rapidly evolving genus, *Orionastraea* is important for stratigraphy of the Brigantian of Great Britain, the area of its highest abundance. It also serves as a good biostratigraphic tool for other areas of its occurrence; even scanty material allows precise correlation based on evaluation of evolutionary advancement of a species. Thus, *Orionastraea* from the Moscow Basin resemble the British *Orionastraea* confined to the fauna I of MITCHELL (1989), whereas the species from the Donets Basin erroneously identified by VASILYUK (1964) as *O. placenta* and occuring at a higher level is evolutionary more advanced and very close to *O. prerete* characteristic of the fauna J of northern England. The presence of this species in the middle part of the lower Vg subzone (in the Limestone B_3) indicates that the base of the Mezha Formation comprising the lower Vg and the upper Vg subzones cannot lie very high in the Brigantian and most probably approximates to the base of the Mikhailov horizon of the Moscow Syneclise as it has been supposed by HECKER, M. (2002) (Fig. 1).

In spite of its scarcity, the material of *Orionastraea* from the Moscow Basin allows study of variability demonstrating that the specimens from the Msta River attributed by DOBROLYUBOVA (1958) to *O. phillipsi*, *O. rareseptata* DOBROLYUVOBA, 1958 and *O. heteroseptata* DOBROLYUVOBA, 1958 belong to the same species.

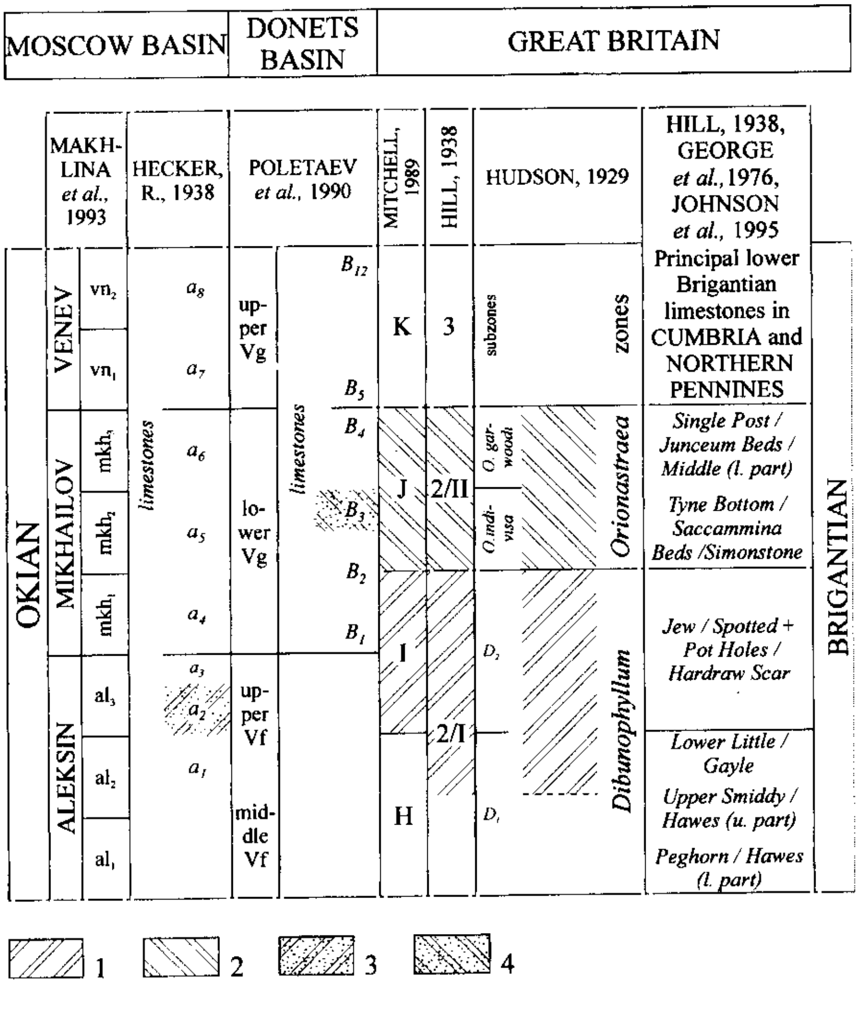


Figure 1.- Correlation of the uppermost Viséan (Brigantian) stratigraphic units of the Moscow and Donets Basins with reference to some rugose coral zonations adopted in Great Britain at different times, and principal lower Brigantian limestones in northern England. 1: rugose coral fauna I of MITCHELL (1989) and its equivalents in the other rugose coral zonations considered. 2: rugose coral fauna J of MITCHELL (1989) and its equivalents in the other rugose coral zonations considered. 1 + 2: range of *Orionastraea* in Great Britain. 3: range of *Orionastraea* in the Moscow Basin. 4: occurrence of *Orionastraea* in the Donets Basin.

Figura 1.- Correlación de las unidades estratigráficas del Viseense terminal (Brigantiense) de las cuencas de Moscú y Donetz, con referencia a algunas zonaciones de corales rugosos definidas en Gran Bretaña en diferentes fechas, y principales calizas del Brigantiense inferior del norte de Inglaterra. 1: fauna I de corales rugosos de MITCHELL (1989) y sus equivalentes en las otras zonaciones de corales rugosos referidas. 2: fauna J de corales rugosos de MITCHELL (1989) y sus equivalentes en las otras zonaciones de corales rugosos referidas. 1+ 2: rango de Orionastraea en Gran Bretaña. 3: rango de Orionastraea en la Cuenca de Moscú. 4: distribución de Orionastraea en la cuenca del Donetz.

Many species assigned to the genus are obviously synonyms. There is no doubt that for *Orionastraea* from the British Isles a revision of all types followed by careful studies of variability is required. As a first step, the collection of *Orionastraea* stored in the Natural History Museum, London has been examined in order to outline patterns of variability and evolution of the genus. It contains great number of the types and topotypes of most of the species and varieties described from Great Britain

Institutional abbreviations: PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow; BM, National History Museum, London; SM, Sedgwick Museum, Cambridge; IRScNB, Belgian Royal Institute of Natural Sciences, Brussels.

SYSTEMATIC DESCRIPTION

Suborder LITHOSTROTIONINA
SPASSKY & KACHANOV, 1971
Family Lithostrotionidae D'ORBIGNY, 1852
Genus *Orionastraea* SMITH, 1917

1916 *Orionastraea* SMITH, p. 3.
1917 *Orionastraea* SMITH, p. 294.
1926 *Orionastraea* SMITH; HUDSON, p. 145.
1929 *Orionastraea* SMITH; HUDSON, p. 441.
1940 *Orionastraea* SMITH (partim); HILL, p. 157.
1952 *Orionastraea* SMITH (partim); LECOMPTE, p. 473.
1956 *Orionastraea* SMITH (partim); HILL, p. F283.
1958 *Orionastraea* SMITH; DOBROLYUVOBA, p. 199.
1966 *Paraorionastraea* LIN (partim); reference not traced, quoted from YÜ *et al.*, 1983.
1970 *Orionastraea* SMITH (partim); KATO & MITCHELL, p. 47.
1974 *Orionastraea* SMITH (partim); JULL, p. 72.
1981 *Orionastraea* SMITH (partim); HILL, p. F381.
1983 *Orionastraea* SMITH (partim); YÜ *et al.*, p. 139.
1983 *Paraorionastraea* LIN (partim); YÜ *et al.*, p. 140.
1983 *Vesiorionastraea* YÜ, LIN, SHI, HUANG *et* YU (partim), p. 146.
1999 *Pleionastraea* NUDDS, p. 223.

Type species: Sarcinula phillipsi MCCOY, 1849, p. 125; Upper Grey Limestone, lower Brigantian; Haford-y-Calch, Corwen, North Wales.

