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Biform tabularia and periaxial cones in *Lonsdaleia* McCoy, 1849 (Rugosa)

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ABSTRACT. Biform tabularia in rugose corals show different orientations of peripheral parts of tabulae situated on opposite sides of minor septa. Periaxial cones form irregular conical structures partly enclosing other structural elements of axial column and represent combination of steeply elevated, vertically extended axial parts of tabulae or periaxial tabellae with elongated axial tabellae. Both structures are characteristic of cerioid genus *Cystolonsdaleia* Fomichev, 1953, but also develop within the limits of variability in *Lonsdaleia* McCoy, 1849, including in some cerioid *Lonsdaleia (Actinocyathus)* d'Orbigny, 1849 species, thus suggesting that *Cystolonsdaleia* could have evolved from *Actinocyathus*. Among *Lonsdaleia* species from the uppermost Viséan-lower Serpukhovian of the Moscow Basin, biform tabularia are documented in *L. (Actinocyathus) crassiconus* (McCoy, 1849), *L. (A.) lativesiculosa* (Dobrolyubova, 1958), and *L. (Actinocyathus)* sp. A; periaxial cones in *L. (A.) bronni* (Milne Edwards et Haime, 1851) and *L. (A.) rossicus* (Stuckenberg, 1904); both biform tabularia and periaxial cones are documented in *L. (A.) floriformis* (Martin, 1809), *L. (A.) borealis* (Dobrolyubova, 1958), *L. (A.) subtilis* (Dobrolyubova, 1958), *L. (A.) gorskyi* (Dobrolyubova, 1958), *L. (A.) sarytschevae* (Dobrolyubova, 1958), *L. (Actinocyathus)* sp. A, and *L. (Lonsdaleia) duplicata* (Martin, 1809).

KEYWORDS: *Lonsdaleia*, morphology, uppermost Viséan-Serpukhovian, Moscow Basin, *Cystolonsdaleia*.

1. Introduction

The term *biform tabularium* was introduced by Weyer (1972) for different orientations, or *positions* in the sense of Sutherland (1965), of peripheral parts of tabulae in rugose corals situated on opposite sides of minor septa, those declined adaxially on one side of a given minor septum (*Position I*) and elevated on the other (*Position II*). First discovered in solitary genus *Ditoecholasma* Simpson, 1900 from the Upper Silurian of Oklahoma by Sutherland (1965), different orientations of peripheral part of tabulae were soon documented by Weyer (1972) in fourteen solitary genera and in one cerioid Upper Ordovician genus, *Crenulites* Flower, 1961, later in Upper Carboniferous *Cystolonsdaleia* Fomichev, 1953 and *Petalaxis* Milne Edwards & Haime, 1852 by Bamber & Fedorowski (1998) (Figs 1B, 1C), in fourteen Lower Permian colonial genera by Fedorowski et al. (2007), and in Lower Carboniferous *Actinocyathus* d'Orbigny, 1849 from the uppermost Viséan (Brigantian)-Serpukhovian of the Moscow Basin by Hecker (2010).

The term *periaxial cones* was introduced by Bamber & Fedorowski (1998) for components of axial structure in the genus *Cystolonsdaleia* representing combination of steeply elevated, vertically extended axial parts of tabulae with elongated axial tabellae. In this genus, periaxial cones form irregular, incomplete conical structures partly enclosing other structural elements of discontinuous and variable axial column (median lamella, radial and lateral lamellae, and discontinuous series of axial tabellae, Fig. 1E). Periaxial cones were also documented in few

