Parallel evolution in European rugose corals of the genus *Lonsdaleia* McCoy, 1849 (Lower Carboniferous).

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Abstract

Two lineages, both leading to cerioid and subcerioid species, can be discerned in the evolution of the genus *Lonsdaleia* McCoy, 1849: *L. (Lonsdaleia) duplicata* (MARTIN, 1809) gave rise to the subgenus *Actinocyathus* D'ORBIGNY, 1849 (considered here as a subgenus of *Lonsdaleia*) at the beginning of the latest Viséan in northern Europe, and *L. (Lonsdaleia) redondensis* sp. nov. or a related species possibly evolved into *L. (Serraphyllum)* subgen. nov. near the Viséan/Serpukhovian transition in South France. Three new species of the genus *Lonsdaleia* are described from the uppermost Viséan and Serpukhovian of the Montagne Noire (South France), including two species assigned to the subgenus *L. (Serraphyllum)*. Two species of the subgenus *L. (Actinocyathus)* are redescribed from the Serpukhovian of the Moscow Basin. Parallel evolution in *Actinocyathus* and *Serraphyllum* during the Serpukhovian is discussed.

Key-words: *Lonsdaleia* – evolution – variability – Lower Carboniferous – Europe

Résumé

Deux lignées conduisant chacune à des espèces subcérioïdes et cérioïdes peuvent être reconnues dans l'évolution du genre *Lonsdaleia* MCCOY, 1849: la première donne naissance, dans le nord de l'Europe, au début du Viséen terminal et au départ de l'espèce fasciculée *L. (Lonsdaleia) duplicata* (MARTIN, 1809), à *Actinocyathus* D'ORBIGNY, 1849 (considéré ici comme un sous-genre de *Lonsdaleia*); la seconde donne probablement naissance, dans le sud de la France, lors de la transition du Viséen au Serpukhovien et au départ de *L. (Lonsdaleia) redondensis* sp. nov. ou d'une espèce proche de celle-ci, à *L. (Serraphyllum)* subgen. nov. Trois nouvelles espèces du Viséen terminal et du Serpukhovien de la Montagne Noire (sud de la France) et appartenant au genre *Lonsdaleia* sont décrites; deux d'entre elles sont attribuées au sous-genre *L. (Serraphyllum)*. Deux espèces appartenant au sous-genre *L. (Actinocyathus)* du Serpukhovien du Bassin de Moscou sont redécrites. L'évolution parallèle d' *Actinocyathus* et de *Serraphyllum* pendant le Serpukhovien est discutée.

Mots-clefs: *Lonsdaleia* – évolution – variabilité – Carbonifère inférieur – Europe

Introduction

The objectives of the present paper are: to discuss evolution in *Lonsdaleia* MCCOY, 1849 leading to cerioid and subcerioid species; to demonstrate parallel evolution in *Lonsdaleia* during the Serpukhovian; and to describe new species belonging to this genus.

L. (Actinocyathus) was derived from *L. (Lonsdaleia) duplicata* (MARTIN, 1809) (SMITH, 1916) at the very beginning of the latest Viséan and ranges from the uppermost Viséan through the Serpukhovian. Various species belonging to this subgenus can be found in Great Britain, Belgium, Poland, the East European Platform, the Urals and China (MCCOY, 1849; MILNE-EDWARDS & HAIME, 1851, 1852; STUCKENBERG, 1895, 1904; SMITH, 1916; GORSKY, 1938; HILL, 1940; DOBROLYUBOVA, 1958; VASILYUK, 1960; POTY, 1981; YÜ *et al.*, 1983; KOZYREVA, 1984, etc.). This subgenus reached its maximum abundance and diversity in the Moscow Basin, where it comprised nine species (HECKER, 1997).

L. (Lonsdaleia) has the same range as *L. (Actinocyathus)* and is reported from the same areas (*ibid.*), and also from Spain, South France (SEMENOFF-TIAN-CHANSKY & OVTRACHT, 1965; PERRET & SEMENOFF-TIAN-CHANSKY, 1971; POTY *et al.* (2002), and from Nova Scotia (POTY, in press).

Four *Lonsdaleia* species are characteristic of the uppermost Viséan and Serpukhovian of the Montagne Noire (South France). Three of them, including two species assigned to the subgenus *L. (Serraphyllum)* subgen. nov., are described in the present paper by the senior author. *Serraphyllum* is restricted to the Serpukhovian. It is distinguished by a fasciculate to subcerioid habitus and exhibits similarities with some Serpukhovian *Actinocyathus*. In corallite morphology and in patterns of variability it approaches two Serpukhovian species belonging to the *L. (Actinocyathus) floriformis* species-group – *L. (A.) borealis* (DOBROLYUBOVA, 1958) and *L. (A.) rossica* (STUCKENBERG, 1904). Therefore, updated descriptions, documenting the variability are given herein by the junior author, based on the material from the Moscow Basin.

Repositories

The collections are housed in the Laboratory of Animal and Human Palaeontology, Liège University (L.P.U.Lg.), and in the Palaeontological Institute, Russian Academy of Sciences (PIN) as part of the collections registered under n° 703, 704, 705, 1562. The abbreviation CNIGRM denotes the Central Scientific-Research Geological Exploration Museum, St. Petersburg.

Geological and palaeogeographical setting

The *Lonsdaleia* species described in this paper were collected in the southeastern part of the Montagne Noire (Mont Peyroux nappe and Cabrières slices) in the bodies of massive limestones ("Calcaires à *Productus*") corresponding to olistoliths (ENGELS *et al.*, 1981) (Fig. 1). These limestones, deposited in shallow-water environments, are almost totally composed of boundstones constructed mainly by microbialites and secondarily by corals, bryozoans and sponges. They are divided into two formations: the Roque Redonde Formation and the Roc de Murviel Formation, dated as latest Viséan (Upper Warnantian, Coral Zone RC8, Foraminifer Subzone Cf6δ) and Serpukhovian (Coral Zone "RC9", Foraminifer Zone Cf7), respectively (POTY *et al.*, 2002) (Fig. 2).

The Roque Redonde Formation has yielded rugose corals belonging to the genera *Aulokoninckophyllum* SANDO, 1976, *Axophyllum* MILNE-EDWARDS & HAIME, 1850, *Clisiophyllum* DANA, 1846, *Dibunophyllum* THOMSON & NICHOLSON, 1876, *Diphyphyllum* LONSDALE, 1845, *Haplolasma* SEMENOFF-TIAN-CHANSKY, 1974, *Kizilia* DEGTYAREV, 1965, *Lithostrotion* FLEMING, 1828, *Lonsdaleia* (*Lonsdaleia*), *Melanophyllidium* KROPACHEVA, 1966, *Nemistium* SMITH, 1928, *Palaeosmilia* MILNE-EDWARDS & HAIME, 1848, *Palastraea* MCCOY, 1851, *Pareynia* SEMENOFF-TIAN-CHANSKY, 1974, *Semenoffia* POTY, 1981, *Siphonodendron* MCCOY, 1849, *Siphonophyllia* SCOULER, 1844, and *Solenodendron* SANDO, 1976. The occurrence of *Lonsdaleia*, *Nemistium* and *Palastraea* is characteristic of the RC8 Coral Zone (POTY, 1985; CONIL *et al.*, 1990), indicating the latest Viséan age of the formation. No lonsdaleids with a cerioid habitus have been recorded from this interval.

The Roc de Murviel Formation has yielded species belonging to *Axophyllum*, *Clisiophyllum*, *Corwenia* SMITH & RYDER, 1926, *Dibunophyllum*, *Diphyphyllum*, *Gangamophyllum* GORSKY, 1938, *Haplolasma*, *Kizilia*, *Lithostrotion*, *Lonsdaleia* (*Lonsdaleia*), *L.* (*Serraphyllum*), *Palaeosmilia*, *Palastraea*, *Si-*

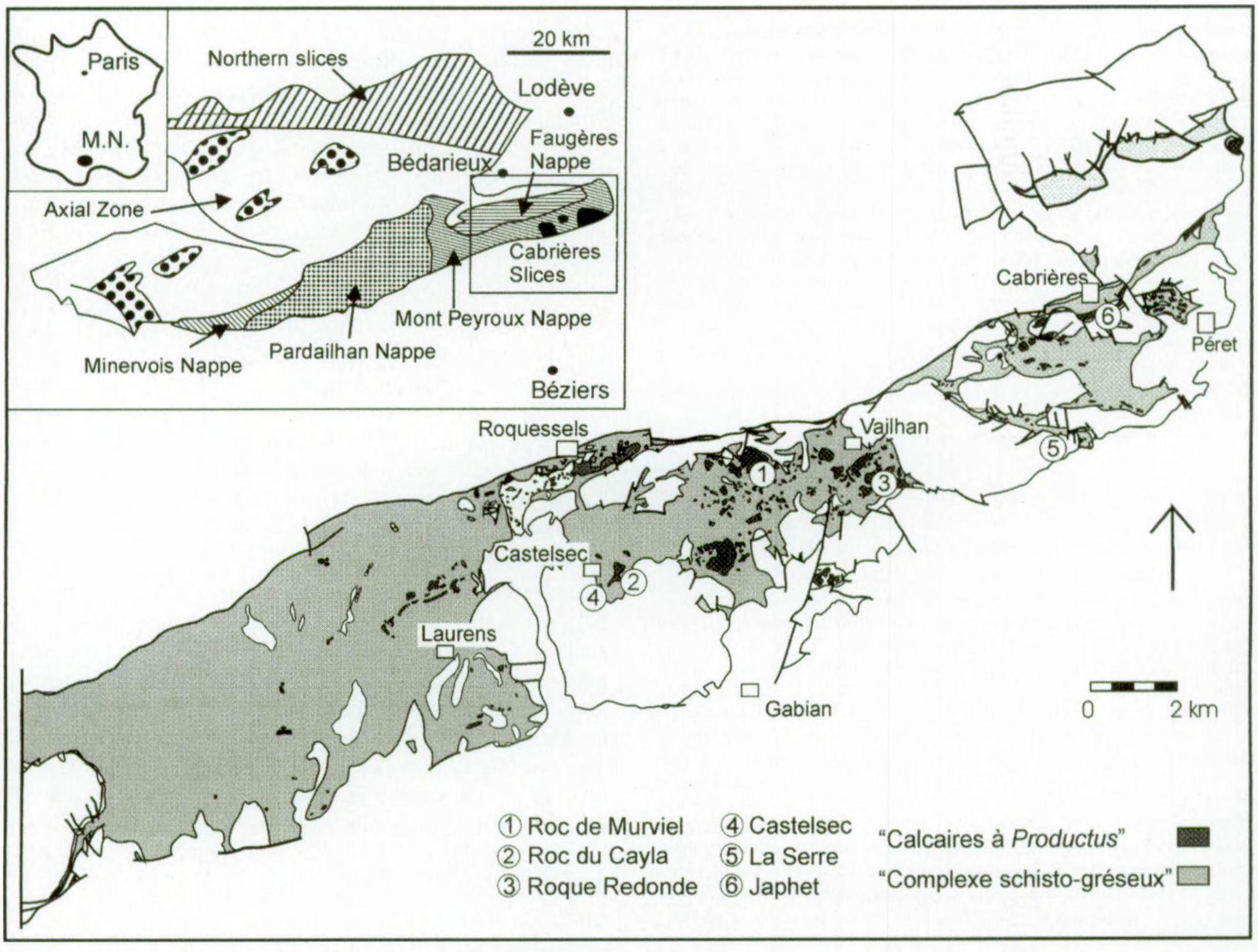

Fig. 1 — Location map of the Upper Viséan and Serpukhovian limestones ("Calcaires à *Productus*") on the southeastern edge of the Montagne Noire. Main sections containing rugose corals are indicated.

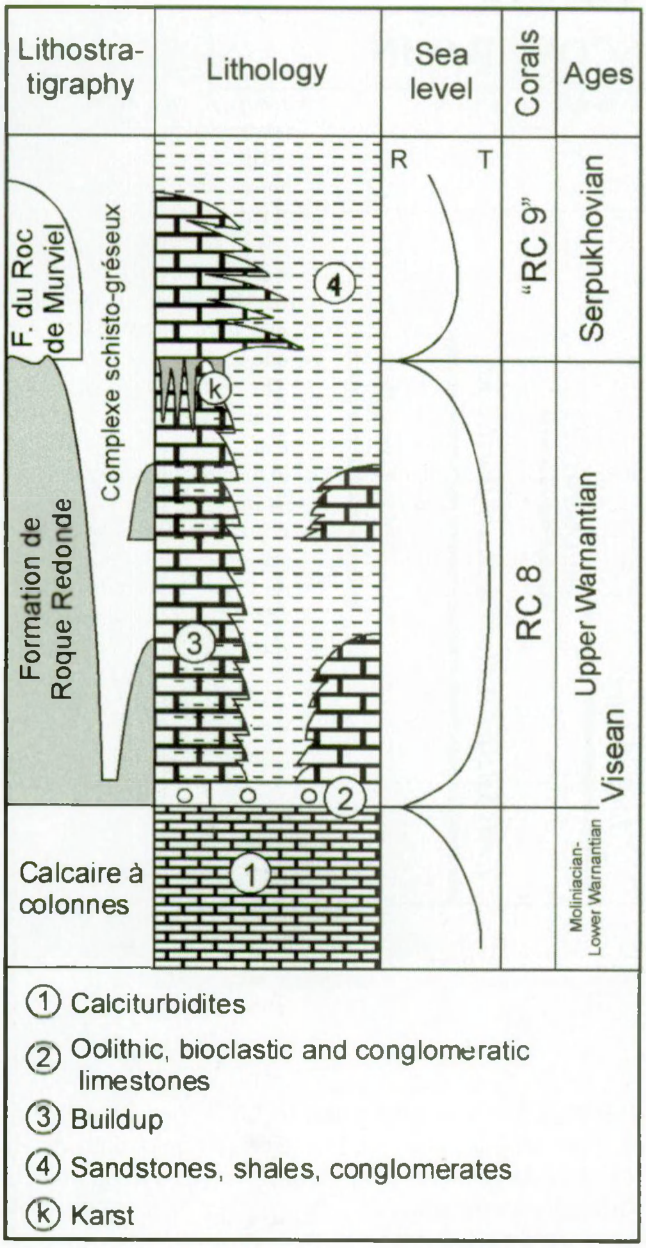

Fig. 2 — Stratigraphy and lithology of the formations of the Upper Viséan and Serpukhovian of the Montagne Noire in their reconstructed original position before being reworked into flysch during the Variscan orogeny.

phonodendron, and to an undescribed colonial heterocoral genus. Some species constituting this association are reported from the Ardengost Limestone in the High Pyrenees (PERRET & SEMENOFF-TIAN-CHANSKY, 1971) and from Lanet, Mouthoumet Massif, Hautes Corbières (SEMENOFF-TIAN-CHANSKY & OVTRACHT, 1965). In the Montagne Noire, the first cerioid lonsdaleids appear in this formation.