Species assigned: Sarcinula phillipsi MCCOY, 1849, *S. placenta* MCCOY, 1849, *S. tuberosa* MCCOY, 1849, *Lithostrotion ensifer* MILNE-EDWARDS & HAIME, 1851, *Orionastraea indivisa* HUDSON, 1926, *O. edmondsi* HUDSON, 1929, *O. edmondsi* var. *laciniosa* HUDSON, 1929, *O. garwoodi* HUDSON, 1929, *O. garwoodi* var. *pristina* HUDSON, 1929, *O. garwoodi* var. *sera* HUDSON, 1929, *O. rete* HUDSON, 1929, *O. prerete* HUDSON, 1929, *O. phillipsi* MCCOY in HILL, 1940, *O. magna* KATO & MITCHELL, 1970, *O. rareseptata* DOBROLYUBOVA, 1958, *O. kurakovensis* DOBROLYUBOVA, 1958, *O. placenta* MCCOY *in* VASSILYUK (1964).

Many of the species mentioned are synonyms (see section «Patterns of variability in *Orionastraea*»).

Diagnosis (emended): pseudocerioid, astraeoid, thamnasterioid or aphroid Lithostrotionidae; vestigial corallite walls may be present; major and minor septa long including confluent or discontinuous towards periphery, seldom degenerated; columella, if present, formed by the axial end of the counter septum; tabulae complete or incomplete, conical to convex; dissepiments variable in shape, secondary dissepiments often present.

Remarks: it is generally accepted that *Orionastraea* is related to *Lithostrotion* and evolved from it by a gradual degeneration of corallite wall. Taking into account similar tabularia diameter and number of septa, NUDDS (1975, 1999) considered *Lithostrotion decipiens* (MCCOY, 1849) as the ancestral species of all *Orionastraea* except for *O. magna* and *O. ensifer* var. *matura*. For these two taxa characterized by larger tabularia and higher number of septa, he erected the genus *Pleionastraea* NUDDS, 1999 (= Gen. n. A NUDDS, 1980) with *Orionastraea magna* as the type species. According to NUDDS, *Pleionastraea* evolved from the larger species of *Lithostrotion* - *L. vorticale* (PARKINSON, 1808) - by following an evolutionary trend of corallite wall breakdown. *Pleionastraea matura* (= *O. ensifer* var. *matura*) possessing a vestigial corallite wall and columella is considered in this lineage as an intermediate stage between cerioid columellate *Lihostrotion vorticale* and astraeoid-thamnasterioid *Pleionastraea magna* (= *Orionastraea magna*) lacking corallite walls and columella.

Only two specimes of *O. ensifer* var. *matura* (the holotype and paratype) have been available to NUDDS (1999), both coming from the derived limestone boulder in the Namurian Upper Bowland Shales at Black Gill Beck, Settle. NUDDS (*ibid.*) estimated the age of these specimens as equating to the Lower Hawes Limestone (lowermost Brigantian) based on the common occurrence of a Brigantian fauna and nodules of *Girvanella* indicating the level of the *Girvanella* Band. In the type area of the Brigantian (Cumbria), the laterally persistent *Girvanella* Band occupies the topmost position in the Peghorn Limestone correlating with the lower part of the Hawes Limestone of North Yorkshire (GEORGE *et al.*, 1976;

JOHNSON *et al.*, 1995). HUDSON (1929, p.445) also recorded *Orionastraea ensifer* var. *matura* from the «lower part of D1 zone» at High Hill, settle but the specimens are reported missing (NUDDS, 1999). It should be mentioned that the lower limit of the D1 zone as recognized by HUDSON in North Yorkshire has a position higher that the base of the Asbian as defined in the type area (Cumbria). It approximates to the base of the D1 zone of VAUGHAN (1905) (see Table 1 in GEORGE *et al.*, 1976) corresponding to the lower limit of the Cf6 foraminiferal subzone, and to the lower limit of the fauna G of MITCHELL (RILEY, 1993). One can assume that *O. ensifer* var. *matura* entered in the upper Asbian and ranged through the lowermost Brigantian correlating with the lower part of the fauna H of MITCHELL, and with the lowermost part of the Cf6d foraminiferal subzone.

HUDSON (1929, p.445) regarded *Orionastraea ensifer* var. *matura* as a «definite earlier variant of *O. ensifer*» pointing at the «more pronounced epitheca» of the former as the most important distinctive character, and considering differences in size of tabularia and septal number less significant. NUDDS (1999) attaches more importance to the fact that *Lithostrotion vorticale* and *Pleionastraea matura* are identical in size of tabularia and septal number correctly inferring that *P. matura* differs from *Lithostrotion vorticale* only in incomplete corallite walls. *L. vorticale* in Europe ranges from the upper part of the Cf5 foraminiferal zone (upper Livian) through the lower part of the Cf6d foraminiferal subzone (POTY, 1993). In general, it is not a highly variable species, typically shows stout columellae, well developed and often beaded corallite walls, and rather regular dissepimentaria. Nevertheless, sometimes *L. vorticale* can demonstrate intracolonial variability possibly related to growth periodicity. It involves columellae, corallite walls and dissepimentaria. Variability of this kind can be observed in the specimen IRScNB I.G.3440-4 (upper part of the Cf 6g foraminiferal subzone, «F» - «H» Quarry, south of Visé, Belgium). The two transverse thin sections cut from this specimen and figured by POTY (1981, Pl. V, Figs. 2a, b) look rather different. Corallites in one of them (Fig. 2a) are larger due to wider dissepimentaria, show thin columellae and very thin walls. Like in the transverse thin section of the holotype of *Orionastraea ensifer* var. *matura* (HUDSON, 1929, Pl. IV, Fig. 4; NUDDS,1999, Pl. 1, Fig.1), these walls become discontinuous between some corallites for short intervals. The corallites in another section (POTY, 1981, Pl. V, Fig. 2b) are much smaller due to narrower dissepimentaria. They show thick to thin but always continuous walls, and columellae varying from thin to very thin, almost disappearing, thus resembling columellae in the transverse thin section of the holotype of *Orionastraea ensifer* var. *matura* (see NUDDS,1999, Pl.1, Fig.1). *O. ensifer* var. *matura* demonstrates striking similarity to *Lithostrotion vorticale* in longitudinal section as well, therefore it should be considered as its junior synonym.

All records of *O. magna* are from the *Orionastraea* Band of Settle district, North Yorkshire (KATO & MITHELL, 1970; NUDDS, 1999) which is developed at the very top of the Hardraw Scar Limestone (HICKS, 1959), i.e. occupies the highest position in the fauna I of MITCHELL. NUDDS (1999) gives the range of this species as equating to the Hardraw Scar Limestone and maintains that it has evolved from *Pleionastraea matura* occuring in the Lower Hawes Limestone (lowermost Brigantian). However, the two limestones (Upper Hawes and Gayle) developed in North Yorkshire between the Lower Hawes and the Hardraw Scar (GEORGE *et al.*, 1976; JOHNSON *et al.*, 1995) and lacking *Pleionastraea* are not considered.

Orionastraea magna is obviously the *Orionastraea* species closely related to some other representatives of the genus from northern England confined to the same interval. Thus, its corallites resemble some corallites in thin sections of the holotype of *O. edmondsi*, particularly large corallites in transverse sections BM R26471 and BM R26474 figured by HUDSON (1929, Pl. III, Figs. 3a, b), in large (sometimes oval) and poorly defined tabularia, in similar number of major septa and degenerated minor septa, and in irregular dissepimentaria. Therefore the genus *Pleionastraea* based on this species is to be considered as the junior synonym of *Orionastraea.*

Paraorionastraea LIN, 1966 is also synonymous with *Orionastraea.* Its type species *Sarcinula placenta* is extremely close to *S. phillipsi*, the type species of *Orionastraea*, and differs from it mainly in the absence of a columella. *Vesiorionastraea* YÜ, LIN, SHI, HUANG *et* YU, 1983 based on *Orionastraea heteroseptata* is another junior synonym of *Orionastraea.* The holotype of *O. heteroseptata* represents the example of variability of *O. rareseptata* with strongly pronounced aphroid tendency.

Distribution: uppermost Viséan, lower Brigantian. Jew Limestone and its equivalents; Bristol area, North Wales, Cumbria, North Yorkshire, Southern Uplands, Northern Ireland, Great Britain. Simonstone Limestone through the lower part of the Middle Limestone and equivalents; Cumbria, North Yorkshire, Great Britain; Central South Region, Republic of Ireland. Upper Crook Burn Limestone; western Northumberland, Great Britain. Uppermost Viséan; Aleksin horizon; north-western and southern parts of the Moscow Syneclise, Russia. Uppermost Viséan; Lublin region, Poland. Lower V_g subzone, Mezha Formation; Donets Basin, Ukraine.