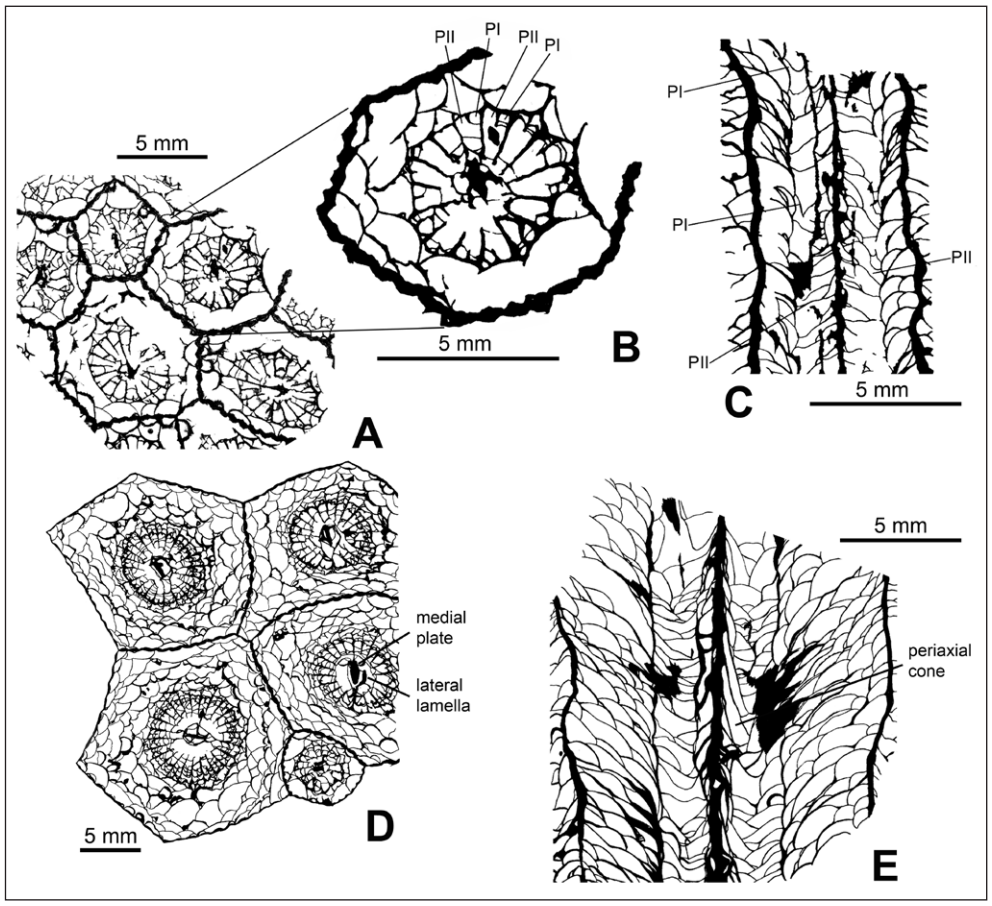

Figure 1. A-C: *Petalaxis maccoyanus* (Milne Edwards et Haime, 1851). A: Transverse section. B: Transverse section showing biform morphology of tabularium. C: Longitudinal section showing biform morphology of tabularium. D-E: *Cystolonsdaleia lutugini* Fomichev, 1953. D: Transverse section. C: Longitudinal section showing periaxial cones on right side of axial column. Legend: PI, tabellae or peripheral parts of tabulae in Position I; PII, tabellae or peripheral parts of tabulae in Position II. (After Bamber & Fedorowski, 1998).

Actinocyathus species from the Moscow Basin (Hecker, 2010).

The objectives of the present paper are: to confirm presence of biform tabularia and periaxial cones in the genus *Lonsdaleia*, and to discuss systematic value of these characters.

The study is based on the collection housed in the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, as part of the collections registered under No. PIN 703, 705 and 1562.

2. Material

The genus *Lonsdaleia* McCoy, 1849 belongs to the family Axophyllidae Milne Edwards & Haime, 1851 and is distinguished by well-defined continuous axial column of dibunophylloid type comprising a median lamella, septal lamellae and typically regularly conical axial tabellae (Pl. 2D). The other diagnostic characters include indistinct to small cardinal fossula, indistinct to well-developed minor septa, concave, subhorizontal or variously declined, commonly complete periaxial tabellae and dissepimentarium dominated by transeptal dissepiments. Increase is typically lateral.

The genus comprises three subgenera: typically fasciculate *Lonsdaleia* and typically cerioid *Actinocyathus* d'Orbigny, 1849, both widely distributed in the uppermost Viséan (Brigantian) of Europe and Asia, and *Serraphyllum* Poty in Poty & Hecker, 2003 having both fasciculate and cerioid habitus, and reported so far from the Serpukhovian of Montagne Noire, South France only (see Poty & Hecker, 2003 for details).

In the subgenus *Actinocyathus*, two species-groups, each representing a separate trend of evolution within the subgenus, are distinguished (Hecker, 1997). The *A. floriformis* (Martin, 1809) group is characterized by its consistently short, commonly indistinct minor septa, and by its highly variable axial structures, whereas the *A. crassiconus* (McCoy, 1849) species-group is distinguished by its consistently developed, commonly long minor septa, and by less variable axial structures, usually showing regularly conical, crowded axial tabellae.

		biform tabularia	periaxial cones
	Lonsdaleia (Lonsdaleia) duplicata	present	present
***A. floriformis* species-group**	***L. (Actinocyathus) floriformis***	present	present
	L. (A.) bronni	not detected	present
	L. (A.) borealis	present	present
	L. (A.) rossica	not detected	present
A. crassiconus species-group	***L. (A.) crassiconus***	present	not detected
	L. (A.) gorskyi	present	present
	L. (A.) subtilis	present	present
	L. (A.) lativesiculosa	present	not detected
	L. (A.) sarytschevae	present	present
	***L. (A.)* sp. A** *in* Hecker (2010)	present	present
	***L. (A.)* sp. B** *in* Hecker (2010)	present	not detected

Table 1. Biform tabularia and periaxial cones in *Lonsdaleia* species from the Moscow Basin.