The material for the two *Lonsdaleia (Actinocyathus)* species redescribed in this paper comes from the Serpukhovian deposits of the Moscow Basin (Tarusa through the Protva horizons) (Fig. 3). In the Serpukhovian, this area indicated a very special set of environments (OSIPOVA & BELSKAYA, 1965, 1969; OSIPOVA *et al.*, 1983), which was especially characteristic of Steshevo time (Fig. 4).

Actinocyathus rossicus has been recorded only from the southern part of the basin. Most records are from bedded crinoidal limestones with abundant corals, brachiopods and bryozoans (upper Steshevo horizon). These limestones are interpreted as deposits of the zone of bottom currents bordering the lagoon confined to the shoals in the outer zone of the near-shore part of the basin (OSIPOVA & BELSKAYA, 1965). Two principal localities for this type of habitat are at the village of Luzhki and near the village of Toropovo. Solitary species belonging to the genera *Pseudozaphrentoides* STUCKENBERG, 1904 and *Turbinatocaninia* DOBROLYUBOVA, 1970 dominate among rugose corals in both localities; *Actinocyathus rossicus* is the only non-fasciculate species ever reported from Toropovo and Luzhki. Thickness of limestones exposed at Luzhki is 6 m, and colonies of *A. rossicus* are confined to two levels – one in the lower two meters, another in the upper two meters (IVANOV, 1928). Steshevo deposits exposed near Toropovo are 7 m thick and consist of bedded crinoidal limestones alternating with thin layers of marls. Two beds of limestones with abundant *Diphyphyllum*, *Nemistium*, *Pseudozaphrentoides* and *Turbinatocaninia*, each 0.4 - 0.5 m thick, may be discerned; *Actinocyathus rossicus* is restricted to the lower of these two beds (OSIPOVA, 1997). Only two specimens of this species were found in the Tarusa horizon (at the locality near the village of Voskresenskaya and in the Zabor'e quarry). They are confined to detrital and foraminiferal limestones interpreted as the open-sea deposits by OSIPOVA & BELSKAYA (1965).

Records of *A. borealis* in the Moscow Basin are predominantly from its northwestern and western parts. Most of the specimens were collected around the town of Borovichi (northwestern part of the basin) from bedded bioclastic limestone with abundant chaetetids, syringoporids and *Diphyphyllum* (top of the Steshevo horizon). This limestone unit, 2.0 - 2.2 m thick, is interpreted as deposits of the offshore part of the basin characterized by active hydrodynamics. As suggested by OSIPOVA & BELSKAYA (1965) and OSIPOVA (1997), these deposits were confined to habitats in the zone of bottom currents. In Steshevo time, these habitats in the northwestern part of the basin were not affected by the influence of the coast (terrigenous supply, recurrent increase of magnesium content, etc.) and therefore were especially favourable for rugose and tabulate corals. The most characteristic occurrences of this type of environment are: the locality at the village of Podbor'e, and few localities on the Msta River, 12 - 20 km southwest of Borovichi, including the localities on the Sukhaya Poneredka Brook, near the villages of Maly Porog and Marinskoe. Only a few specimens of this species were collected from the limestones confined to environments distinguished by active hydrodynamics, but affected by recurrent increase of magnesium content in Protva time or by terrigenous supply in Tarusa and Steshevo times. The characteristic occurrences of the former type of environment are: the localities on the Ragusha River and near the town of Uglovka, and the locality near the village of Zarech'e (northwestern and western parts of the basin, respectively). The characteristic occurrences of the latter type of environment are on the Tutoka River (northwestern part of the basin, Tarusa and Steshevo horizons). Also, not many specimens were collected from deposits of the near-shore shallow-water part of the basin represented by limestones alternating with sands and silts. In the northwestern part of the basin,

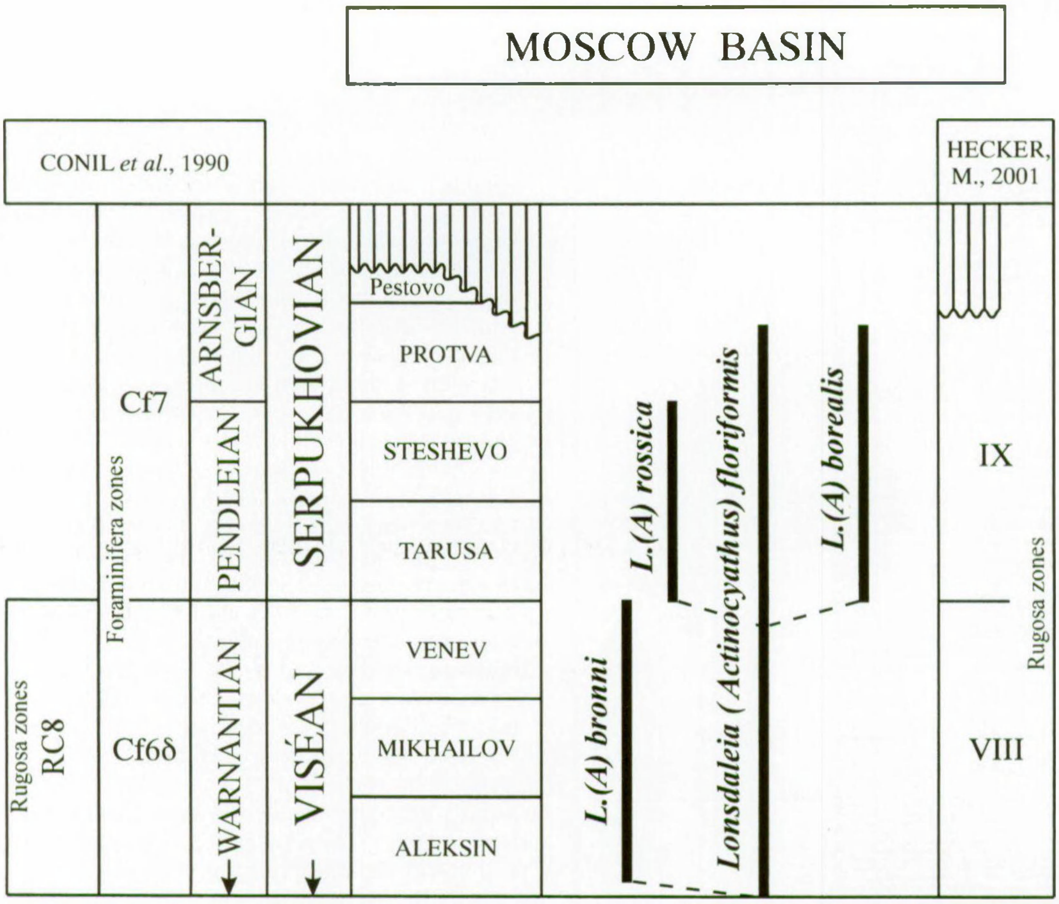

Fig. 3 — Range and phyletic relations of species of the *Lonsdaleia (Actinocyathus) floriformis* group in the Moscow Basin during latest Viséan and Serpukhovian (partly after HECKER, 1997).

the characteristic occurrences of this type of environment are at the village of Slizikha and on the Mokraya Poneredka Brook (Steshevo horizon), and in the western part – the locality at the village of Baranova Gora (Tarusa horizon). In the southern part of the basin, records of *Actinocyathus borealis* are extremely rare and associated with deposits of the open-sea zone; one specimen was collected in the Pogorel'skoe quarry (Tarusa horizon), another – on the Osetr River (Steshevo horizon).

Taxonomy

Genus *Lonsdaleia* McCoy, 1849

DIAGNOSIS: Fasciculate, subcerioid or cerioid. Increase lateral, nonparricidal. Axial column usually well-defined, more or less complex and thickened, comprising a medial plate connected to the cardinal and/or to the counter septum, radial lamellae, and axial tabellae, or sporadically reduced to a medial plate or absent. Minor septa indistinct to well developed. Dissepimentarium dominated by transeptal dissepiments. Cardinal fossula indistinct, uncommonly inconspicuous. Periaxial tabellae slightly concave, subhorizontal or declined outward or inward, commonly complete.

REMARKS: The emended genus includes species of *Serraphyllum* subgen. nov., and of *Actinocyathus* considered here as a subgenus, both exhibiting a cerioid trend in their variable growth habit.

Subgenus *Lonsdaleia* McCoy, 1849

DIAGNOSIS: *Lonsdaleia*, typically with fasciculate, less commonly subcerioid growth habit. Medial plate usually connected to the cardinal septum. Cardinal fossula indistinct.

REMARKS: Some undescribed species of fasciculate *Lonsdaleia* are found in the Lower Carboniferous deposits of the Montagne Noire, of which only one, *L. (Lonsdaleia) redondensis* sp. nov. is described here as being relatively close to *L.* (*Serraphyllum*) *serraensis* subgen. et sp. nov.

Lonsdaleia (Lonsdaleia) redondensis sp. nov.
Plate 1, Figures 1-3; Figures 5, 6 (*partim*)

SYNONYMY

? 1935 *Lonsdaleia duplicata* (Martin) – BÖHM, p. 156, pl. 9, fig. 3.

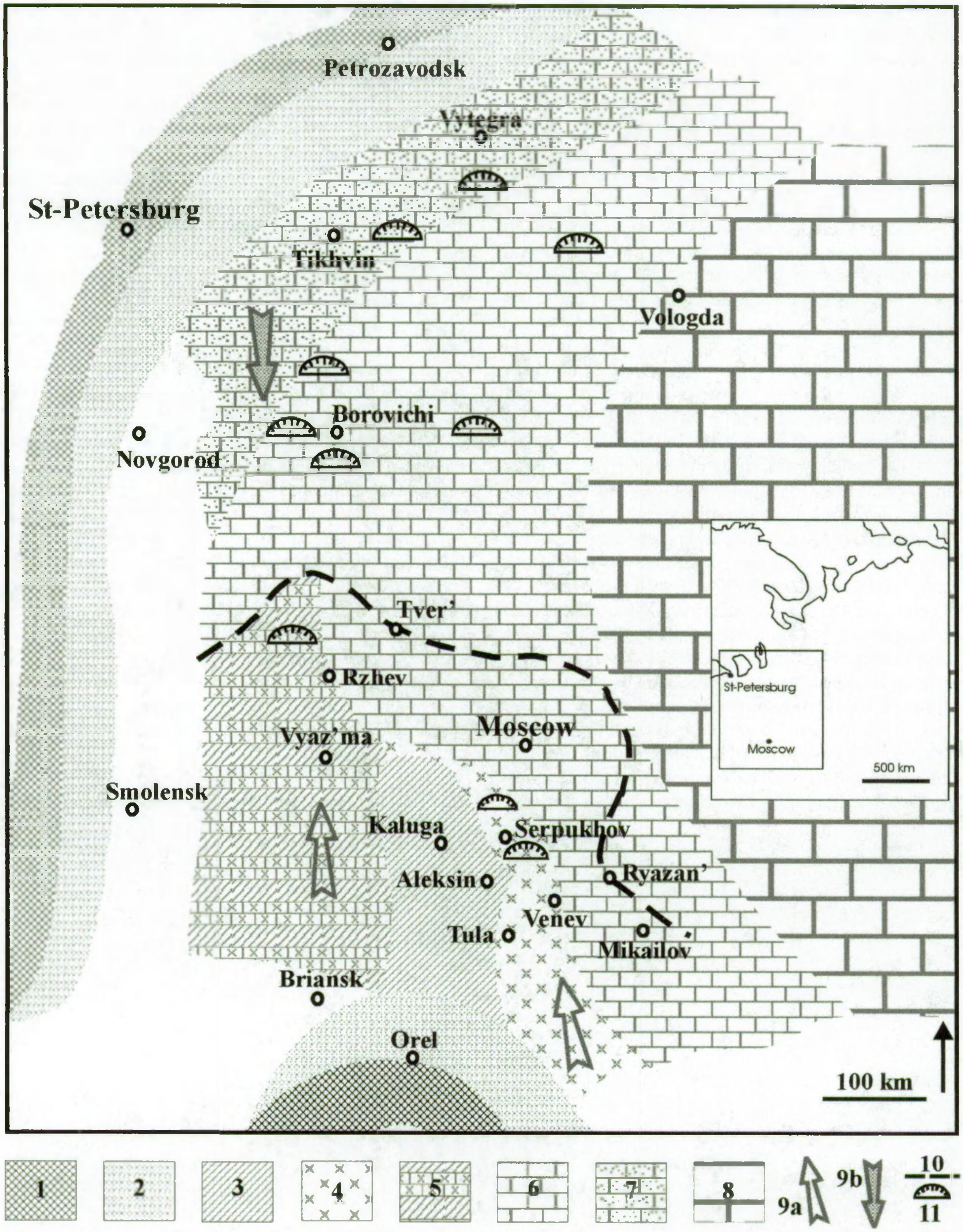

Fig. 4 — Palaeogeographical map for Moscow Basin in Steshevo time (modified from OSIPOVA & BELSKAYA, 1970). Legend: 1: land; 2: deltaic marine sands and silts; 3: argillaceous and dolomitic lagoon sediments; 4: crinoid calcareous sediments on shoals; 5: crinoid calcareous sediments alternating with argillaceous and dolomitic lagoon sediments; 6: calcareous detrital and foraminiferal sediments; 7: marine calcareous sediments alternating with deltaic sands and silts; 8: marine calcareous sediments without detailed facies characteristics; 9: directions of currents: a – principal current responsible for terrigenous supply, b – currents bordering lagoon; 10 – limit of lagoon sediments at end of Steshevo time; 11 – main habitats of the *Lonsdaleia (Actinocyathus) floriformis* species-group.

HOLOTYPE: Specimen L. P. U. Lg. R.R.1994-282 (colony with three transverse and three longitudinal thin sections); Roque Redonde Formation, Upper Warnantian (uppermost Viséan), South France, Montagne Noire, Vailhan, Roque Redonde old quarry, unit 13, thirty m above the base of the section.

MATERIAL: Holotype only.

DIAGNOSIS: *Lonsdaleia* with corallites up to 7.6 mm in diameter and up to 18 septa of both orders. Tabularium diameter up to 4.2 mm. Minor septa well developed and relatively long. Dissepimentarium wide. Outer and inner walls usually thick.