Orionastraea rareseptata DOBROLYUBOVA, 1958
(Pl. 1, Figs. 1 - 3; Pl. 2, Figs. 1 - 2)

1958 *Orionastraea phillipsi* (MCCOY): DOBROLYUBOVA, p. 201; Pl. XXXIV, Fig. 2a, b; Pl. XXXV, Fig. 1
1958 *Orionastraea rareseptata* DOBROLYUBOVA, p. 205; Pl. XXXVII, Fig. 1a, b.
1958 *Orionastraea heteroseptata* DOBROLYUBOVA, p. 206; Pl. XXXVIII, Fig. 1a, b.
1977 *Orionastraea* cf. *ensifer* (MILNE-EDWARDS & HAIME); NGUEN, p. 348; Pl. 7, Fig. 4a, b.
1977 *Orionastraea* aff. *kurakovensis* DOBROLYUBOVA; NGUEN, p. 349; Pl. 8, Fig. 2; Pl. 9, Fig. 4a, b.
1977 *Orionastraea* aff. *magna* KATO & MITCHELL; NGUEN, p. 350; Pl. 8, Fig. 1a-c.

Holotype: Orionastraea rareseptata DOBROLYUBOVA, 1958. Specimen PIN 705/115 with three transverse and three longitudinal thin sections (same registration numbers). Two of the thin sections (one transverse and one longitudinal) were figured by DOBROLYUBOVA (1958; Pl. XXXVII, Fig.1a, b).

Stratum typicum: Limestone a_2, upper part of the Aleksin horizon, uppermost Viséan (Brigantian).

Locus typicus: Msta River near Vittsy Mine, 8 km SE of the town of Borovichi, north-western part of the Moscow Syneclise.

Material: four specimens; locality and age as for the holotype. Specimen PIN 705/112 with two transverse and two longitudinal thin sections (same registration numbers); specimen PIN 705/114a with four transverse thin sections (same registration numbers); specimen PIN 705/114b with four transverse thin sections (same registration numbers). These three specimens were attributed by DOBROLYUBOVA (1958) to *O. phillipsi* (MCCOY), and some of the thin sections were figured by her: Pl. XXXIV, Fig. 1a, b (PIN 705/112); Pl. XXXV, Fig. 1 (PIN 705/114b). Specimen PIN 705/113 with one transverse and one longitudinal thin sections (same registration numbers) is the type and unique specimen on which DOBROLYUBOVA (1958) based her new species *O. heteroseptata* (*ibid.*, p. 206; Pl. XXXVIII, Fig. 1a, b).

Diagnosis: aphroid, partly thamnasterioid-astracoid *Orionastraea* with thin vestigial corallite walls, columella thin to absent, 14-17 major septa, minor

PLATE 1

Figs. 1 - 3. - *Orionastraea rareseptata* DOBROLYUBOVA, 1958. Uppermost Viséan, Aleksin horizon, Limestone a_2; north-western part of the Moscow Syneclise, Msta River near Vittsy Mine, 8 km SE of the town of Borovichi.

Fig. 1. - Holotype, PIN 705/115; 1a, transverse thin section; 1b, c, longitudinal thin sections. Aphroid colony, major septa often restricted to tabularia, columellae lacking in most of the corallites. Sections represented on fig.1a, b have been figured by DOBROLYUBOVA, 1958, pl. XXXVII, fig. 1a, b.

Fig. 2. - PIN 705/114a; colony with septa of both orders developed and columellae often present. Successive transverse thin sections demonstrating intracolonial variability: 2a, aphroid, partly thamnasteriod; 2b, thamnasterioid with weakly developed aphroid interruption of septa.

Fig. 3. - PIN 705/114b; transverse thin section. Astraeoid-thamnasteriod colony with weakly developed aphroid interruption of septa, septa of both orders developed, columellae present in all corallites. This section has been figured by DOBROLYUBOVA, 1958, pl. XXXVI, fig. 1; the specimen has been attributed by her to *O. phillipsi*.

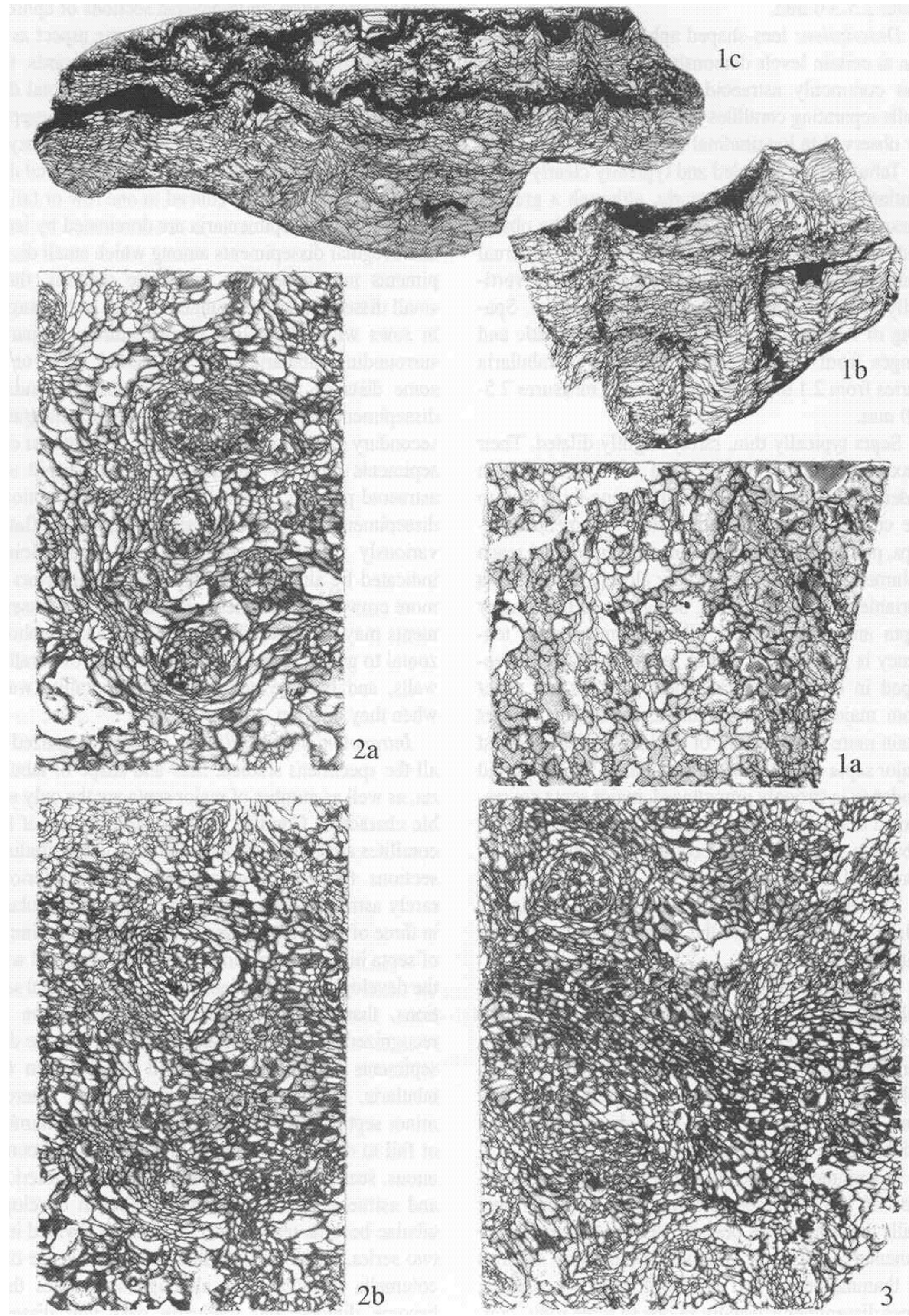
Figs. 1 – 3. *Orionastraea rareseptata* DOBROLYUBOVA, 1958. Viseense terminal, Horizonte Aleksin, Caliza a_2; noroeste de la Sinclisa de Moscú, Río Msta, próximo a la Mina Vittsy, a 8km al sureste de Borovichi.

LÁMINA 1

Fig. 1. Holotipo, PIN 705/115; 1a, sección transversal; 1b, c, secciones longitudinales. Colonia afroide, septos mayores frecuentemente limitados al tabulario, columnillas ausentes en la mayoría de los coralitos. Las secciones representadas en las figuras 1 a,b proceden de DOBROLYUBOVA, 1958, lám. XXXVII, fig. 1 a, b.

Fig. 2. – PIN 705/114a; colonia con los dos órdenes de septos desarrollados y con columnillas frecuentemente presentes. Secciones seriadas transversales mostrando la variabilidad intracolonial: 2a, afroide, parcialmente thamnasterioide; 2b, thamnasterioide con débil desarrollo de interrupciones afroides de los septos.

Fig. 3. – PIN 705/114b; sección transversal. Colonia astreoide-thamnasterioide con débil desarrollo de interrupciones afroides de los septos, los dos órdenes de septos desarrollados, columnillas presentes en todos los coralitos. Esta sección ha sido figurada por DOBROLYUBOVA, 1958, lám. XXXVI, fig. 1, ejemplar atribuido por esta autora a *O. phillipsi*.


1c
1b
2a
1a
2b
3

septa often less in number or absent, tabularium diameter 2.5-3.0 mm.

Description: lens-shaped aphroid colonies which can at certain levels demonstrate thamnasterioid and less commonly astraeoid tendency. Thin vestigial walls separating corallites are always present but better observed in longitudinal sections.

Tabularia are rounded and typically clearly differentiated from dissepimentaria, although a gradual passage of dissepiments into tabulae can be observed sometimes in longitudinal sections. Internal wall thin, rarely slightly dilated, formed by vertically inclined inner margins of dissepiments. Spacing of tabularia is very variable characteristic and ranges from 1.5 to 12 mm. Diameter of tabularia varies from 2.1 to 3.2 mm and usually measures 2.5-3.0 mm.

Septa typically thin, rarely slightly dilated. Their maximum number varies from 14 to 17 of both orders. Major septa extend half to one-third way to the centres of the tabularia; when columella develops, part of them (very seldom all major septa) reach columella or approaches it very closely. Minor septa variable in number, often being fewer than major septa and even absent. When thamnasterioid tendency is pronounced, minor septa can be well developed in dissepimentaria where they do not differ from major septa. In tabularia, minor septa never attain more than one half of the length of the shortest major septa or just penetrate tabularia. When aphroid tendency is strongly pronounced, major septa are restricted to the innermost series of dissepiments and to tabularia, and minor septa commonly reduce in number or fail to develop.

The columella (when present) is thin or slightly dilated, connected with the counter septum only or with few major septa.

Tabulae complete or incomplete, spaced rather irregularly from 0.25 to 1.0 mm (usually 0.25-0.5 mm) apart. In the absence of a columella, they are subhorizontal or slightly concave, rarely gently convex. When columella is present, tabulae become tent-shaped, seldom divided in two series with abaxially declined axial tabellae and flattened periaxial tabellae.

Dissepiments typically thin, except for inner margins of the innermost dissepiments forming inner walls that sometimes become slightly dilated. Dissepimentaria extremely variable. In transverse sections of thamnasterioid and astraeoid parts of colonies, inner dissepiments usually in one to three rows, concave towards the axis. Towards the periphery dissepiments increase in size, become irregular and random in orientation. In transverse sections of aphroid parts, inner dissepiments have the same aspect as in thamnasterioid and astraeoid parts; towards the periphery they pass through irregular transeptal dissepiments of second order into irregular transeptal dissepiments of first order. When aphroid tendency is especially strongly pronounced, inner interseptal dissepiments may become reduced to one row or fail to develop, and dissepimentaria are dominated by large and irregular dissepiments among which small dissepiments may appear. In transverse sections, these small dissepiments are rounded to oval and arranged in rows which look like chains entirely or partly surrounding tabularia next to internal walls or at some distance from them. Semicircular secondary dissepiments on primary dissepiments, elongated secondary dissepiments lining septa, and buttress dissepiments typically develop in thamnasterioid and astraeoid parts of colonies. In longitudinal sections, dissepiments are different in size and irregular, flat to variously inflated. Sometimes weak «periodicity» indicated by alternation of rather irregular layers of more crowded flat and less crowded inflated dissepiments may be discernible. These layers are subhorizontal to gently depressed in the absence of corallite walls, and become upturned to the corallite walls when they develop.

Intracolonial variability: it can be recognized in all the specimens studied. Size and shape of tabularia, as well as number of major septa are the only stable characters. Corallite walls separating part of the corallites are always present, although in longitudinal sections they are discontinuous. Thamnasterioid, rarely astraeoid tendency seem to appear irregularly in three of the four specimens studied, and continuity of septa in dissepimentaria is directly connected with the development of this tendency. In longitudinal sections, thamnasterioid and astraeoid parts can be recognized due to the presence of small globose dissepiments sometimes intersected by septa. In the tabularia, major septa can vary in length, whereas minor septa are always short, but can vary in number or fail to develop. Columella, if present, is discontinuous, seems to be more common in thamnasterioid and astraeoid parts of colonies. When it develops, tabulae become tent-shaped, sometimes divided into two series. Variability of tabulae in the absence of a columella is rather low, although sometimes they become divided and gradually pass into dissepiments. Compared to the other structures, dissepiments on the periphery of corallites demonstrate the highest intracolonial variability. They vary from rather regular interseptal dissepiments typically associated with secondary dissepiments (in thamnasterioid and astraeoid parts of colonies) to large irregular dissepiments of second order lacking secondary dissepiments (in aphroid parts). In longitudinal sections, layers of dissepiments are always upturned to corallite walls, and in adjacent corallites they usually are inclined towards tabularia at different angles.

Intercolonial variability within a biotope: a gradual passage from aphroid, partly thamnasterioid-astraeoid colonies to colonies with strongly developed aphroid tendency can be observed. The former show longer major septa (both in dissepimentaria and in tabularia), better developed minor septa, regular inner dissepiments in three or two rows and concave towards the axis, peripheral dissepiments strongly affected by intracolonial variability. Also, in some corallites discontinuous columellae with tabulae upturned to them are discernible. In the colonies with strongly pronounced aphroid tendency, major septa are often restricted to tabularia and very short, minor septa are fewer or lacking, tabulae are typically horizontal to concave, columella is absent, inner dissepiments are in one row or lacking, and peripheral dissepiments are less variable.

Remarks: O. rareseptata resembles *O. kurakovensis* in the type of colony but differs in smaller tabularia, lower septal number, minor septa often less developed, columella sometimes present, tabulae less regular and often incomplete, and secondary dissepiments better developed.

In size of tabularia, septal number, and in the patterns of variability, *O. rareseptata* is close to the *Orionastraea* from the Jew Limestone and its equivalents in England which are most probably conspecific although described under different names: *O. ensifer, O. phillipsi, O. edmondsi, O. edmondsi* var. *laciniosa* (see section «Variability in *Orionastraea*»). However, *O. rareseptata* never has such a stout columella as the types and some topotypes of *O. ensifer* and *O. phillipsi*. It also does not show herringbone dissepiments (even when minor septa fail to develop). Besides, in *O. rareseptata*, vestigial corallite walls are always present, dissepimentaria are more variable, and aphroid tendency is often stronger pronounced.

The four specimens from the uppermost Viséan of Lublin region, Poland identified by NGUEN (1977) as *O.* cf. *ensifer* (one specimen), *O.* aff. *kurakovensis* (two specimens), and *O.* aff. *magna* (one specimen) all belong to *O. rareseptata*. They are identical in size of tabularia, septal number, do not differ in other characters and demonstrate the same patterns of variability as the specimens from the Msta River. As regards the age of the Polish specimens, it may be considered as approximating to the age of the Russian specimens based on very similar rugose assemblage, especially on the common occurrence of *Nemistium dobrolyubovae* reported by NGUEN (*ibid.*) from the same interval. This species is restricted to the uppermost Viséan, and in the Moscow Syneclise, it has its acme in the Aleksin horizon. In the north-west of the Moscow Syneclise, both *N. dobrolyubovae* and *Orionastraea rareseptata* are confined to the Limestone a_2 only.