DESCRIPTION: Fasciculate colony some tens of cm high and wide. Corallites up to 7.6 mm in diameter with up to 18 septa of both orders. Length of major septa in tabularium approximates one-third - two-thirds of its radius. They do not reach axial structure except for cardinal septum, which may be connected with medial plate. Thickness of major septa at inner margin of dissepimentarium varies from 0.03 to 0.2 mm and decreases towards their inner ends. Minor septa commonly well developed, penetrate tabularium one-half to two-thirds length of major septa. Both major and minor septa may extend into dissepimentarium, reaching outer wall, or forming crests on dissepiments. Axial structure varies from simple medial plate to thickened complex structure approximating one-third of tabularium diameter in width, or fail to develop; when present, composed of irregular medial plate, up to 10 radial lamellae and irregular, densely packed and steeply conical axial tabellae. Periaxial tabellae complete, seldom divided, variable in shape: concave, horizontal, slightly declined outward, or declined inward at angles up to 60° and upturned near axial structure. They number 15 - 20 per one cm of corallite length. Dissepimentarium wide, from one-third to one-half of corallite radius in width, dominated by wide transeptal dissepiments, may contain interseptal dissepiments. In longitudinal section dissepiments are in one or two series, abaxially declined, elongate to subglobose. Their length varies from 0.5 to 5 mm, and spacing - from 0.2 to 1 mm. Inner margin of dissepimentarium more or less thickened (0.05 - 0.3 mm). Outer wall festooned, 0.15 - 0.6 mm thick. Youngest offsets separated from the parent corallite are at least 1.6 - 2 mm in diameter and show 9 - 11 major septa.

REMARKS: *Lonsdaleia (Lonsdaleia) redondensis* sp. nov. resembles *L. (L.) corbariensis* SEMENOFF-TIAN-CHANSKY & OVTRACHT, 1965 in having well developed minor septa and thickened inner and outer walls, but the latter species has wider corallites (up to 15 mm) and tabularia, and higher septal numbers (up to 32). *L. duplicata* as interpreted by BÖHM (1935) could be conspecific with *L. (L.) redondensis*, since it exhibits the same corallite and tabularium diameters, wide dissepimentarium and well-developed minor septa. However, its septal number is higher (up to 20 septa of both orders).

OCCURRENCE: As for the holotype.

Subgenus *Serraphyllum* subgen. nov.

Type species
Lonsdaleia (Serraphyllum) serraensis subgen. et sp. nov.

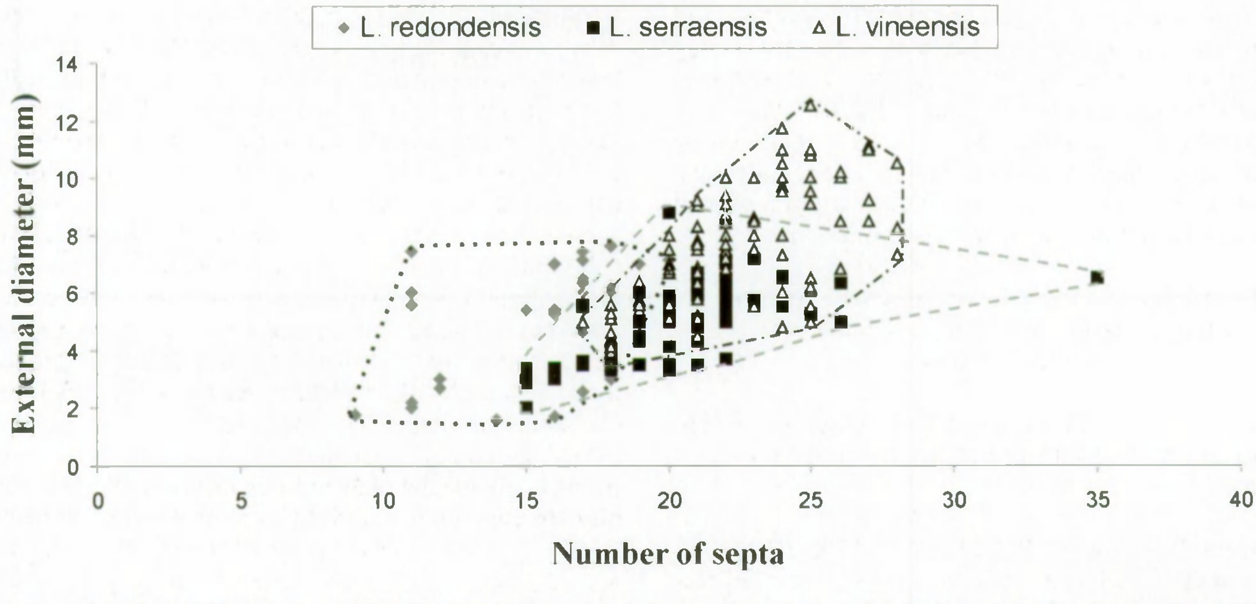

Fig. 5 — Relationship between corallite diameter and number of major septa in *Lonsdaleia (Lonsdaleia) redondensis* sp. nov., *L. (Serraphyllum) serraensis* subgen. et sp. nov. and *L. (S.) vineensis* subgen et sp. nov.

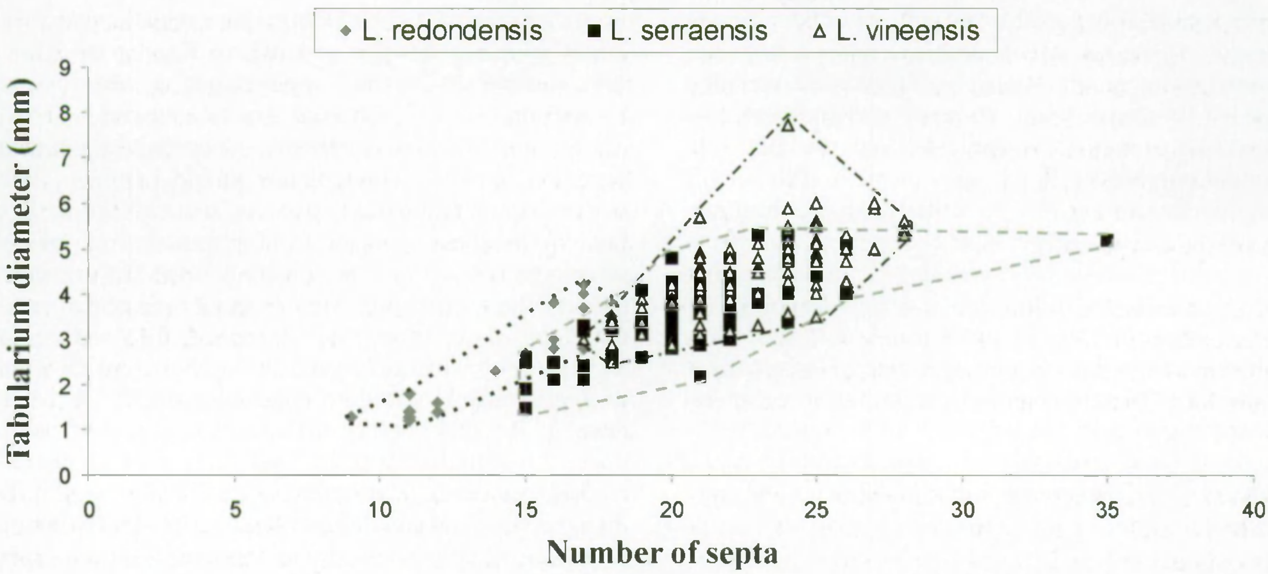

Fig. 6 — Relationship between tabularium diameter and number of major septa in *Lonsdaleia (Lonsdaleia) redondensis* sp. nov., *L. (Serraphyllum) serraensis* subgen. et sp. nov. and *L. (S.) vineensis* subgen et sp. nov.

Species included: Lonsdaleia (Serraphyllum) vineensis subgen. et sp. nov

DERIVATIO NOMINIS: From the La Serre Mountain, south-eastern part of the Montagne Noire, where the subgenus is common.

DIAGNOSIS: *Lonsdaleia* having both fasciculate and cerioid habitus. Cardinal fossula inconspicuous to small. Outer wall commonly strongly thickened.

REMARKS: *Serraphyllum* is established to include species of *Lonsdaleia* exhibiting a cerioid trend within their range of variability and, as a result, characterized by fasciculate, fasciculate-subcerioid, fasciculate-subcerioid-cerioid and cerioid colonies. So far, *Serraphyllum* is recorded only in the Serpukhovian of the Montagne Noire. Similarities between its type species *Lonsdaleia (Serraphyllum) serraensis* subgen. et sp. nov. and fasciculate *L. (Lonsdaleia) redondensis*, reported from a lower level (uppermost Viséan) in the same area, suggest that *Serraphyllum* could arise from the latter or a closely related species.

Lonsdaleia (_Serraphyllum_) _serraensis_ sp. nov.
Plate 1, Figures 4-6, Plate 2, Figures 1-3;
Figures 5, 6 (*partim*)

DERIVATIO NOMINIS: From the La Serre Mountain, south-eastern part of the Montagne Noire, where the species is common.

HOLOTYPE: Specimen L. P. U. Lg. L. S.1992-1/100 (colony with three transverse and four longitudinal thin sections); Roc de Murviel Formation, Serpukhovian, South France, Montagne Noire, vineyard 500 m E. of the La Roquette farmhouse and 100 m S. of the Devonian/Carboniferous boundary stratotype at La Serre.

MATERIAL: Eight specimens (see Appendix 1) with twenty-one transverse and eleven longitudinal thin sections.

DIAGNOSIS: *Serraphyllum* with corallites having maximum width 5-8 mm where cerioid and maximum diameter up to 8.9 mm where fasciculate. Diameter of tabularium 3.4-5.8 mm. Major septa 20-26 in number. Minor septa very short to indistinct. Dissepimentarium narrow.

DESCRIPTION: Colonies irregular, fasciculate, fasciculate-subcerioid and cerioid, varying in height from few centimeters to one meter. Corallites with maximum width 5-8 mm where cerioid, and maximum diameter up to 8.9 mm where fasciculate. Major septa number up to 20-26, may be developed in inner dissepimentarium, do not reach axial structure except for cardinal septum which is commonly connected with medial plate. Cardinal fossula poorly discernible. Length of other major septa within tabularium not more than two-thirds of its radius. Thickness of major septa at inner margin of dissepimentarium varies from 0.05 to 0.5 mm and decreases towards their inner ends. Minor septa commonly indistinct, less commonly developed as septal crests on dissepiments or extending shortly in tabularium. Axial structure varies from simple medial plate to more or less thickened complex structure up to one-third corallite diameter in width, or fails to develop; where present, composed of irregular medial plate, up to 14 radial lamellae and steeply conical axial tabellae. Periaxial tabellae, where associated with complex axial structure, are complete, seldom divided, slightly declined outwards or inwards, or horizontal, and number 24-40 per one cm of corallite length. Where axial structure lacking or represented by simple plate, complete to divided tabulae develop. They are variable (flat, concave, subhorizontal or steeply elevated towards axial plate) and number 10-20 per one cm of corallite length. Dissepimentarium narrow, no wider than one-third corallite radius, dominated by wide transeptal dissepiments, may comprise interseptal dissepiments. In longitudinal section dissepiments in one - two series, abaxially declined at angles of 40°-70°, globose to elongate. Their length varies from 0.5 to 4 mm, and spacing – from 0.2 to 0.5 mm. Inner margin of dissepimentarium more or less thickened (up to 0.35 mm). Outer wall festooned, 0.03 - 0.5 mm thick. Increase lateral. Youngest offsets separated from parent corallite at least 2 mm in diameter and show 12-14 major septa.

REMARKS: The smallest distance between two sides of a corallite in transverse section, or between a side and a corner, is adopted here as the width of the corallite in a cerioid colony.

Serraphyllum serraensis differs from *S. vineensis* subgen. et sp. nov. in having smaller corallites with narrower tabularia, lower septal number and more weakly developed minor septa. It resembles *Lonsdaleia redondensis* sp. nov. where it has fasciculate habitus, but shows larger corallites with a higher septal number and also is distinguished by the weak development of its minor septa.

OCCURRENCE: South France, southeastern part of the Montagne Noire, Roc de Murviel Formation, Serpukhovian.

Lonsdaleia (Serraphyllum) vineensis sp. nov.
Plate 2, Figures 4-8, Plate 3, Figures 1-4;
Figures 5, 6 (*partim*)

DERIVATIO NOMINIS: From the vineyard near the La Roquette farmhouse, where the holotype has been found.

HOLOTYPE: Specimen L. P. U. Lg. L. S.1995-1/354 (colony with three transverse and six longitudinal thin sections); Roc de Murviel Formation, Serpukhovian, South France, Montagne Noire, vineyard 500 m E. of the La Roquette farmhouse and 100 m S. of the Devonian/ Carboniferous boundary stratotype at La Serre.

MATERIAL: Fifteen specimens (see Appendix 2) with thirty-one transverse and twenty-nine longitudinal thin sections.

DIAGNOSIS: *Serraphyllum* with corallites having maximum width 9.2-11.7 mm where cerioid and maximum diameter 9.5-12.5 mm where fasciculate. Diameter of tabularium 5-7.5 mm. Major septa 24-29 in number. Minor septa short. Dissepimentarium narrow.

DESCRIPTION: Colonies fasciculate, fasciculate-subcerioid and cerioid, large (up to 40 cm wide). Corallites with maximum width 9.2-11.7 mm where cerioid, and maximum diameter 9.5-12.5 mm where fasciculate. Major septa number 24-29, may be developed in inner dissepimentarium, do not reach axial structure except for cardinal septum which is commonly connected with medial plate. Cardinal fossula poorly discernible. Length of other major septa in tabularium not more than two-thirds of its radius. Thickness of major septa at inner margin of dissepimentarium varies from 0.05 to 0.5 mm and decreases towards their inner ends. Minor septa developed as septal crests on dissepiments and extending very shortly in tabularium to indistinct. Axial structure may reach width of approximately one-third corallite diameter, or fail to develop. It is more or less thickened, composed of medial plate, 12-20 radial lamellae and more or less densely packed conical axial tabellae. Radial lamellae may be disrupted by axial tabellae on periphery of axial structure. Complete, seldom divided and commonly sagging periaxial tabellae associated with complex axial structure; slightly declined toward dissepimentarium, horizontal or more or less strongly declined to axis and number 16-30 per one cm of corallite length. Dissepimentarium narrow, width no more than one-third corallite radius, dominated by wide transeptal dissepiments, may contain interseptal dissepiments. In longitudinal section dissepiments in one or two series, abaxially declined (from angle 40°-60° to subvertical), commonly elongate and more or less densely packed; length varies from 1 to 5 mm, and spacing - from 0.3 to 0.7 mm. Inner margin of dissepimentarium more or less thickened (up to 0.4 mm). Outer wall festooned, 0.01 - 0.7 mm thick. Increase lateral or intermural. Youngest offsets separated from parent corallite show minimum diameter (or minimum width where increase intermural) of 2.5 - 4 mm and 15-18 major septa.

REMARKS: *Serraphyllum vineensis* is distinguished from *S. serraensis* by larger corallites, a wider tabularium, a higher septal number and stronger development of minor septa.

OCCURRENCE: South France, southeastern part of the Montagne Noire, Roc de Murviel Formation, Serpukhovian.

Subgenus *Actinocyathus* D'ORBIGNY, 1849

DIAGNOSIS: *Lonsdaleia*, typically with cerioid, less commonly subcerioid to fasciculate growth habit. Cardinal fossula indistinct to small. Periaxial tabellae commonly complete, seldom divided. Dissepimentarium commonly wide.

REMARKS: According to HILL (1981), the medial plate in late stages may remain continuous with the cardinal septum. However, it may be also continuous with the counter septum or both the cardinal and counter septa. This observation agrees with illustrations published by JULL (1967), KHOA (1977) and SCRUTTON (1983).

Lonsdaleia (Actinocyathus) borealis
(Dobrolyubova, 1958)
Plate 4, Figures 1-10, Plate 5, Figures 1-8

Synonymy

v. 1845 *Lithostrotion emarciatum* - Lonsdale, p. 603, figs. a-f on p. 603 [non *Astraea emarcida* (= *A. emarciata*) Fisher von Waldheim, 1837 = *Petalaxis*].

v. 1845 *Lithostrotion floriforme*, J. Fleming - Lonsdale, p. 608, figs. a-c on p. 609 [non *Lithostrotion floriforme* (Martin) *in* Fleming (1828) = *Lonsdaleia (Actinocyathus) floriformis*].

p 1846 *Lithostrotion floriforme* - von Keyserling, p. 154, pl. 1, figs. 1 a-c (only).

non 1849 *Strombodes emarciatum* (Lonsd. Sp.) - McCoy, p. 136 [= *Lonsdaleia (Actinocyathus) floriformis*].

non 1851 *Strombodes emarciatum* (Lonsd. Sp.) - McCoy, p. 103 [= *Lonsdaleia (Actinocyathus) floriformis*].

v. 1904 *Lonsdaleia papillata* Edwards & Haime *non* Fischer - Stuckenberg, p. 38, pl. 3, fig. 6.

v non 1916 *Lonsdaleia floriformis floriformis* Martin - Smith, p. 247, pl. 19, figs. 1-5 [= *Lonsdaleia (Actinocyathus) floriformis*].

v. 1916 *Lithostrotion emarciatum* (Lamark) *in* Lonsdale, 1845 = *Lonsdaleia floriformis floriformis* Martin - Smith, p. 257, pl. 21, fig. 1.

v. 1941 *Lonsdaleia floriformis* Martin, 1809 - Gorsky, p. 69, pl. 9, figs. 4, 5a- b.

v p. 1958 *Lonsdaleia similis* n. sp. - Dobroluybova, p. 56, text-figs. 5-7, pl. 5, figs. 1a-b.

v p. 1958 *Lonsdaleia papillata* Edwards *et* Haime, 1851 - Dobrolyubova, p. 62, text-fig. 8, pl. 6, figs. 1a-b.

v p. 1958 *Lonsdaleia modesta* n. sp. - Dobroluybova, p. 66, text-fig. 9, pl. 6, figs. 2a-b.

v p. 1958 *Lonsdaleia floriformis floriformis* (Martin) - Dobrolyubova, p. 71; non text-figs. 11-12, pl. 8, figs. 1a-d, 2a-d, 3a-b [= *Lonsdaleia (Actinocyathus) floriformis*].

v p. 1958 *Lonsdaleia rossica rossica* Stuckenberg - Dobrolyubova, p. 76; non text-figs. 13-16, pl. 9, figs. 1, 2a-c, 3a-b, pl. 10, fig. 1 [= *Lonsdaleia (Actinocyathus) rossica*].

v p*. 1958 *Lonsdaleia rossica borealis* n.sp. - Dobrolyubova, p. 82, text-figs. 17 - 18, pl. 9, figs. 1a-b, 2a-b, 3.

v. 1958 *Lonsdaleia rossica minor* n. sp. - Dobrolyubova, p. 85; text-figs. 17 - 18, pl. 10, figs. 4a-g.

v p. 1958 *Lonsdaleia ornata* n. sp. - Dobrolyubova, p. 93; non text-fig. 20, pl. 12, figs. 1a-b [= *Lonsdaleia (Actinocyathus) ornata*].

v. 1984 *Actinocyathus donensis* n. sp. - Kozyreva, p. 53, pl. 5, fig. 1.

v. 1984 *Actinocyathus densicolumnatus* n. sp. - Kozyreva, p. 55, pl. 5, figs. 4a-b.

v. 1984 *Actinocyathus veidelevkensis* n. sp. - Kozyreva, p. 56, pl. 5, fig. 5.

v p. 1992 *Lonsdaleia floriformis* (Martin) - Hecker, pl. 4, figs. 4, 5, 6a-b (only).

v. 1997 *Actinocyathus borealis* (Dobrolyubova, 1958) - Hecker, pl. 1, fig. 4.

Holotype: *Lonsdaleia rossica borealis* Dobrolyubova, 1958. Specimen PIN 705/108 (fragment of colony with one transverse and one longitudinal thin sections); upper part of Steshevo horizon, top lower Serpukhovian, northwestern part of Moscow Basin, unspecified locality on Msta River, 12 - 20 km southwest of town of Borovichi.

Material: Eighty-three specimens (fragments of colonies and complete colonies) (see Appendix 3) with 220 thin sections. The material contains figured thin sections, including types. Those by Dobroluybova (1958) are as follows: PIN 705/191, holotype (pl. 5, fig. 1a, fig. 1b = text-fig. 5) and PIN 705/110 (text-figs. 6a-d, 7a-f) as *Lonsdaleia similis* sp. nov.; PIN 705/343 (pl. 6, figs. 1a-b) and PIN 705/344 (text-figs. 8a-b) as *L. papillata* Edwards & Haime, 1851; PIN 705/155, holotype (pl. 6, figs. 2a-b) and PIN 705/132 (text-figs. 9a-b) as *L. modesta* sp. nov.; PIN 705/8 (pl. 10, fig. 3), PIN 705/142, (text-figs. 17a-b) and PIN 705/154 (text-figs. 18a-c) as *L. rossica borealis* ssp. nov.; PIN 705/188, holotype (pl. 10, figs. 4a-j) as *L. rossica minor* ssp. nov. The following sections have been figured as *L. floriformis* (Martin) - PIN 705/697 (Hecker, 1992, pl. 4, fig. 4), PIN 705/153 (*ibid*., pl. 4, fig. 5), PIN 703/2929 (*ibid*., pl. 4, figs. 6a-b); and as *Actinocyathus borealis* (Dobrolyubova, 1958) - PIN 705/157 (Hecker, 1997, pl. 1, fig. 4).

Diagnosis: *Actinocyathus* with corallites having diagonals 9-15 mm. Diameter of tabularium 5-6.5 mm. Major septa 19-23 in number. Minor septa short to indistinct.

Description: Colonies cerioid, of medium size (up to 15 cm in diameter), domal, seldom semisphaerical, exceptionally subcerioid. Calices more or less deep, having diagonals 9 - 15 mm, seldom up to 18 mm, pentagonal to octagonal in outline. Calicular pits 5-7 mm in diameter, commonly deep, with almost vertical walls. Calicular platforms from almost horizontal to gently abaxially sloping, varying in width from approximately the same diameter of calicular pits to being 2-2.5 times as narrow, with major septa extending across them (more commonly in colonies with narrow platforms) or discernible only in proximity of calicular pits, locally accompanied by weakly pronounced minor septa. Axial structures columnar or laterally flattened, with rounded upper surfaces, reaching borders of calicular pits or projecting higher, at level of corallite walls. Corallite walls raised, often thickened, commonly sinuous, and seldom simple.

Inner walls thin to dilated. Diameter of tabularia typically measures 5-6.5 mm. Major septa typically thin and straight, seldom sinuous, commonly 19-23 in number, one-third to two-thirds (commonly one-half) tabularium radius, may penetrate dissepimentaria, locally reaching outer walls, locally dilated in tabularia, rarely - in dissepimentaria.

Cardinal septum commonly not discernible, rarely connected to medial plate, locally thinner and/or shorter than other major septa. Inconspicuous cardinal fossula seldom present. Counter septum commonly not discernible, locally longer than other major septa and connected to medial plate. Other major septa may closely approach axial structures and locally join few radial lamellae. Minor septa never dilated, variable in number, commonly fewer than major septa, or indistinct. They are developed as ridges on inner wall, rarely increase in length and attain half-length of major septa in tabularia and very rarely develop in innermost parts of dissepimentaria. Axial structures variable, rounded to oval in outline, attaining half to one-fourth tabularium diameter. Rounded and subrounded axial structures approximate half of tabularium diameter, typically show long, lens-shaped or thin, straight or sinuous medial plate, 10 to 20 thin or slightly dilated near medial plate and strongly bifurcating radial lamellae, and widely conical, spaced 0.25-0.4 mm apart axial tabellae. Narrower and regularly oval axial structures attaining approximately one-third tabularium diameter show thin or lens-shaped, straight or sinuous medial plate, fewer (6-12), commonly thin and straight radial lamellae, and more steeply elevated axial tabellae. Narrowest axial structures, approximating one-fourth tabularium diameter, commonly show 4 to 6 radial lamellae, and less regularly spaced axial tabellae. Periaxial tabellae subhorizontal or slightly declined abaxially, commonly gently sagging, generally spaced rather regularly, 0.5-1.0 mm apart, but in some colonies they may be packed either more tightly or loosely (1.5-2.0 mm apart). Dissepiments commonly thin except for locally slightly dilated, vertically inclined inner margins of innermost dissepiments. Dissepimentaria vary in width, usually attain one-fourth to one-fifth of corallite diagonals, commonly dominated by irregular first order transeptal dissepiments, which in transverse section strongly vary in size and may be partly replaced, more often near inner walls, by second order transeptal dissepiments. In longitudinal section dissepiments variously inflated, almost horizontal to abaxially declined at angles of 20°-40°.

VARIABILITY: Intracolonial variability is especially well expressed in the dissepimentaria and axial structures. Dissepiments vary in sloping and in size, and major septa may become better pronounced in dissepimentaria with transeptal dissepiments decreasing in size and attaining a more regular aspect. Variability in the axial structures commonly involves the medial plate changing from straight to sinuous and from thin to slightly dilated, and the radial lamellae varying in number and in aspect (more or less straight or bifurcating). The major septa vary in length and thickness, and the minor septa - in length. Rarely, an inconspicuous cardinal fossula may develop in some corallites. The sizes of the tabularia were generally not affected by intracolonial variability.

The highest intracolonial variability involving dissepimentaria, axial structures and septa was typical for colonies from the most favourable habitats in the offshore part of the basin characterized by active hydrodynamics (Pl. 4, Figs. 1-4; Pl. 5, Figs. 1-3). Calices in these colonies may vary in depth, and axial structures - in height. Calicular platforms may vary in width, and major septa that extended across them - in length. Also, weakly developed minor septa may appear in the inner parts of calicular platforms. Colonies in similar habitats distinguished by recurrent increase in magnesium content had rather stable axial structures, whereas their dissepimentaria noticeably varied in width and in size of dissepiments. Their major septa varied from being thin and restricted to the tabularia to being strongly dilated and well pronounced in the dissepimentaria, and their minor septa varied in number and length (Pl. 5, Figs. 6,7). In other offshore habitats, in the near-shore habitats and in the open sea, the intracolonial variability was relatively low and mostly involved axial structures (Pl. 4, Fig. 4; Pl. 5, Figs. 4,5).

Intercolonial variability within a biotope was especially characteristic of colonies from the most favourable habitats in the offshore part of the basin. Colonies differed in the prevailing depth of their calices, although some of them exhibited calices of variable depth, and they also differed in the predominant height and shape of their axial structures. It is noteworthy, that colonies from this habitat showed the highest variability in size of tabularia: some of them were dominated by corallites with tabularia measuring 5 - 6 mm (Pl. 4, Fig. 5; Pl. 5, Fig. 2), others - by corallites with tabularia measuring 5.5 - 7 mm (Pl. 4, Figs. 9,10; Pl. 5, Figs. 1-3). Partly as a result of this, but chiefly because of differences in expansion of the calicular platforms, colonies differed in the prevailing size of their corallites. No correlation between the degree of complexity of the axial structures and the aspect of the dissepimentaria can be detected. In some colonies, with corallites exhibiting the most sophisticated axial structures, the dissepimentaria are wide and dominated by large, irregular transeptal dissepiments (Pl. 4, Figs. 1, 2). In other colonies, corallites show both complicated axial structures and narrow dissepimentaria composed of relatively small and flat transeptal dissepiments (Pl. 4, Figs. 9, 10). Also, the corallites of some colonies have both simple axial structures and dissepimentaria dominated by large, irregular first order transeptal dissepiments (Pl. 4, Figs. 3, 4). In the offshore habitats characterized by recurrent increase in magnesium content, colonies may rarely have developed subcerioid habitus. In other aspects, the intercolonial variability within a biotope followed the same pattern as in the colonies from the most favourable habitats, but was less pronounced. It mostly involved the size of corallites, which differed in various colonies because of differences in prevailing size of the tabularia and dissepimentaria. Axial structures in some colonies were wide and very complicated, in others - narrower and with fewer radial lamellae. In other habitats, the intercolonial variability within a biotope was low and mostly involved the dissepimentaria, which in some colonies were dominated by larger and more irregular first order transeptal dissepiments, in others - by smaller and more regular ones (Pl. 4, Fig. 5; Pl. 5, Fig. 4).

Three groups can be discerned within the species, which suggests intraspecific variability. The first group comprises colonies from the offshore habitats characterized by active hydrodynamics and not affected by terrigenous supply from the continent. As a whole, this group is distinguished by high intercolonial variability involving corallite size. However, its intracolonial variability is not uniform and is more strongly pronounced in colonies from the most favourable habitats characteristic of Steshevo time (Pl. 4, Figs. 1-3, 9, 10; Pl. 5, Figs. 1-3). The second group includes colonies from the least favourable offshore habitats, at times affected by terrigenous supply (Pl. 4, Figs. 7-8). These colonies are dominated by relatively small corallites with the tabularia 4.5-6 mm in diameter and with commonly rather narrow dissepimentaria, not exceeding one-fifth of the corallite diagonals in width. Their dissepimentaria are usually composed of second order transeptal dissepiments, thus allowing pronounced extension of the major septa, which may reach the outer walls. Minor septa commonly occur and may be rather long, approaching half the length of the major septa within the tabularia. Their axial structures are rounded to oval, commonly complicated and wide, attaining one-half to one-third of the tabularium diameter. Colonies from the open sea habitats closely approach this group and differ only in having shorter minor septa in their dissepimentaria. The third group includes colonies from the near-shore shallow-water habitats and is distinguished by corallites with tabularia commonly measuring 5.5 - 6.5 mm in diameter, major septa mostly restricted to the tabularia, minor septa very poorly developed, dissepimentaria commonly dominated by transeptal dissepiments, and commonly rounded to subrounded axial structures. This group is characterized by low intracolonial variability, which mostly involves radial lamellae varying in number and shape (Pl. 5, Figs. 4, 5, 8).