Distribution: upper part of the Aleksin horizon, uppermost Viséan (lower Brigantian); Msta River near Vittsy Mine, 8 km SE of the town of Borovichi, north-western part of the Moscow Syneclise. Uppermost Viséan (lower Brigantian); Lublin region, Poland.

Orionastraea kurakovensis DOBROLYUBOVA, 1958 (Pl. II, Fig. 3)

1958 *Orionastraea kurakovensis* DOBROLYUBOVA, p. 203; Pl. XXXVI, Fig. 1a, b.

Holotype: Orionastraea kurakovensis DOBROLYUBOVA, 1958. Specimen PIN 703/4968 with one transverse and one longitudinal thin sections (the same registration number), both figured by DOBROLYUBOVA (1958; Pl. XXXVI, Fig. 1a, b).

Stratum typicum: Aleksin horizon, uppermost Viséan (Brigantian).

Locus typicus: MOGK Quarry near Kurakovo railroad station, 25 km SW of the city of Tula, southern part of the Moscow Syneclise.

Material: the holotype only.

Diagnosis: aphroid, partly weakly astraeoid *Orionastraea* with thin vestigial corallite walls, no columella, 18-22 septa of both orders, tabularium diameter 3.5-4.5 mm.

Description: the only specimen represents part of a tabular aphroid, partly weakly astraeoid colony. About half of the corallites are separated by thin vestigial walls while dissepimentaria of the others are continuous.

Tabularia are round to oval and clearly differentiated from dissepimentaria both in transverse and longitudinal sections. Internal wall thin or slightly dilated, formed by vertically inclined inner margins of dissepiments. Tabularia are spaced 2.5-7.5 mm apart, their diameter is 3.5-4.5 mm.

Septa are thin, their maximum number varies from 18 to 22 of both orders. Major septa extend one-third way to the centre of tabularium and sometimes are slightly dilated near internal wall. Minor septa extend to inner row of dissepiments, just penetrating tabularium or fail to reach it. Septa, especially minor septa, are usually discontinuous at peripheral ends, but in some corallites part of major septa demonstrate astraeoid elongation.

Tabulae are usually complete broad flattened domes, rarely subhorizontal or incomplete, spaced 0.3-0.75 mm apart.

Dissepiments typically thin except for inner margins of innermost dissepiments forming inner walls that sometimes are slightly dilated. In transverse section, inner dissepiments usually in one to three rows, concave towards the axis. Dissepiments become less regular towards the periphery of corallites and commonly pass through transeptal dissepiments of second order into large irregular transeptal dissepiments of first order. Secondary dissepiments on primary dissepiments as well as buttress dissepiments are present but extremely rare. In longitudinal section, dissepiments are different in size and irregular, flat to variously inflated. They are arranged in more or less regular layers which are subhorizontal to gently domed when corallite walls are missing, or become upturned to the walls if they develop.

Variability: not studied on account of scarcity of the material.

Remarks: O. kurakovensis resembles *O. rareseptata* in the type of colony, but differs in larger tabularia, higher septal number, minor septa better developed, columella absent, tabulae generally complete and more regular, and secondary dissepiments poorly developed.

In the size of tabularia, septal number, and in absence of a columella, *O. kurakovensis* resembles *O. magna* from the top of the Hardraw Scar Limestone of North Yorkshire. However, it differs in the type of colony, in tabularia better differentiated and closer spaced, and in secondary dissepiments poorly developed.

Distribution: Aleksin horizon, uppermost Viséan (lower Brigantian); MOGK Quarry near Kurakovo railroad station, 25 km SW of the city of Tula, southern part of the Moscow Syneclise.

PLATE 2

Figs. 1 - 2. - *Orionastraea rareseptata* DOBROLYUBOVA, 1958. Uppermost Viséan, upper part of the Aleksin horizon, Limestone a_2; northwestern part of the Moscow Syneclise, Msta River near Vittsy Mine, 8 km SE of the town of Borovichi.

Fig. 1. - PIN 705/112; 1a, transverse thin section; 1b, longitudinal thin section. aphroid, partly thamnasterioid colony, columellae present. These sections have been figured by DOBROLYUBOVA, 1958, pl. XXXIV, fig. 2a, b; the specimen has been attributed by her to *O. phillipsi.*

Fig. 2. - PIN 705/113; 1a, transverse thin section; 1b, longitudinal thin section. Colony with strongly pronounced aphroid tendency: almost all major septa restricted to tabularia, minor septa less in number than major and often lacking, columellae lacking. These sections have been figured by DOBROLYUBOVA, 1958, pl. XXXVIII, fig. 1a, b; the specimen is the holotype of *O. heteroseptata* DOBROLYUBOVA, 1958.

Fig. 3. - *Orionastraea kurakovensis* DOBROLYUBOVA, 1958. Uppermost Viséan, Aleksin horizon; southern part of the Moscow Syneclise, MOGK Quarry near Kurakovo railroad station, 25 km SW of the city of Tula. Holotype, PIN 703/4968; 3a, transverse thin section; 3b, longitudinal thin section. These sections have been figured by DOBROLYUBOVA, 1958, pl. XXXVI, fig. 1a, b.

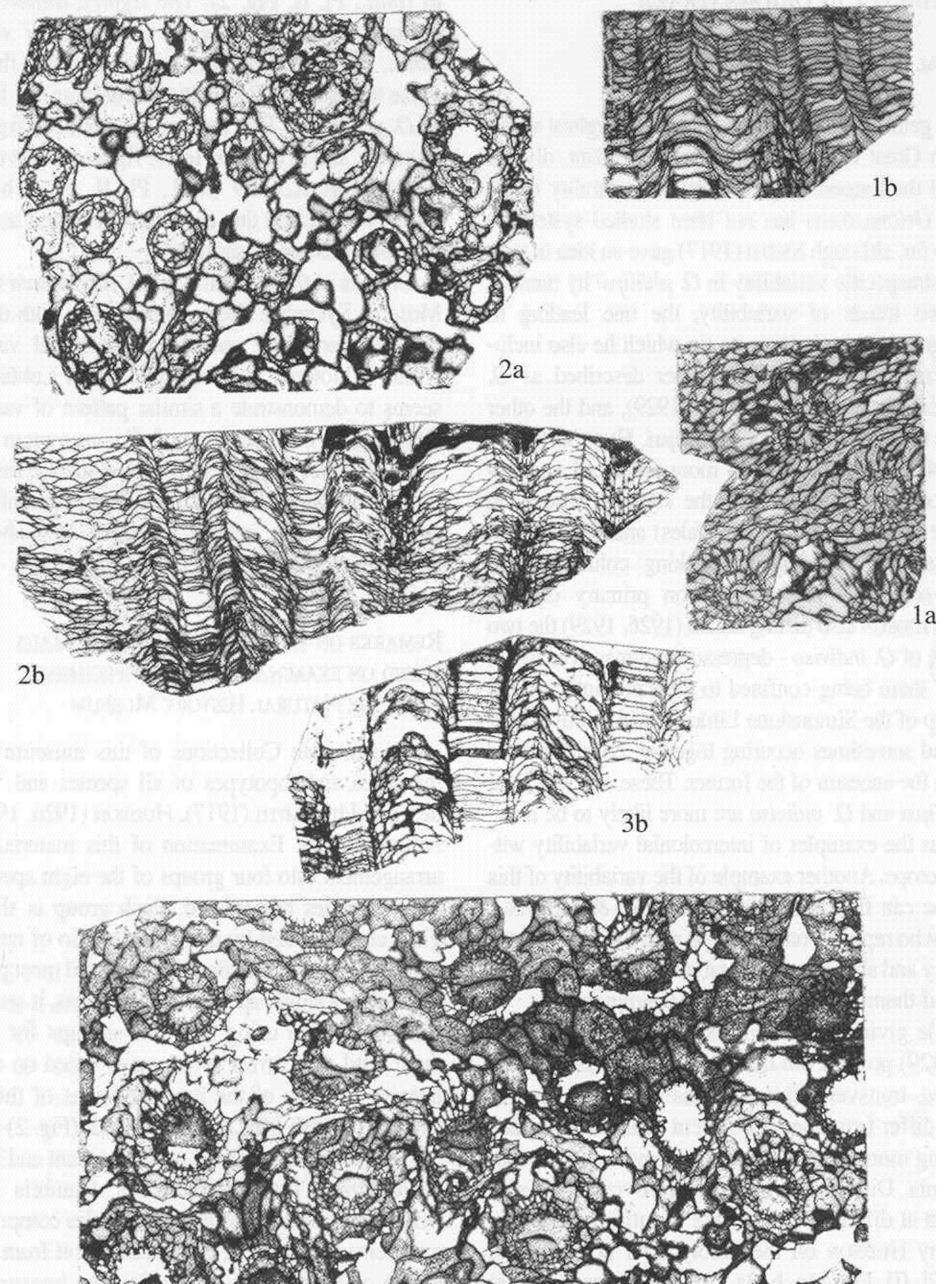
LÁMINA 2

Figs. 1 – 2. – *Orionastraea rareseptata* DOBROLYUBOVA, 1958. Viseense terminal, tramo superior del horizonte Aleksin, Caliza a_2; noroeste de la Sinclisa de Moscú, Río Msta, próximo a la Mina Vittsy, a 8km al sureste de Borovichi.

Fig. 1. PIN 705/112; 1a, sección transversal; 1b, sección longitudinal. Colonia afroide, paracialmente thamnasterioide, columnillas presentes. Estas secciones han sido figuradas por DOBROLYUBOVA, 1958, lám. XXXIV, fig. 2 a, b; ejemplar atribuido por esta autora a *O. phillipsi.*

Fig. 2. – PIN 705/113; 1a, sección transversal; 1b, sección longitudinal. Colonia con acusada tendencia afroide: la mayoría de los septos están limitados al tabulario, septos menores menos numerosos que los mayores y frecuentemente ausentes, columnillas ausentes. Secciones figuradas por DOBROLYUBOVA, 1958, lám. XXXVIII, fig. 1 a, b; este ejemplar ha sido designado como holotipo de *O. heteroseptata* DOBROLYUBOVA, 1958.

Fig. 3. – *Orionastarea kurakovensis* DOBROLYUBOVA, 1958. Viseense terminal, horizonte Aleksin; sureste de la Sinclisa de Moscú, Cantera MOGK, próxima a la estación de ferrocarril de Kurakovo, 25 km al suroeste de Tula. Holotipo, PIN 703/4968; 3a, sección transversal; sección longitudinal. Secciones figuradas por DOBROLYUBOVA, 1958, lám. XXXVI, fig. 1 a, b.


1b
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1 cm

VARIABILITY IN *ORIONASTRAEA*

GENERAL REMARKS

The genus *Orionastraea* exhibited its highest variability in Great Britain where it was abundant, diverse and had the longest range. However, variability in the British *Orionastraea* has not been studied systematically so far, although SMITH (1917) gave an idea of probable intraspecific variability in *O. phillipsi* by mentioning two trends of variability, the one leading to convergence with *O. placenta* (in which he also included forms from North Wales later described as *O. edmondsi* var. *laciniosa* HUDSON, 1929), and the other leading to *O. ensifer*. For *O. phillipsi*, HUDSON (1929, p.444, 452, 453) reported «a more advanced variety» which occurred together with the «typical variety» in the type area (Corwen, North Wales) and without it in Cumbria. This «variety» is lacking columella and shows secondary dissepiments on primary dissepiments. HUDSON also distinguished (1926, 1929) the two varieties of *O. indivisa* - depressed and massive, and in spite of them being confined to the same interval and area (top of the Simonstone Limestone in North Yorkshire) and sometimes occuring together, considered the latter as the ancestor of the former. These «varieties» of *O. phillipsi* and *O. indivisa* are more likely to be interpreted as the examples of intercolonial variability within a biotope. Another example of the variability of this kind one can find in the paper by KATO & MITCHELL (1970) who reported one paratype with marked aphroid tendency and slightly smaller tabularia among typically astraeoid-thamnasterioid types of *O. magna*.

While giving the diagnosis of *O. phillipsi*, HUDSON (1929) pointed out that in many species of *Orionastraea*, transverse thin sections cut at the base of colony differ from the sections cut near distal surface in having more confluent septa and more regular dissepiments. Differences between transverse thin sections cut at different levels were beautifully demonstrated by HUDSON on the holotype of *O. edmondsi* (*ibid.*, Pl. III, Figs. 1a, b, 3a, b). One can assume that he exemplified the intracolonial variability in *Orionastraea*, although he did not define this phenomenon in that way. However, he did not recognize similar phenomenon in *O. garwoodi* and established two varieties, *O. garwoodi* var. *pristina* and *O. garwoodi* var. *sera*. The figured part of the transverse thin section of the holotype of the former (*ibid.*, Pl. III, Fig. 4a) is identical with the lower part of the figured transverse thin section of the paratype of *O. garwoodi* (*ibid.*, Pl. II, Fig. 2). The figured transverse thin section of the holotype of *O. garwoodi* var. *sera* (*ibid.*, Pl. II, Fig. 3) does not differ from the transverse thin section BM R26498 cut from the holotype of *O. garwoodi*. This section has not been figured by HUDSON, and in contrast to the figured transverse thin section BM R26499 (*ibid.*, Pl. II, Fig. 1b), looks more complicated due to better developed secondary dissepiments lining septa.

Studies of the variability of *O. rareseptata* from the Moscow Syneclise allows to recognize both the intracolonial variability and the intercolonial variability within a biotope. *O. rareseptata* from Lublin region seems to demonstrate a similar pattern of variability. Comparison of specimens of *O. rareseptata* in both areas does not provide sufficient evidence for discerning the intraspecific (modificational) variability. This is most probably related to rather low abundance and/or high specialization of this species.

REMARKS ON VARIABILITY IN ORIONASTRAEA BASED ON EXAMINATION OF THE SPECIMENS FROM THE NATURAL HISTORY MUSEUM

Coelenterate Collections of this museum include the types and topotypes of all species and varieties described by SMITH (1917), HUDSON (1926, 1929) and NUDDS (1999). Examination of this material allows arrangement into four groups of the eight species and three varieties represented. Each group is short-ranging, characterized by quite stable ratio of number of major septa to tabularium diameter, and most probably represents a single species. Nevertheless, it seems reasonable to keep using the term «group» for most of them until the correct synonymies based on comprehensive revision of the representatives of this genus from the British Isles are established. (Fig. 2)

The first «group» is the most abundant and includes *Orionastraea* from North Wales, Cumbria and the Bristol area. Material from North Wales comprises one transverse thin section, BM R42396, cut from the lectotype of *O. phillipsi*, SM 213a; two transverse thin sections, BM R4510, labelled *O. phillipsi*; the paratype of *O. edmondsi* var. *laciniosa* (specimen BM R4412, one transverse and three longitudinal thin sections, BM R4412b); one transverse thin section, BM R4359, labelled *O. edmondsi* var. *laciniosa*. From Cumbria comes the holotype of *O. edmondsi* (specimen BM R26466-9, nine transverse, BM R26470-R26474, R26479-R26482, and four longitudinal thin sections, BM R26475-R26478). Material from the Bristol area inclu-

taxa included	type of colony	diameter of tabularium	number of major septa	axial structure	tabulae	secondary dissepiments	corallite walls	range	geographical distribution
O. ensifer *O. phillipsi* *O. edmondsi* *O. edmondsi* var. *laciniosa*	pseudocerioid astraeoid, astraeoid-thamnasterioid, thamnasterioid, thamnasterioid-aphroid	2.5-3.5	15-18	columella, a few major septa joined in the centre, lacking	complete or incomplete	not numerous; on primary dissepiments, lining septa, buttress	vestigial or lacking	H?-I	Bristol area, North Wales, Cumbria
O. prerete *O. rete* *O. indivisa*	thamnasteroid-astraeoid, astraeoid, aphroid-thamnasteriorid, aphroid with degenerated septa	1.5-2.0	12	lacking	incomplete	rare; on primary dissepiments	lacking or vestigial	top I-J	North Yorkshire Cumbria
O. garwoodi *O. garwoodi* var. *pristina* *O. garwoodi* var. *sera*	astraeoid-thamnasteriorid	2.0-2.5	12-14	a few major septa joined in the centre, lacking	incomplete	common; on primary dissepiments lining septa	lacking	J	North Yorkshire Cumbria