REMARKS: The first record of corals here assigned to *Lonsdaleia (Actinocyathus) borealis* was provided by LONSDALE (1845). He recognized the two species, *Lithostrotion floriforme* and *L. emarciatum*, among specimens from the Msta River and its tributaries, not far from Borovichi collected in 1840 by the expedition of Murchison. By that time the former species was recognized as characteristic for the Mountain Limestone of England. The latter species was considered by LONSDALE as conspecific with *Astraea emarcida* (= *A. emarciata*) as interpreted by FISCHER VON WALDHEIM (1837) in fact a *Petalaxis* from the Upper Carboniferous (Moscovian, Podol'sk or Myachkovo horizons) of the Moscow area. All specimens from the Murchison Collection (Natural History Museum, London) figured and described by LONSDALE as *Lithostrotion emarciatum* (LONSDALE, 1845, p. 603, figs. a-f on p. 603) and *L. floriforme* (*ibid.*, p. 608, figs. a-e on p. 609) belong to *Lonsdaleia (Actinocyathus) borealis*. From the same area, this species was erroneously described by STUCKENBERG (1904) as *Lonsdaleia papillata* Edwards & Haime *non* Fischer. *L. papillata* in the sense of MILNE-EDWARDS & HAIME (1852) (= *Lonsdalia papillata* MILNE-EDWARDS & HAIME, 1851) is *L. (Actinocyathus) floriformis* with tabularia 7-8 mm in diameter, 22 to 24 septa of both orders and axial structures approximately 2.5 mm in diameter containing few radial lamellae, whereas *Cyathophyllum papillatum* FISCHER von WALDHEIM, 1837 is probably a *Petalaxis* from the Myachkovo horizon of the Moscow area.

For *Actinocyathus* from the lower Serpukhovian of the northwestern and western parts of the Moscow Basin, DOBROLYUBOVA (1958) adopted the name *Lonsdaleia papillata* Edwards & Haime, and established two new species *L. similis* and *L. modesta* and two new sub-species *L. rossica borealis* and *L. rossica minor*. The holotype of *L. rossica borealis* (*ibid.*, pl. 4, figs. 1, 2) shows corallites with wide, rounded and highly complicated axial structures, major septa mainly restricted to the tabularium, minor septa very short to indistinct, and dissepimentaria dominated by large, irregular, strongly inflated first order transeptal dissepiments. The holotype of *L. rossica minor* (*ibid.*, pl. 4, fig. 7) also has corallites with rather complicated axial structures, but its major septa are more strongly developed in the tabularia, minor septa are commonly present, and its dissepimentaria are dominated by smaller and more regular first order transeptal dissepiments. The holotype of *L. modesta* (*ibid.*, pl. 4, figs. 3, 4) is similar to the holotype of *L. rossica borealis* in the type of dissepimentaria present and in having its major septa mostly restricted to the tabularia and its minor septa very short to indistinct, but shows small axial structures with few radial lamellae. The holotype of *L. similis* (*ibid.*, pl. 4, figs. 5, 6) represents a fragment of a colony encompassing the zone of intensive budding; therefore it shows many small corallites with axial structures incompletely developed. The mature corallites in this specimen are very similar to those in the holotype of *L. modesta*. Some specimens attributed by DOBROLYUBOVA to *L. papillata* are very similar to the holotype of *L. rossica minor*, differing from it only in having more variable axial structures, minor septa very short to indistinct, major septa locally more strongly developed in the dissepimentaria, and more numerous second order transeptal dissepiments (*ibid.*, pl. 4, fig. 8). Others approach the holotype of *L. rossica borealis* in the size and aspect of their axial structures (*ibid.*, pl. 4, figs. 9, 10). All of them differ from the specimen figured by MILNE-EDWARDS & HAIME (1851, pl. 11, figs. 2, 2a) as *L. papillata* in having smaller corallites with smaller tabularia, fewer major septa, minor septa commonly not well expressed, and complicated axial structures with numerous and commonly bifurcating radial lamellae. All of the above mentioned taxa established by DOBROLYUBOVA, as well as *L. papillata* in the sense of STUCKENBERG and DOBROLYUBOVA, were considered conspecific by HECKER (1997), as representing various aspects of the variability of *Actinocyathus borealis*. This specific name was considered as the most appropriate choice, since the holotype of *Lonsdaleia rossica borealis* exhibits all distinctive characters of the species and comes from the area and stratigraphic interval of its maximum abundance. Besides, the type series of *L. rossica borealis*, represented by thirty-six specimens, contains specimens showing all aspects of variability and includes only one specimen belonging to another species, whereas the type series of *L. similis* and *L. modesta* include many specimens belonging to different species.

Three species established by KOZYREVA (1984) on the material from the southern part of the Voronezh Basin fit the variability of *L. (Actinocyathus) borealis*. These are: *Actinocyathus donensis* based on two specimens from the lower Serpukhovian, *A. densicolumnatus* based on three specimens from the lower upper Serpukhovian, and *A. veidelevkensis* based on one specimen from the same interval. *A. donensis* shows corallites with diagonals 8 - 14 mm, tabularia 6.5 - 7 mm in diameter, 19 - 24 major septa commonly reaching the outer wall, minor septa commonly indistinct, dissepimentaria rather narrow and dominated by irregular transeptal dissepiments of both orders, and axial structures subrounded to oval, rather complicated, containing curved and locally bifurcating radial lamellae. *A. densicolumnatus* shows corallites with diagonals 10- 13 mm, tabularia 5 - 6 mm in diameter, 19 - 22 major septa rarely reaching the outer wall, minor septa indistinct, periaxial tabellae subhorizontal to abaxially declined, spaced 0.5 - 1 mm apart, dissepimentaria dominated by rather regular first order transeptal dissepiments, and axial structures rounded and subrounded, rather complicated, with numerous bifurcating radial lamellae and regularly spaced conical axial tabellae. *A. veidelevkensis* has corallites with tabularia 6.5 - 7 mm in diameter, 19 - 25 major septa locally reaching outer wall, minor septa indistinct, dissepimentaria dominated by rather irregular first order transeptal dissepiments, and axial structures wide, rounded to subrounded, with numerous, locally bifurcating radial lamellae.

Actinocyathus borealis differs from *A. floriformis* in having fewer septa, smaller tabularia and more variable axial structures, which may exhibit more numerous and bifurcating radial lamellae. It is close to *A. rossicus* in size of tabularia and septal number, but differs in having smaller corallites with narrower and more variable dissepimentaria and less variable periaxial tabellae. Also, *A. borealis* shows less variability in its axial structures than does *A. rossicus* and thus approaches *Serraphyllum vineensis*.

OCCURRENCE: Moscow Basin: southern part, Tarusa and Steshevo horizons, lower Serpukhovian; northwestern part, Tarusa through Protva horizons, lower Serpukhovian - lower part of upper Serpukhovian; western part, Tarusa and Protva horizons, lower part of lower Serpukhovian, lower part of upper Serpukhovian. Voronezh Basin, southern part: lower Serpukhovian - lower part of upper Serpukhovian. Central Urals, eastern slope: base of lower Serpukhovian. Southern Urals, eastern slope: upper part of Kizel Formation, Serpukhovian.

Lonsdaleia (Actinocyathus) rossica
(STUCKENBERG, 1904)
Plate 6, Figures 1-7

SYNONYMY

- v* 1904 *Lonsdaleia rossica* n. sp. - STUCKENBERG, p. 41, pl. 9, figs. 1a-d.
- v. 1904 *Lonsdaleia Muschketowi* n. sp - STUCKENBERG, p. 42, pl. 9, figs 2a -c.
- v p. 1958 *Lonsdaleia rossica rossica* Stuckenberg, 1904 - DOBROLYUBOVA, p. 76, text-figs. 13-16, pl. 9, figs. 1, 2a-c, 3a-b, pl. 10, fig. 1.
- v. 1984 *Actinocyathus sidenkoi* n. sp. - KOZYREVA, p. 54, pl. 5, figs. 2a-c.
- v. 1987 *Actinocyathus rossicus* (Stuck.) - IWANOWSKI, p. 32, pl. 19, figs. 2a- b, 3a-b.
- v p. 1992 *Lonsdaleia floriformis* (Martin) - HECKER, pl. 3, figs. 2a-b (only).
- v. 1997 *Actinocyathus rossicus* (Stuckenberg, 1904) - HECKER, pl. 1, fig. 3.

LECTOTYPE: SD DOBROLYUBOVA (1958, p. 75). *Lonsdaleia rossica* STUCKENBERG, 1904. Specimen CNIGRM 336/74 (colony with one transverse and one longitudinal thin sections); upper part of Steshevo horizon, top lower Serpukhovian, southern part of Moscow Basin, left bank of Oka River at village of Luzhki, 12 km SE. of town of Serpukhov.

MATERIAL: Forty-four specimens (fragments of colonies and complete colonies) (see Appendix 4) with 124 thin sections. The material includes specimens figured by DOBROLUYBOVA (1958) as *Lonsdaleia rossica rossica* STUCKENBERG, 1904: colony PIN 703/2736 (pl. 9, figs. 1a-b), and thin sections PIN 703/36 (pl. 9, fig. 1), PIN 703/43 (pl. 9, figs. 2a-c), PIN 703/5094 (pl. 9, figs. 3a-b = text-figs. 13 a-b), PIN 703/36b (text-fig. 14), PIN 703/44 (text-figs. 15 a-h, 16 a-b). Also figured are thin sections PIN 703/2737, as *L. floriformis* (Martin) (HECKER, 1992, pl. 13, figs. 2a-b), and PIN 703/5094, as *Actinocyathus rossicus* (STUCKENBERG, 1904) (HECKER, 1997, pl. 1, fig. 3).

DIAGNOSIS: *Actinocyathus* with corallites having diagonals 12-25 mm. Diameter of tabularium 5-6 mm. Major septa 19-24 in number. Minor septa short to indistinct. Dissepimentarium very wide, up to half corallite diagonal.

DESCRIPTION: Colonies cerioid, large (up to 40 cm in diameter, commonly 18-20 cm), 4 to 10 cm thick, bulbous to almost tabular, with upper surface almost flat to gently convex. Calices shallow, having diagonals 10 to 30 mm, commonly 12-25 mm, pentagonal to septagonal in outline. Calicular pits shallow but sharply marked off from calicular platforms by a change in slope, usually measuring 5-6 mm. Calicular platforms variable in width, almost flat or gently sagging, seldom slightly sloping abaxially, with major septa commonly extending across them, and minor septa locally discernible in their inner parts. Axial structures commonly projecting higher than corallite walls, columnar or laterally flattened, with upper surfaces rounded or bearing ridges corresponding to medial plate. Corallite walls raised, thin and simple to thick and sinuous.

Inner walls thin, rarely slightly dilated. Diameter of tabularia usually 5-6 mm. Major septa typically thin or slightly dilated, straight, commonly 19-24 in number. They are mostly restricted to tabularia and vary in length from half to one-third of tabularium radius. Major septa may penetrate inner dissepimentaria. Cardinal septum commonly not discernible, rarely connected to medial plate, locally thinner and/or shorter than other major septa. Inconspicuous cardinal fossula seldom present. Counter septum commonly not discernible, locally longer than other major septa and connected to medial plate. Minor septa never dilated, developed as ridges on inner wall, rarely traced into innermost parts of dissepimentaria, variable in number, commonly fewer than major septa or indistinct. Axial structures commonly present and extremely variable, rounded to oval in outline, attaining one-third, rarely half of tabularia diameter. Oval axial structures commonly show long, straight or gently sinuous, thin to slightly dilated medial plate, 4 to 7, straight or sinuous, locally bifurcating radial lamellae, and elevated, spaced 0.3-0.5 mm apart axial tabellae. In axial structures of this aspect, radial lamellae may decrease in number, axial tabellae may become irregular and loosely spaced, and medial plate - strongly curving. Rounded axial structures show thin to variably dilated, straight or curving medial plate, 15 to 25, thin or dilated near medial plate, consistently strongly bifurcating radial lamellae, and regular, steeply elevated and more closely spaced (0.2-0.3 mm apart) axial tabellae. Also, medial plate may become short and therefore indiscernible from radial lamellae; in transverse sections such axial structures demonstrate a tangle-like structure. Seldom, axial structures fail to develop, and one septum (counter?), which is elongated, locally slightly dilated at its axial end and curved, extends far in tabularia. Periaxial tabellae complete, seldom divided, subhorizontal, slightly declined abaxially or adaxially, usually gently sagging, commonly spaced irregularly 0.5-1.0 mm apart, less commonly 1.5-2.0 mm apart. Dissepiments commonly thin except for locally slightly dilated vertically inclined inner margins of innermost dissepiments. Dissepimentaria wide, up to half, commonly one-third corallite diagonals, dominated by large, irregular first order transeptal dissepiments, which in longitudinal sections, appear variously inflated to flat, almost horizontal to abaxially declined at angles of 20°-30°. Interseptal dissepiments and second order transeptal dissepiments may appear sporadically in innermost parts of dissepimentaria.

VARIABILITY: Intracolonial variability can be recognized in all specimens studied. The highest variability is exhibited by axial structures, which commonly differ in most of adjacent corallites and may repeatedly change at maturity along individual corallites from more complex to less complex. Dissepimentaria vary in width as well as in shape and slope of dissepiments, tabulae vary in shape and spacing, and septa - in length (Pl. 6, Figs. 1-3). Inconspicuous cardinal fossulae may develop. In some colonies a weak "periodicity" may be discerned in longitudinal sections indicated by alternation of rather irregular layers of more crowded, flat and less crowded, inflated dissepiments. Size of tabularia and the number of major septa are the most stable characters. Intracolonial variability can be observed in calices, involving the shape of the axial structures as well as the width and aspect of the calicular platforms, which may be more or less flat and bear variably pronounced septa.

Intercolonial variability within a biotope may be observed in the material from both principal localities of the species: at Luzhki and Toropovo. Colonies vary in size and shape - from bulbous to almost tabular. Also, a gradual passage is evident, from colonies dominated by corallites with generally numerous bifurcating radial lamellae and regular, closely spaced axial tabellae (Pl. 6, Figs. 2, 7), to colonies dominated by corallites with strongly simplified axial structures showing irregular medial plate, few and irregular, locally disappearing radial lamellae and rather regular axial tabellae (Pl. 6, Fig. 1). In colonies of the former type, the major septa are commonly longer, the minor septa more commonly develop and the dissepiments are less inflated. Corallites in colonies with simplified axial structures commonly exhibit short major septa, indistinct minor septa and larger, more inflated dissepiments.