Figure 2.- Characteristic *Orionastraea* «groups» represented in the Coelenterata Collections of the Natural History Museum, London. Range is indicated in terms of the rugose coral faunas of MITCHELL (1989).
Figura 2.- «Grupos» característicos de Orionastraea *representados en las colecciones de celentéreos del Museo de Historia Natural de Londres. El rango está indicado en los términos de las faunas de corales rugosos de* MITCHELL *(1989).*

des one transverse thin section, BM R4577, labelled *O. radiata* and nine thin sections labelled *O. ensifer*: BM R15288 (transverse); BM R17084a (transverse); BM R17087 (two transverse and one longitudinal); BM R17090 (transverse); BM R19735 (transverse) and BM R19736 (longitudinal), both cut from the same specimen; BM 56740 (transverse). Six out of the twenty-six thin sections examined have been figured by SMITH (1917): BM R42396 (Pl. XXIII, Fig. 2); BM R4412b (Pl. XXIII, Figs 8,9); BM R4510 (Pl. XXIV, Fig. 1); BM R17084a (Pl. XXIV, Fig. 3); BM R17087 (Pl. XXIV, Fig. 4). Five sections have been figured by HUDSON (1929): BM R26480 and BM R26481 (Pl. III, Figs. 1a, b); BM R26475 (Pl. III, Fig. 2); BM R26471 and BM R26474 (Pl. III, Fig. 3a, b).The holotype of *O. edmondsi* comes from the from the upper part of the fauna I of MITCHELL (1989). It is confined to the *Orionastraea* Band developed at the top of the Pot Holes Limestone equating with the upper part of the Hardraw Scar Limestone. All North Wales records are from the «coral bed» at the top of the Upper Grey Limestone. According to GEORGE *et al.* (1976), this limestone correlates with the Hardraw Scar, and according to SOMERVILLE (pers. com.), the «coral bed» shows affinity with the Simonstone Limestone, thus approximating the upper part of the fauna I or the lower part of the fauna J of MITCHELL. However, HUDSON (1929) considered this bed as having a position lower than the Hardraw Scar based on the occurrence of *O. edmondsi* var. *laciniosa* adopted by him as the ancestor of *O. edmondsi*. The material from the Bristol area belongs to the classical D2 fauna of VAUGHAN (1905) attributed by MITCHELL to his fauna I.

This «group» is characterized by 15-18 septa of both orders, tabularia of medium size (typically 2.5-3.5 mm), axial structures varying from stout columella to few major septa joined in the center, or absent, tabulae complete or divided into two series, inner dissepiments typically concave towards the axis, secondary dissepiments (on primary dissepiments, lining septa and buttress) not numerous but always present. It includes pseudocerioid to astraeoid colonies with corallites separated by vestigial walls and typically possessing columellae (*ensifer* type), astraeoid-thamnasterioid colonies with corallites showing rare traces of walls and commonly developing collumellae (*phillipsi* type), predominantly astraeoid or predominantly thamnasterioid colonies with the counter septa extending far in tabularia and slightly dilated (*laciniosa* type), and generally aphroid colonies with thamnasterioid parts, few major septa sometimes joining in the center and extremely rare traces of corallite walls (*edmondsi* type). Colonies from North Wales and Cumbria demonstrate the three latter types with intermediate forms. Among colonies from the Bristol area, the *ensifer* type dominates, but thamnasterioid and aphroid colonies with corallites lacking columellae are also present. They resemble *O. edmondsi* var. *laciniosa* and *O. edmondsi* but have better developed corallite walls. It seems possible to recognize within this widely distributed «group» intraspecific variability with two modifications: one restricted to the Bristol area, another - to North Wales and Cumbria. The former differs from the latter chiefly in better developed corallite walls.

Members of the first «group» are also characterized by high intracolonial variability which involves various structures depending on the type of colony. In all types of colonies, however, septa, especially minor septa, vary in length, and peripheral dissepiments - in orientation. In astraeoid and thamnasterioid colonies, axial structures may vary from stout columellae to a few major septa joined at the centre or are lacking. Commonly, the elongated and slightly dilated counter septum is present in some corallites, whereas in the others only few major septa extend into tabularia. In aphroid colonies, axial structures are typically lacking, tabulae are random in orientation and seldom divided. When axial structures develop, tabulae are often abaxially declined, commonly divided into flattened periaxial and tent-shaped axial series. Aphroid tendency seems to occur sporadically in this «group», being especially characteristic for *O. edmondsi*. Both in the holotype of this species and in some thin sections labelled *O. ensifer*, this tendency is affected by intracolonial variability and becomes better pronounced in upper parts of colonies. Nevertheless, transeptal dissepiments in colonies attributed to this «group» are never large, rather regular and commonly develop on the periphery of corallites. In the patterns of variability this «group» resembles *O. rareseptata* although it does not have an aphroid tendency so strongly pronounced.

The second «group» includes the holotype of *O. prerete* (specimen BM R26483-5, two transverse, BM R26484 and BM R26486, and one longitudinal thin section, BM R26487); the holotype of *O. rete* (specimen BM R26492, one transverse, BM R26494, and one longitudinal thin section, BM R26495), the holotype of *O. indivisa* (specimen BM R26483-5, two transverse, BM R25236 and BM R25237, and one longitudinal thin section, BM R25238), the paratype of *O. indivisa* (specimen BM R25239, one transverse, BM R25240, and one longitudinal thin section, BM R25241), specimen BM R25242 identified by HUDSON (1929) as *O.* aff. *indivisa* and one longitudinal thin section, BM R25243, cut from it, specimen BM R26541 labelled *Orionastraea* sp. and one transverse thin section, BM R26596, cut from it. Six out of the twelve thin sections examined have been figured by HUDSON (1926): BM R25236-R25238 (Pl. VIII, Fig. 1a, b, c); BM R25240 and BM R25241 (Pl. VIII, Fig. 2a, b); BM R25243 (Pl. VIII, Fig. 3). Four thin sections have been figured by HUDSON (1929): BM R26486 and BM R26487 (Pl. I, Fig. 1a, b); BM R26494 and BM R26495 (Pl. I, Fig. 2a, b). All material comes from North Yorkshire. The types of *O. prerete* and *O. indivisa* are from the Simonstone Limestone equating with the lower part of the fauna J of MITCHELL (1989), whereas the holotype of *O. rete* is from the lower part of the Middle Limestone, that is from the upper part of this fauna.

All members of this «group» are lacking axial structures. They have small tabularia (1.5-2.0 mm in diameter), septa low in number (maximum 24 in total) and never extending well into tabularium, tabulae incomplete and typically concave, inner dissepiments concave towards the axis and partly or completely replaced by small vesicles preventing septal penetration into tabularium. Variability in type of colony is especially characteristic, and the «group» includes thamnasterioid-astraeoid colonies with rare traces of corallite walls (*prerete* type), thamnasterioid-astraeoid partly aphroid colonies (*rete* type), and very special kind of aphroid colonies with irregular dissepimentarium and septa so strongly degenerated that in certain thin sections they give an impression of being missing (*indivisa* type). For the latter NUDDS (1979a) introduced the name indivisoid and suggested that corallites in such colonies did not develop septa. Intracolonial variability in the second «group» is less important and mostly involves septa which vary in number and length. Dissepimentarium is generally more variable in colonies of the *rete* type. It shows irregularly oriented interseptal peripheral dissepiments associated with secondary dissepiments which become partly replaced by large irregular transeptal dissepiments.