Intraspecific variability could be suggested by the aspect of two groups, which both occur in habitats within the outer zone of the near-shore part of the basin and are differentiated by their septal numbers and type of increase. Corallites in colonies found at Luzhki and Venev Monastyr' are usually characterized by 19 - 23 major septa (Pl. 6, Figs. 1, 2), whereas those in colonies from the locality near Toropovo commonly have up to 25 major septa (Pl. 6, Fig. 7). Together with typical for the genus lateral increase, with young corallites arising in the transeptal dissepiments of the parent, about thirty per cent of colonies from Luzhki and the colony from Venev Monastyr' at late stages of astogeny exhibit a very special type of increase in which young corallites appear as "bubbles" between the walls of adjacent corallites. It was presented by DOBROLYUBOVA (1958) as extracalicular lateral increase, interpreted by JULL (1967) as intermural increase and later reinterpreted by FEDOROWSKI & JULL (1976) as coenenchymal increase. This type of increase was most probably connected with some extrinsic factors and should not be interpreted as a proof of full integration of polyps within colonies of this species distinguishing it from the other *Lonsdaleia*.

REMARKS: STUCKENBERG (1904), from material from Luzhki, established *Lonsdaleia rossica* on three specimens, CNIGRM 336/73 - 75, and *L. mushketowi* - on one specimen, CNIGRM 336/76. According to him, the former species is distinguished by 22-26 major septa and gently sagging calicular platforms, and the latter - by 18-22 major septa and flat calicular platforms, slightly declined abaxially. DOBROLYUBOVA (1958) suggested that both taxa are synonymous and IWANOWSKI (1987) supported this. Thin sections of the lectotype of *L. rossica* (*ibid.*, pl. 19 , figs. 3a-b) and of the holotype of *L. mushketowi* (*ibid.*, pl. 19 , figs. 3a-b) exhibit extreme examples of intracolonial variability within a biotope, characteristic of *Actinocyathus rossicus* from Luzhki. The lectotype of *Lonsdaleia rossica* shows 19 - 24 major septa, with minor septa fewer but present, complex, rounded axial structures with numerous bifurcating radial lamellae and closely spaced axial tabellae, and first order transeptal dissepiments replaced by second order transeptal dissepiments in the innermost parts of the dissepimentaria. In the holotype of *L. mushketowi* major septa number 19 - 21 and are mostly restricted to the tabularia, minor septa are indistinct, axial structures are strongly simplified, possessing a few irregular radial lamellae and loosely spaced axial tabellae, and the dissepimentarium is dominated by large, strongly inflated first order transeptal dissepiments.

The earliest record of *L.(A.) rossica* is from the lower Tarusa (Pl. 6, Figs. 5, 6); this colony approaches *Actinocyathus floriformis* in tabularium size and shows closer similarity to its ancestral species than the colony from the top Tarusa (Pl. 6, Fig. 3), and especially to the colonies from the Steshevo horizon. This could indicate, that decrease in tabularium size characteristic of this species in Steshevo time may be interpreted as an adaptation to the very special environment close to the lagoon, where it dominated among cerioid rugose corals. Later, it could have experienced a stronger influence from the adjacent lagoon, which was progressively expanding during the early Serpukhovian.

Actinocyathus sidenkoi KOZYREVA, 1984 based on a single specimen from the Serpukhovian from the southern part of the Voronezh Basin, is conspecific with *A. rossicus*. In size of tabularia (up to 7 mm) and in its relatively high septal number (20 - 24 major septa), it is close to the colony from the lower Tarusa of the Moscow Basin, but is distinguished by wide, rounded axial structures with numerous irregular bifurcating radial lamellae typical of many colonies from the Steshevo horizon.

Lonsdaleia (Actinocyathus) rossica is distinguished from *L. (A.) floriformis* by larger corallites with smaller tabularia, a lower septal number, wider dissepimentaria, and more variable axial structures, which may exhibit more numerous and bifurcating radial lamellae. It resembles *A. borealis* in tabularium size and septal number, but has larger corallites showing wider, less variable dissepimentaria, but more variable axial columns and periaxial tabellae. In the pattern of variability of its axial structures it approaches *Serraphyllum serraensis*.

OCCURRENCE: Moscow Basin, southern part, Tarusa and Steshevo horizons, lower Serpukhovian; Voronezh Basin, southern part, lower Serpukhovian, possibly lower part of the upper Serpukhovian.

Discussion

The genus *Actinocyathus* was re-established by HILL (1981) to include cerioid species previously attributed to *Lonsdaleia*. Since then, *Lonsdaleia* has remained restricted to fasciculate and subcerioid species. However, *Actinocyathus* and *Lonsdaleia* as interpreted by HILL do not differ in corallite morphology and are closely related. This is suggested by the presence of subcerioid and fasciculate zones in colonies of some *Actinocyathus* species, and by subcerioid zones in colonies of some *Lonsdaleia* species. This also agrees with the hypothesis of SMITH (1916) on the origin of *L. (Actinocyathus) floriformis* (adopted by him as *Lonsdaleia floriformis floriformis*) from *L. (Lonsdaleia) duplicata*, which is supported by the observation that in the Rugosa, fasciculate species may give rise to cerioid species (NUDDS, 1979; POTY, 1993). Therefore, *Actinocyathus* is adopted here as a subgenus of *Lonsdaleia*. The first *Actinocyathus* species, *A. floriformis*, appears near the base of the uppermost Viséan and marks the lower limits of the RC8 Coral Zone of POTY (CONIL *et al.*, 1990), and of Rugose coral zone VIII of HECKER (2001). *A. crassiconus*, which also appears in the uppermost Viséan and differs from *A. floriformis* chiefly in having longer minor septa and more regular axial structures, could have evolved from the same ancestral species, *Lonsdaleia duplicata*, which shows "*floriformis*" and "*crassiconus*" trends in its pattern of intracolonial variability. It is noteworthy, that *Actinocyathus crassiconus* commonly exhibits subcerioid to fasciculate habitus.

Actinocyathus floriformis and *A. crassiconus* probably gave rise to two species-groups, each representing a separate trend of evolution within the subgenus. The former species-group is distinguished by its consistently short, commonly indistinct minor septa, and by its highly variable axial structures. The *A. crassiconus* species-group is characterized by its consistently developed, commonly long minor septa, and by less variable axial structures, usually showing regularly conical, crowded axial tabellae. Species belonging to both species-groups may be found in various areas, but only in the Moscow Basin, where the subgenus has its longest (and uninterrupted) range, do these species-groups show clear differences in corallite morphology and ecological plasticity (HECKER, 1997). However, both species-groups include species showing subcerioid to fasciculate habitus. In the *A. floriformis* species-group such a habitus is shown by *A. bronni* (MILNE-EDWARDS & HAIME, 1851); in the *A. crassiconus* species-group - by *A. sarytchevae* (DOBROLYUBOVA, 1958), in addition to *A. crassiconus*.

Serraphyllum is close to *Actinocyathus* in its corallum habitus, but is separated from that subgenus because of its origin. It is considered as evolving, during the Viséan/Serpukhovian transition, from the uppermost Viséan fasciculate *Lonsdaleia (Lonsdaleia) redondensis* or from a closely related species. Similarities with *L. redondensis* in the morphology of adult corallites and offsets are especially evident when fasciculate colonies or fasciculate parts of colonies of *Serraphyllum serraensis* are considered (Pl. 1, Figs. 1, 2, 5; Pl. 2, Figs. 1, 2), suggesting close relationships between these species. Therefore, *Serraphyllum* probably originating from a species different than that giving rise to *Actinocyathus*, is here interpreted as a taxon convergent with the latter and is adopted as a subgenus of *Lonsdaleia*. It is noteworthy, that the two species of *Serraphyllum* described here are easily distinguishable from both *Lonsdaleia (Actinocyathus)* and *L. (Lonsdaleia)*.

To conclude parallel evolution marked by transformation of two fasciculate species into two subgenera exhibiting both subcerioid and cerioid habitus may be recognized within the genus *Lonsdaleia*: *Actinocyathus* appeared at the beginning of the latest Viséan, and *Serraphyllum* - at the beginning of the Serpukhovian. *Serraphyllum* is morphologically convergent with the *Actinocyathus floriformis* species-group, as indicated by the poor development of its minor septa and the fact that its radial lamellae and axial tabellae are never as regular as in *A. crassiconus* and related species. It closely approaches the two Serpukhovian species, *A. borealis* and *A. rossicus*, in the aspect and patterns of variability of its axial structures. Both *A. rossicus* (Pl. 6, Figs. 1, 2) and *Serraphyllum serraensis* (Pl. 1, Figs. 5, 6) show exceptionally high variability in their axial structures; also, in both species axial structures may be lacking. In *S. vineensis* and *Actinocyathus borealis* the variability in the axial structures is less striking, and in both species it shows a similar pattern. *Serraphyllum serraensis* and *S. vineensis* may develop bifurcating radial lamellae (Pl. 1, Fig. 5; Pl. 2, Figs. 1, 4, 8; Pl. 3, Fig. 4) characteristic of *Actinocyathus borealis* and *A. rossicus* (Pl. 4, Figs. 1, 9; Pl. 2, Figs. 2, 5-8; Pl. 6, Figs. 2, 3, 7). In both *A. borealis* and *A. rossicus* intracolonial variability and variability within a biotope were especially high in habitats where these species dominated. The high variability reported for the two *Serraphyllum* species could indicate that they played an important role in Sepukhovian rugose communities.

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Appendix 1: material studied of *Lonsdaleia (Serraphyllum) serraensis* sp. nov. (coll. L. P. U. Lg.)

Coll. number	Locality	Formation	Area
L.S.1992-1/44 L.S.1992-1/61 L.S.1992-1/85 L.S.1992-1/94 L.S.1992-1/96 L.S. 1992-1/100 (holotype) L.S.1995-1/340	vineyard 500 m E. of the La Roquette farmhouse and 100 m S. of the Devonian/ Carboniferous boundary stratotype at La Serre	Roc de Murviel	South France, Montagne Noire
R.M.1999-33-1-413 R.M.2002-331A/486	southeastern side of the Roc de Murviel hill, 1.2 km S. of Le Mas Rolland		

Appendix 2: material studied of *Lonsdaleia (Serraphyllum) vineensis* sp. nov. (coll. L. P. U. Lg.)

Coll. number	Locality	Formation	Area
L.S.1/295 L.S.1/444 L.S.1992-1/97 L.S.1993-1/328 L.S.1995-1/329 L.S.1995-1/345 L.S.1995-1/352 L.S.1995-1/354 (holotype) L.S.1997-1/445 L.S.1999-1/341 L.S.1999-1/450 L.S.2002/1-491	vineyard 500 m E. of the La Roquette farmhouse and 100 m S. of the Devonian/ Carboniferous boundary stratotype at La Serre	Roc de Murviel	South France, Montagne Noire
R.M.1999-33-1/400 R.M.2002-33-1/479 R.M.2002-33-1/480 R.M.2002-33-1/485	southeastern side of the Roc de Murviel hill, 1.2 km S. of Le Mas Rolland		

Appendix 3: material studied of *Lonsdaleia (Actinocyathus) borealis* (DOBROLYUBOVA, 1958) (coll. PIN)

Coll. number	Locality	Horizon	Area
705/183 705/656-659	Tutoka River, approximately 60 km NE. of town of Boksitogorsk	Tarusa	Moscow Basin, northwestern part
705/132	Msta River, 12 km SW. of town of Borovichi		
705/698	Patrovskiy Brook, 15 S. of the town of Vytegra		
705/188 - 189 705/343 - 345 705/661 - 663 705/670	Tutoka River, approximately 60 km NE. of Boksitogorsk	Steshevo	
705/593 705/686 - 687	Medveditsa River near village of Slizikha		
705/701 705/703	village of Ochep		
705/142 - 159 705/208 705/448 - 460 705/475 705/690 - 691 1562/2511 - 2515	village of Podbor'e, 7 km NW. of Borovichi		
705/8 – 10 705/102 705/108 (holotype) 705/110 705/129 705/132	unspecified localities on Msta River, 12 - 20 km SW. of Borovichi, including locality on Mokraya Poneredka Brook		
705/135 -136 705/138 705/140	Sukhaya Poneredka Brook, 12 km SW. of Borovichi		
705/128	Msta River near village of Marinskoe, 17 km SW. of Borovichi		
705/678	Msta River near village of Maly Porog, 18 km SW. of Borovichi		
705/474	Borehole 192 near Boksitogorsk		
705/652	Ragusha River, 110 km NNW. of Borovichi	Protva	
705/197	town of Uglovka, 30 km SE. of Borovichi		
703/4908 705/191-193 705/368-369 705/682 705/697	left bank of Volga in its upper reaches, village of Baranova Gora, 150 km W. of city of Tver'	Tarusa	Moscow Basin, western part
703/2729	Tsna River near village of Zarech'e	Protva	
1562/2373	left bank of Pronya River, 52 km S. of the city of Ryazan', Pogorel'skoe quarry	Tarusa	Moscow Basin, southern part
1562/1019	Osetr River, 23 km NE. of town of Venev	Steshevo	
704/5044 - 5047 704/5049 - 5054 704/ 5056a	left bank of Don River at village of Kazanskaya	Tarusa-Steshevo	Voronezh Basin, southern part

Appendix 4: material studied of *Lonsdaleia (Actinocyathus) rossica* (STUCKENBERG, 1904) (coll. PIN)

Coll. number	Locality	Horizon	Area
703/2737	Sukhaya Besputa River near village of Voskresenskaya, NW. of town of Venev	Tarusa	Moscow Basin, southern part
703/5094	SE margin of town of Serpukhov, Zabor'e quarry		
703/32 - 36, 36b 703/37 - 43, 43a 703/44 - 51 703/2723 - 2726 1562/1180	left bank of Oka River at village of Luzhki, 12 km SE. of Serpukhov	Steshevo	
703/2734 - 2736 703/5065 - 5074	Sukhaya Besputa River near village of Toropovo, 30 km NW. of Venev		
703/2740	Osetr River at village of Venev Monastyr', 15 km W. of Venev		
704/5062 - 5063	Borehole Valuyki-20	Tarusa-Steshevo	Voronezh Basin, southern part

Explanation of Plates

Plate 1

Lonsdaleia (Lonsdaleia) redondensis sp. nov.

Figs. 1-3 — Holotype L.P.U. Lg. R.R.1994-282: 1 – transverse section, x 3; 2 – transverse section showing variability in axial structures, x 5; 3 – longitudinal section showing variability in periaxial tabellae (declined outwards or inwards, or horizontal), x 5. Upper Warnantian (uppermost Viséan), Roque Redonde Formation, South France, Montagne Noire, Vailhan, Roque Redonde old quarry.