It should be mentioned, that a similar pattern of variability can be observed in another «group» of the British *Orionastraea* comprising *O. placenta*, *O. tuberosa* and *O.* aff. *indivisa* as interpreted by MITCHELL *in*

STEVENSON & GAUNT, 1971. This «group» is not discussed here, since it is not represented in the collection of the Natural History Museum. It resembles the second «group» in the type of colonies (thamnasterioid-astraeoid with traces of corallite walls and colonies of the *indivisa* type) but is distinguished by corallites with bigger tabularia and higher septal number.

The third «group» which may be discerned among *Orionastraea* specimes from the Natural History Museum comprises the holotype of *O. garwoodi* (specimen BM R26497, two transverse, BM R26498 and BM R26499, and one longitudinal thin section, BM R26402), the paratype of *O. garwoodi* (specimen BM R26503 and one transverse thin section, BM R26504), the holotype of *O. garwoodi* var. *pristina* (specimen BM R26461-3, one transverse, BM R26464, and one longitudinal thin section, BM R26465), and the holotype of *O. garwoodi* var. *sera* (specimen BM R26407 and three transverse thin sections, BM R26508-R26510). Six out of the nine thin sections examined have been figured by HUDSON (1929): BM R26502 and BM R26499 (Pl. II, Fig. 1a,b); BM R26504 (Pl. II, Fig. 2); BM R 26510 (Pl. II, Fig. 3); BM R26464 and BM R26465 (Pl. III, Fig. 4a, b). The types of *O. garwoodi* and *O. garwoodi* var. *pristina* come from the lower part of the Middle Limestone in North Yorkshire, i.e. from the interval equating with the upper part of the fauna J of MITCHELL (1989). *O. garwoodi* var. *sera* is based on two specimens from the Fourth Limestone in Cumbria collected «immediately above the sandstone which follows the Pot Holes Limestone» (HUDSON, 1929, p. 454), thus being confined to a rather low level in the fauna J. Nevertheless, HUDSON considered *O. garwoodi* var. *sera* as structurally more advanced compared to *O. garwoodi*, and in the description of the variety (*ibid*., p. 450) indicated, although with a questionmark, a higher level of its occurrence (*junceum* Bed) equating with the upper part of the fauna J.

This «group» is characterized by astraeoid-thamnasterioid colonies, continuous 12-14 septa of both orders, tabularium 2.0-2.5 mm in diameter, the counter septum often extending to the centre and sometimes joining the cardinal septum and a few elongated major septa, tabulae incomplete and random in orientation, inner dissepiments regular and concave towards the axis, peripheral dissepiments typically convex towards the axis. Secondary dissepiments on primary dissepiments and along septa are very characteristic. They are best developed in central part of colonies near their distal surfaces, thus demonstrating intracolonial topomorphic variability and/or intracolonial variability related to astogeny.

The specimen BM R49922 is the only specimen in the collections of the Natural History Museum belonging to *O. magna*. Transverse thin section cut from it, BM R49922a, has been figured by NUDDS (1999, Pl. 1, Fig 5). This species as described by KATO & MITCHELL (1970) and NUDDS (1999) is predominantly astraeoid-thamnasterioid, typically has 15-17continuous major septa and incomplete subhorizontal tabulae. As it has been already mentioned, *O. magna* demonstrates intercolonial variability within a biotope. Intracolonial variability in this species is also marked and mostly involves minor septa varying in number and in length, and dissepimentaria. At their periphery, large irregular interseptal dissepiments of second order may replace interseptal dissepiments which are random in orientation and often associated with secondary dissepiments lining septa.

EVOLUTION IN *ORIONASTRAEA*

Since HUDSON (1926, 1929) published on the British *Orionastraea*, the distribution of the genus in the British Isles has been reinterpreted based on the records from western Northumberland (JOHNSON, 1959), south-east Derbyshire (GEORGE *et al.*, 1976) and Ireland (NUDDS, 1979b). A form transitional between *O. ensifer* and *O. phillipsi* has been reported from in western Northumberland (JOHNSON, 1959) where it occurred in the Upper Crook Burn Limestone correlating with the top of the Hawes Limestone (JOHNSON *et al.*, 1995). Therefore, the possibility that the lowermost occurrence of the genus could be confined to the fauna H of MITCHELL in northern England cannot be excluded. Both records belong to the first «group» as adopted in the present paper. It persisted through the interval of the Brigantian correlated with the fauna I of MITCHELL(1989) and is reported from Bristol area, North Wales, northern England and Southern Uplands (SMITH, 1917; HUDSON, 1929; HILL, 1940). This «group» probably gave rise to *O. rareseptata* reported from the north-west of the Moscow Syneclise and from the Lublin region, and to *O. kurakovensis* restricted to the southern part of the Moscow Syneclise during the first stage of evolution in *Orionastraea*.

The next stage of evolution in the genus was confined to the interval correlating with the topmost part of the Hardraw Scar Cyclothem. Two thamnasterioid-astraeoid species, both lacking axial structures but strongly differing in size of tabularia are reported from this interval in northern England - large *O. magna* (KATO & MITCHELL, 1970; NUDDS, 1999) and small *O. prerete* (HICKS, 1959). The former was extremely short-ranging and occurred at the very top of the Hadraw Scar Limestone in a restricted area of North Yorkshire, the latter belonged to the second «group» discerned in *Orionastraea*. It persisted higher in the Brigantian and represented one of the important elements of the fauna J of MITCHELL (1989) in northern England. It was especially characteristic there for the lower part of this fauna, that is for the *O. indivisa* subzone of HUDSON (1929). This «group» also occurred in central southern region of Ireland (NUDDS, 1979b). A closely related species is reported from the Donets Basin (VASSILYUK, 1964).

It is highly probable that during the same stage of evolution *O. placenta* appeared. It is characteristic of the upper part of the fauna I of MITCHELL (1989) in Derbyshire, occurs there near the top of the Upper Monsal Dale Beds and its equivalents (SMITH, 1917; HUDSON, 1929; STEVENSON & GAUNT, 1971; GEORGE *et al.*, 1976; MITCHELL, 1989), and is adopted also as *O. tuberosa* and *O.* aff. *indivisa*. Records of this species from northern Ireland (NUDDS, 1979b) are possibly confined to the fauna I of MITCHELL.

Exclusively astraeoid-thamnastreioid *Orionastraea* species, typically possessing numerous secondary dissepiments and adopted here as the third «group», appeared at the last stage of evolution of the genus and remained restricted to northern England. According to HUDSON (1929), they were especially characteristic of the lower part of the Middle Limestone (*O. garwoodi* subzone), that is, to the interval equating to the upper part of the fauna J of MITCHELL.

All the «groups» and species that appeared during the two first stages of evolution of the genus often possessed vestigial corallite walls and exhibited aphroid tendency as a result of both intracolonial variability and intercolonial variability within a biotope. In the youngest «group», these characters are not observed. Therefore, the aphroid type of colony does not appear to be the evolutionary most advanced in *Orionastraea*.

CONCLUSIONS

1. *Orionastraea* is a short-ranging genus characteristic of the middle part of the uppermost Viséan (Brigantian). It was abundant and diverse in Great Britain, and also occurred in Ireland, Russia (Moscow Syneclise), Poland (Lublin region) and Ukraine (Donets Basin). *Paraorionastraea*, *Vesiorionastraea* and *Pleionastraea* are here considered to be junior synonyms of *Orionastraea*.
2. Studies of the variability of the Russian *Orionastraea* demonstrate that they belong to the two species: *O. rareseptata* occurring in the north-western part of the Moscow Syneclise, and *O. kurakovensis* occurring in its southern part, both restricted to the upper part of the Aleksin horizon. The former species is also reported from Poland.
3. Examination of *Orionastraea* specimens from the Bristol area, North Wales, Cumbria and North Yorkshire in the Natural History Museum, allows to recognize four short-ranging species, three of which include synonymous species and are adopted here as «groups» until the genus is thoroughly revised and correct synonymies are established. One more «group» was restricted to Derbyshire.
4. Three stages of evolution can be discerned in the genus. Both species reported from Russia seem to have appeared during the first stage of evolution near the lower limit of the rugose coral fauna I of MITCHELL (1989).

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