Lonsdaleia (*Serraphyllum*) *serraensis* subgen. nov., sp. nov.

Fig. 4 — Holotype L.P.U.Lg. L.S. 1992-1/100: transverse section. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, La Serre. x 3.

Figs. 5-6 — L.P.U.Lg. L.S.1992-1/61: transverse sections showing fasciculate and cerioid parts, from one colony. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, La Serre. x 3.

Plate 2

All thin sections are figured at magnification x 5

Lonsdaleia (*Serraphyllum*) *serraensis* subgen. nov., sp. nov.

Fig. 1 — L.P.U.Lg. L.S.1992-1/61: transverse section in part of colony showing corallite lacking axial structure and several offsets (on left), and two corallites with complex axial structures. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, La Serre.

Fig. 2 — L.P.U.Lg. R.M.1999-33-1/413: transverse section from fasciculate colony showing strongly thickened corallites. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, Roc de Murviel.

Fig. 3 — Holotype L.P.U.Lg. L.S. 1992-1/100: longitudinal section. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, La Serre. x 3.

Lonsdaleia (*Serraphyllum*) *vineensis* subgen. nov., sp. nov.

Fig. 4 — L.P.U.Lg. R.M.1999-33-1/400: transverse section from fasciculate colony showing thickened corallites. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, Roc de Murviel.

Fig. 5 — Holotype L.P.U.Lg. L.S.1995-1/354: longitudinal section. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, La Serre.

Fig. 6 — L.P.U.Lg. L.S.1995-1/352: longitudinal section showing variability in periaxial tabellae (declined outwards or inwards, or horizontal). Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, La Serre.

Fig. 7 — L.P.U.Lg. R.M.1999-33-1/400: transverse section in two corallites of fasciculate colony. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, Roc de Murviel.

Fig. 8 — Holotype L.P.U.Lg. L.S.1995-1/354: transverse section in fasciculate part of colony showing lateral increase. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, La Serre.

Plate 3

All thin sections are figured at magnification x 3

Lonsdaleia (*Serraphyllum*) *vineensis* subgen. nov., sp. nov.

Figs. 1, 2, 4 — Holotype L.P.U.Lg. L.S.1995-1/354: 1 – transverse section in fasciculate part of colony, 2 – transverse section in densely packed part of colony, 4 – transverse section in subcerioid to cerioid part of colony. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, La Serre.

Fig. 3 — L.P.U.Lg. L.S.1993-1/328: transverse section of cerioid colony. Serpukhovian, Roc de Murviel Formation, South France, Montagne Noire, La Serre.

Plate 4

Lonsdaleia (Actinocyathus) borealis (Dobrolyubova, 1958)

Figs. 1, 2 — Holotype of *Lonsdaleia rossica borealis* Dobrolyubova, 1958; PIN 705/108: 1 – transverse section, 2 – longitudinal section. Lower Serpukhovian, upper part of Steshevo horizon, northwestern part of Moscow Basin, unspecified locality on Msta River, 12 – 20 km SW. of Borovichi. x 3.

Figs. 3, 4 — Holotype of *Lonsdaleia modesta* Dobrolyubova, 1958; PIN 705/115: 3 – transverse section, 4 – longitudinal section. Lower Serpukhovian, upper part of Steshevo horizon, northwestern part of Moscow Basin, Podbor'e. x 3.

Figs. 5, 6 — Holotype of *Lonsdaleia similis* Dobrolyubova, 1958; PIN 705/191: 5 – transverse section, 6 – longitudinal section. Lower Serpukhovian, Tarusa horizon, western part of Moscow Basin, Baranova Gora. x 3.

Fig. 7 — Holotype of *Lonsdaleia rossica minor* Dobrolyubova, 1958; PIN 705/188: transverse section. Lower Serpukhovian, Tarusa horizon, northwestern part of Moscow Basin, Tutoka River about 60 km NE. of Boksitogorsk. x 3.

Fig. 8 — PIN 705/343: transverse section. Lower Serpukhovian, Steshevo horizon, northwestern part of Moscow Basin, Tutoka River about 60 km NE. of Boksitogorsk. x 2.

Figs. 9, 10 — PIN 705/146: 9 – transverse section, x 2; 10 – longitudinal section, x3. Lower Serpukhovian, upper part of Steshevo horizon, northwestern part of Moscow Basin, Podbor'e. x 3.

Plate 5

All thin sections are figured at magnification x 2

Lonsdaleia (Actinocyathus) borealis (Dobrolyubova, 1958)

Fig. 1 — PIN 705/153: transverse section. Lower Serpukhovian, upper part of Steshevo horizon, northwestern part of Moscow Basin, Podbor'e.

Fig. 2 — PIN 705/157: transverse section. Lower Serpukhovian, upper part of Steshevo horizon, northwestern part of Moscow Basin, Podbor'e.

Fig. 3 — PIN 1562/2514: transverse section. Lower Serpukhovian, upper part of Steshevo horizon, northwestern part of the Moscow Basin, Podbor'e.

Fig. 4 — PIN 705/697: transverse section. Lower Serpukhovian, Tarusa horizon, western part of Moscow Basin, Baranova Gora.

Fig. 5 — PIN 705/686: transverse section. Lower Serpukhovian, Steshevo horizon, northwestern part of Moscow Basin, Medveditsa River near Slizikha.

Figs. 6, 7 — PIN 705/197: successive transverse sections. Upper Serpukhovian, Protva horizon, northwestern part of Moscow Basin, Uglovka.

Fig. 8 — PIN 705/8: transverse section. Lower Serpukhovian, Steshevo horizon, northwestern part of Moscow Basin, Mokraya Poneredka Brook.

Plate 6

All thin sections are figured at magnification x 2.

Lonsdaleia (Actinocyathus) rossica (Stuckenberg, 1904)

Fig. 1 — PIN 703/39: transverse section. Lower Serpukhovian, upper part of Steshevo horizon, southern part of Moscow Basin, left bank of Oka River at Luzhki.

Fig. 2 — PIN 703/36: transverse section. Lower Serpukhovian, upper part of Steshevo horizon, southern part of Moscow Basin, left bank of Oka River at Luzhki.

Figs. 3-4 — PIN 703/5094: 3 – transverse section, 4 – longitudinal section. Lower Serpukhovian, upper part of Tarusa horizon, southern part of Moscow Basin, Zabor'e quarry.

Figs. 5-6 — PIN 703/2737: 5 – transverse section, 6 – longitudinal section. Lower Serpukhovian, Tarusa horizon, southern part of Moscow Basin, Sukhaya Besputa River near Voskresenskaya.

Fig. 7 — PIN 703/5072: transverse section. Lower Serpukhovian, Steshevo horizon, southern part of Moscow Basin, Sukhaya Besputa River near Toropovo.

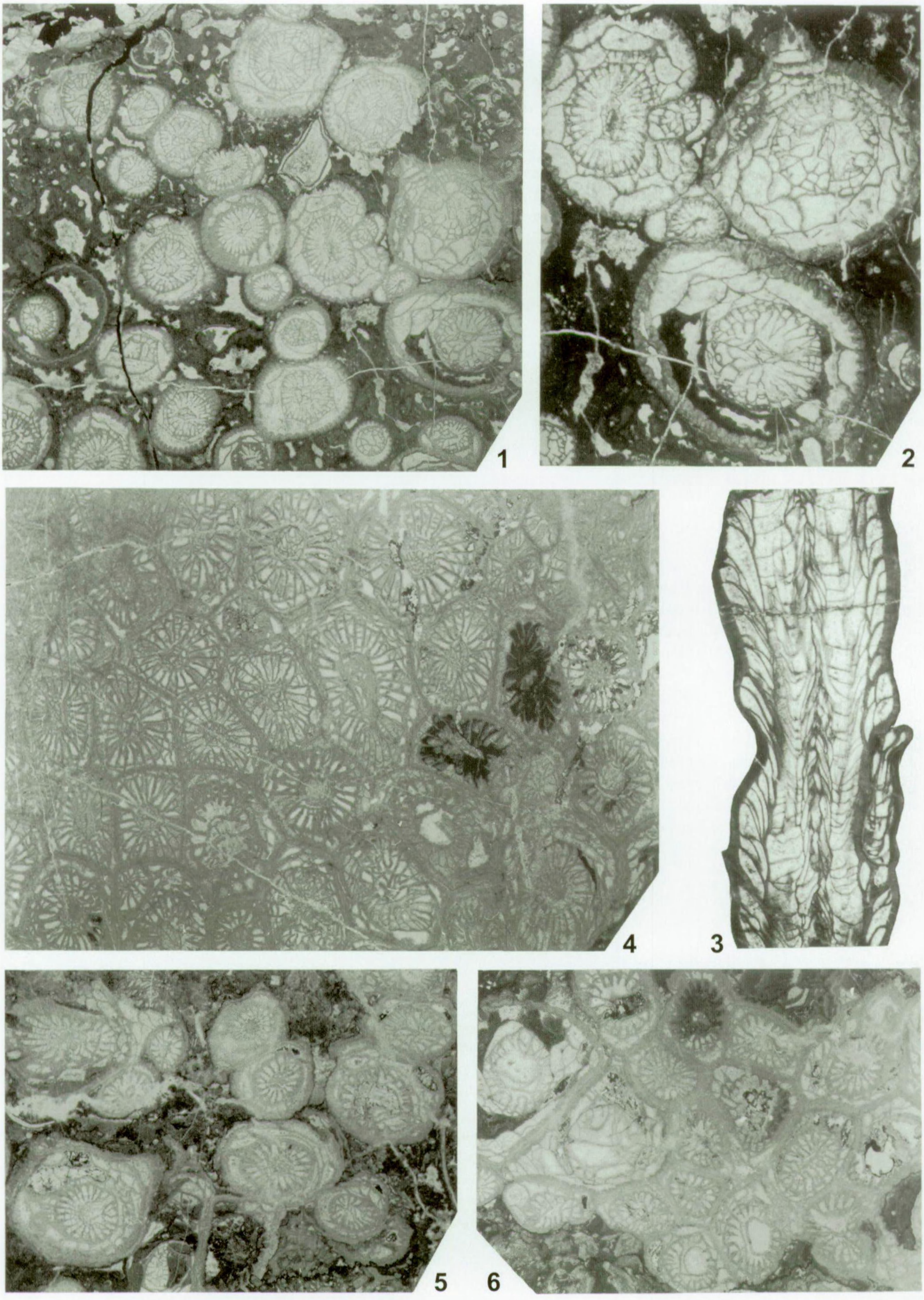

PLATE 1

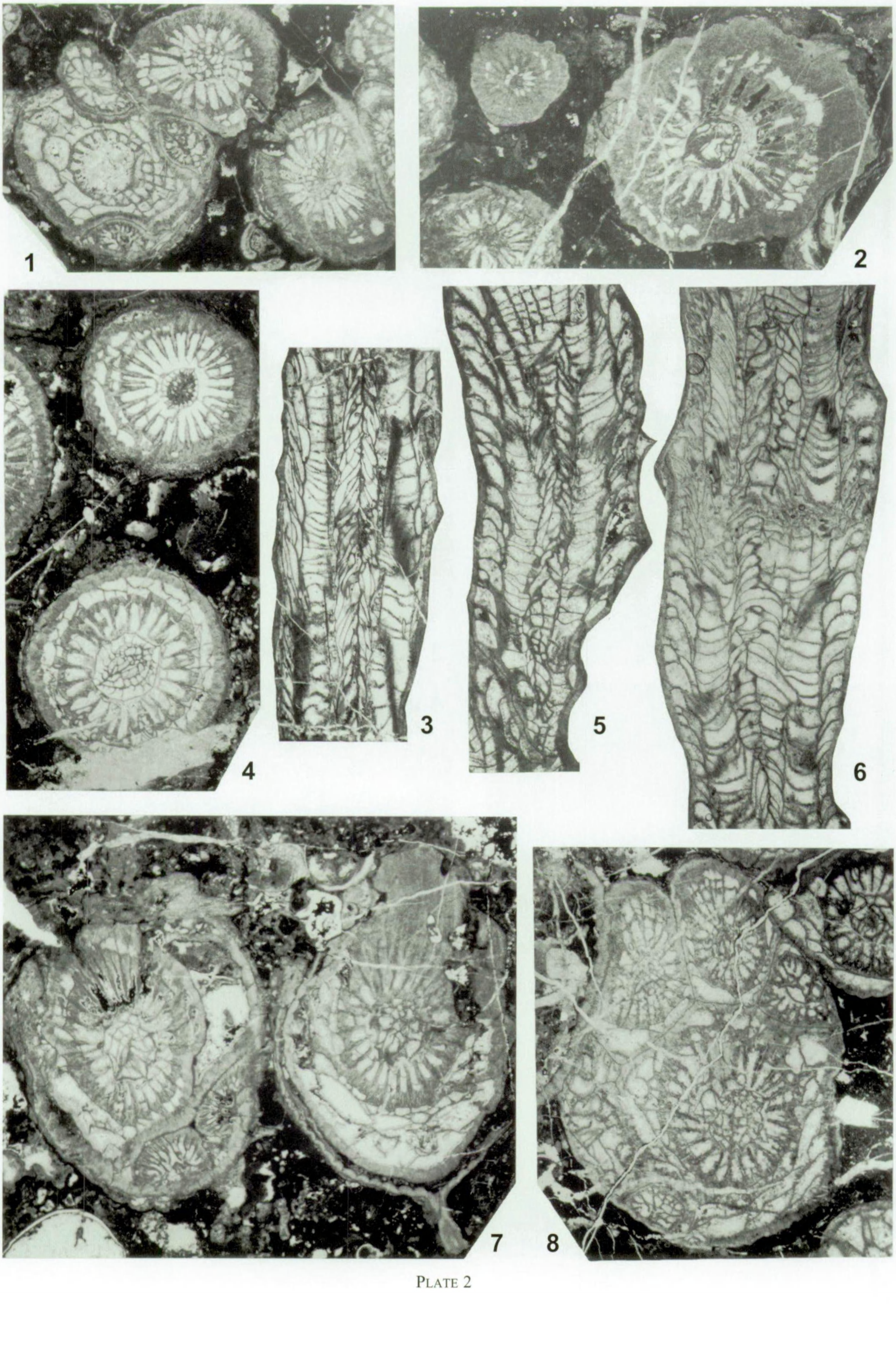

PLATE 2

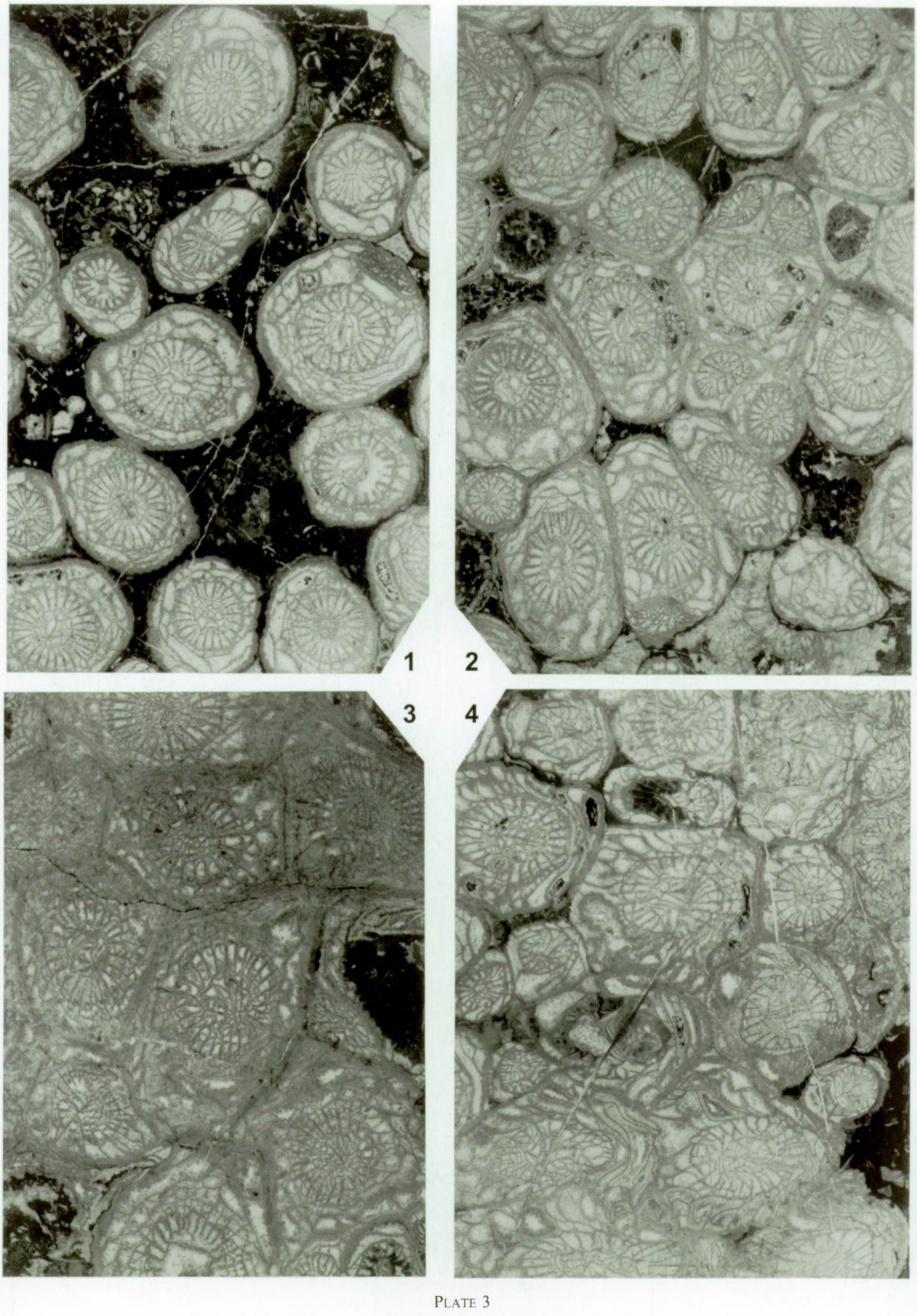

PLATE 3

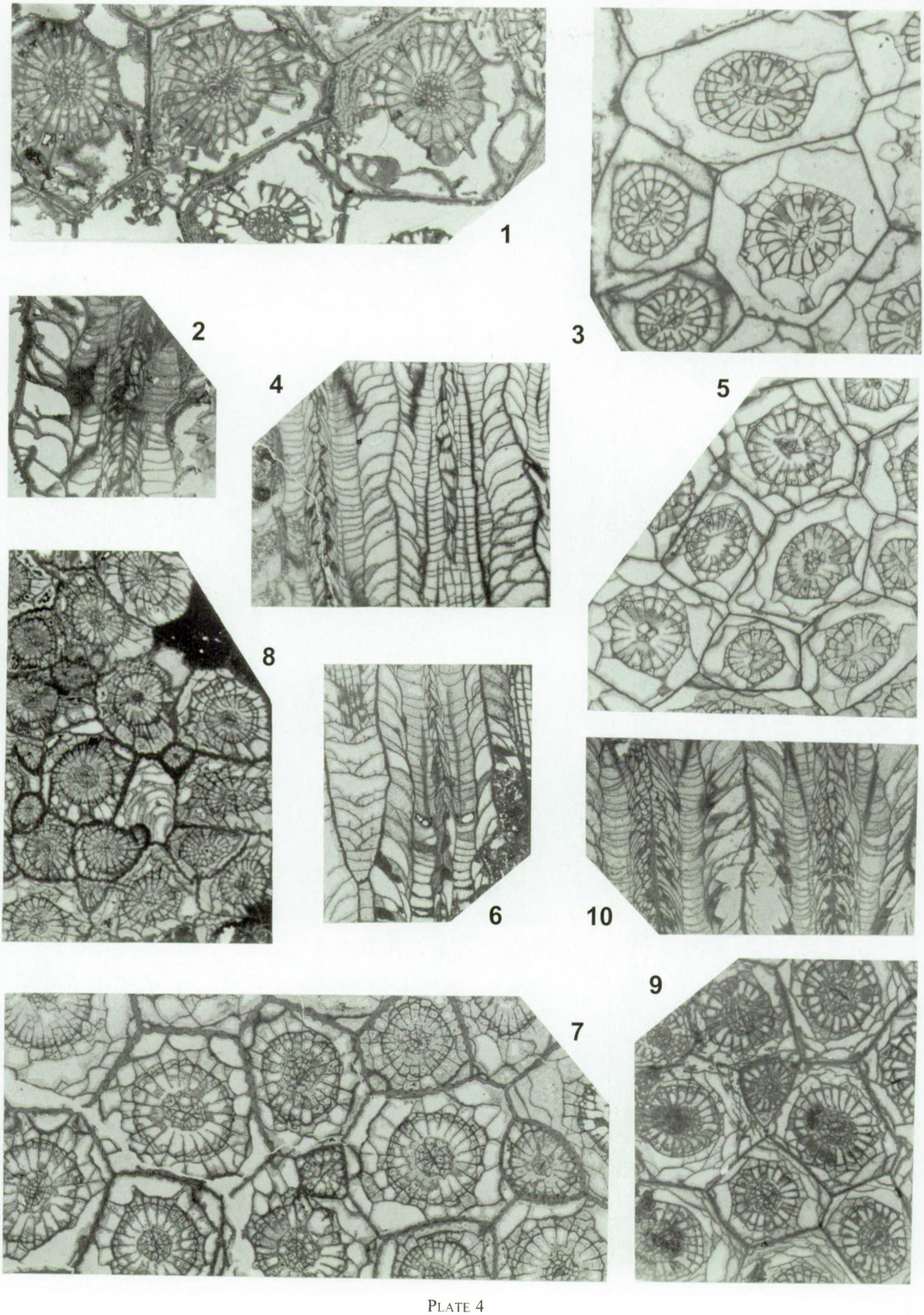

PLATE 4

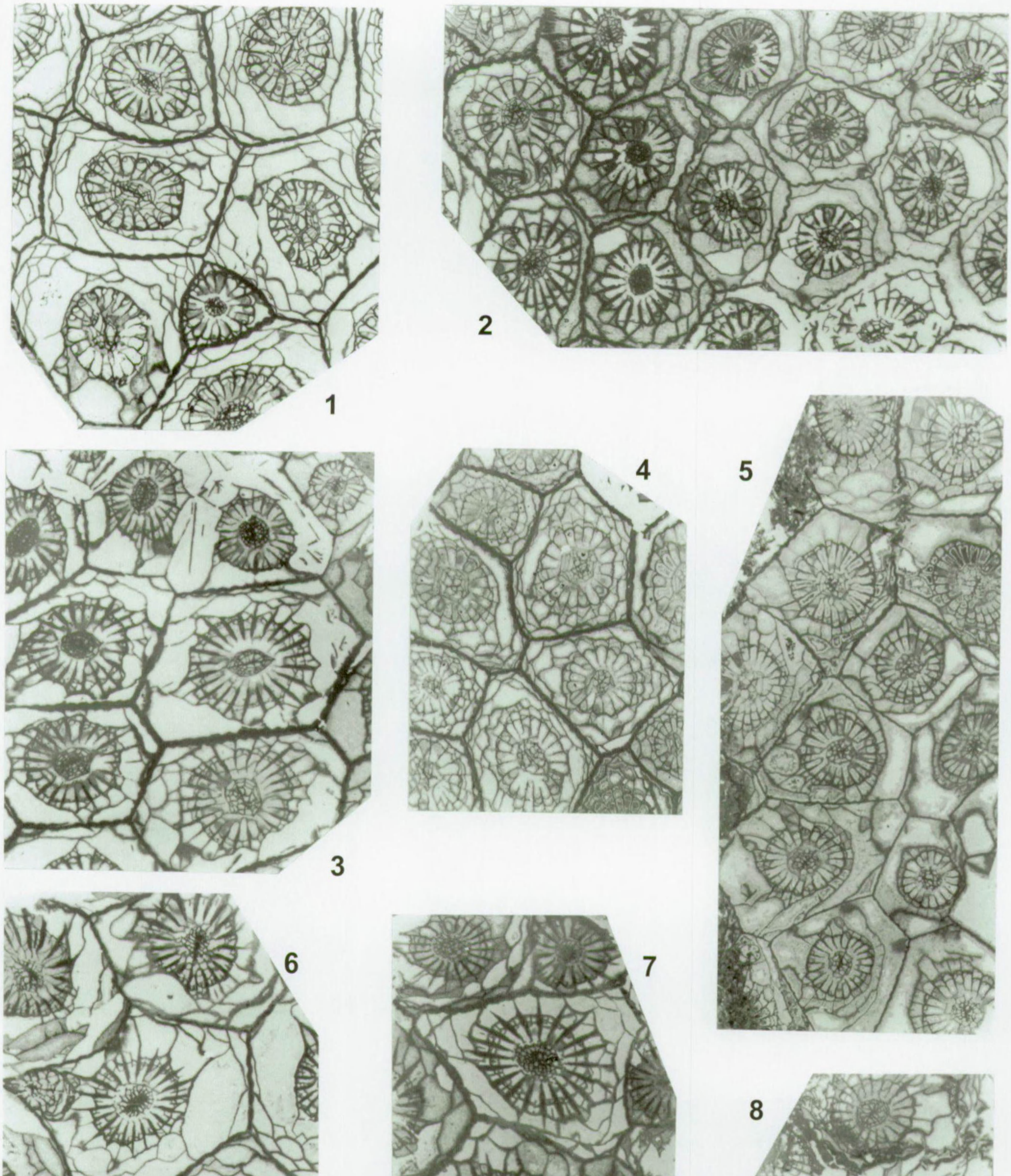

PLATE 5

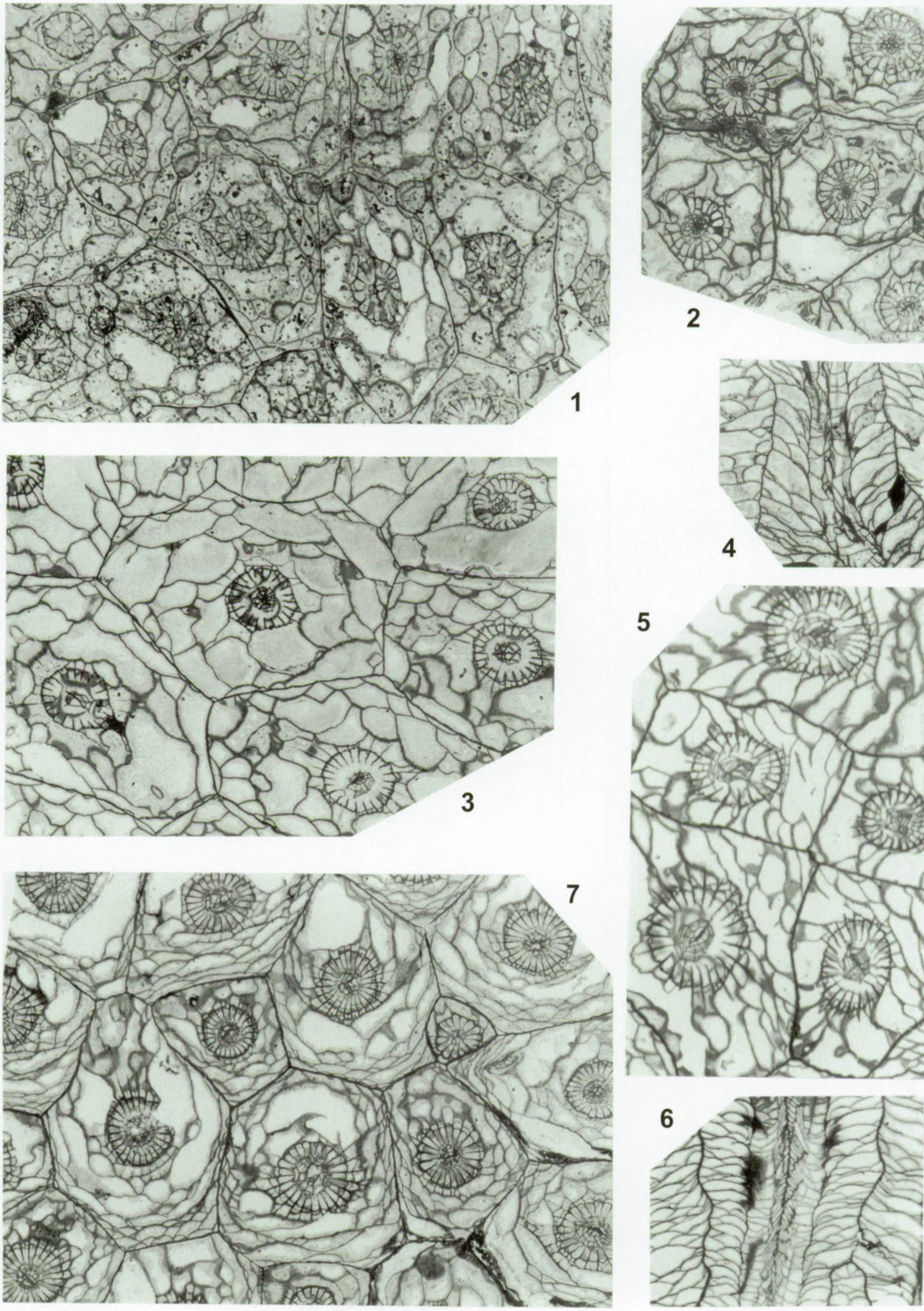

PLATE 6