Among *Lonsdaleia* from the Moscow Basin, biform tabularia are locally developed in *Lonsdaleia duplicata* (Martin, 1809) (Pl. 3A) and in *Actinocyathus* species belonging to both species-groups, *A. floriformis*, *A. borealis* (Dobrolyubova, 1958) (Pl. 1B), *A. crassiconus*, *A. subtilis* (Dobrolyubova, 1958) (Pl. 2B, 2C), *A. gorskyi* (Dobrolyubova, 1958) (Pl. 2H), *A. sarytschevae* (Dobrolyubova, 1958) (Pl. 3E, 3F), *A. lativesiculosus* (Dobrolyubova, 1958), *Actinocyathus* sp. A and *Actinocyathus* sp. B in the sense of Hecker (2010). When biform morphology of tabularium is expressed, periaxial tabellae in Position I are commonly steeper abaxially declined than tabellae in Position II (Pl. 1C). Biform tabularia are especially characteristic for the species comprising the *A. crassiconus* species-group distinguished by minor septa consistently penetrating tabularia (Pl. 2A, 2H, 3D). Biform tabularia are not detected in the two species characterized by systematically indistinct minor septa belonging to the *A. floriformis* species-group, *A. rossicus* (Stuckenberg, 1904) (Pl. 1E) and *A. bronni* (Milne Edwards et Haime, 1851) (Tab. 1).

Periaxial cones in *Lonsdaleia* are composed of fused periaxial and axial tabellae. They are locally developed in *Lonsdaleia duplicata* (Pl. 3B, 3C), *Actinocyathus floriformis*, *A. bronni*, *A. borealis* (Pl. 1C, 1D), *A. rossicus* (Pl. 1F, 1G), *A. subtilis* (Pl. 2E, 2F), *A. gorskyi* (Pl. 2I), A. *sarytschevae* (Pl. 3F) and *Actinocyathus* sp. A. Periaxial tabellae in *Lonsdaleia* typically extend from the dissepimentarium to the outer margin of the axial column and terminate adaxially against an axial tabella, whereas periaxial tabellae forming periaxial cones are steeply elevated near the axial column and merge with elongated axial tabellae joining the median lamella. It is possible to observe a transition from the state when elevated periaxial tabella terminates against an elongated axial tabella to the state when these structures merge to form a periaxial cone (Pl. 1C, 1D, 1F, 1G, 2E, 3B).

Periaxial cones are detected in the majority of the *Actinocyathus* species from the Moscow Basin (Tab. 1), except for *A. crassiconus*, *A. lativesiculosus* and *Actinocyathus* sp. A. *Actinocyathus crassiconus* is characterized by the most regular and well-defined axial column with densely spaced conical axial tabellae. *Actinocyathus lativesiculosus* and *Actinocyathus* sp. A showing marked intracolonial variability involving shape and spacing of axial tabellae and periaxial tabellae (see Hecker, 2010 for details) are represented by scanty material.

3. Discussion

Some published figures of *Lonsdaleia* from the Moscow Basin confirm presence of biform tabularia in *Actinocyathus subtilis* (Dobrolyubova, 1958, pl. 11, figs 1a, 2a, 3a, pl. 12, fig. 1a), *A. sarytschevae* (Dobrolyubova, 1958, pl. 14, fig. 2c), *A. borealis* (Poty & Hecker, 2003, pl. 5, figs 5-6), *A. crassiconus* (Hecker, 2010, fig. 1B) and *Actinocyathus* sp. A (Hecker, 2010, fig. 1H), presence of periaxial cones in *Lonsdaleia duplicata* (Dobrolyubova, 1958, pl. 2, fig. 4b) and *Actinocyathus crassiconus* (Hecker, 2010, fig. 1A), and presence of both biform tabularia and periaxial cones in *A. bronni* (Dobrolyubova, 1958, pl. 6, fig. 3) and *A. gorskyi* (Dobrolyubova, 1958, pl. 13, figs 1a, 1b, 2a, 2b).

Periaxial cones can be easily observed on the published figures of the longitudinal sections of the holotype of cerioid *Lonsdaleia floriformis laticlavia* Smith, 1916 (pl. 19, fig. 11) from the basal Pendleian of Northumberland, North England and "*Lonsdaleia floriformis laticlavia*, but convergent with *crassiconus*" (Smith, 1916, pl. 19, fig. 7) from the Brigantian of Derbyshire.

Bamber & Fedorowski (1998) considered biform tabularium and periaxial cones as the main characters distinguishing *Cystolonsdaleia* from similar cerioid taxa with complex axial structures and transeptal dissepiments, including *Lonsdaleia (Actinocyathus)*.

Biform tabularia, however, are expressed in many rugose species with minor septa long enough to penetrate tabularium as it was demonstrated by Weyer (1972) and Fedorowski et al. (2007). Among the *Actinocyathus* species from the Moscow Basin, biform tabularia were detected even in *A. floriformis* and *A. borealis* with typically short minor septa seldom penetrating tabularium.

Periaxial cones are far less common. In *Actinocyathus*, these structures occasionally develop within the limits of variability of some species. Periaxial cones are best expressed in *A. subtilis*, especially in the colonies form the northwestern part of the Moscow Basin (Pl. 2E, 2F), most probably because this was the area where the species reached the peak of its abundance and showed the highest variability in the Tarusa time (earliest Serpukhovian) (Hecker, 2010), including in the shape of periaxial tabellae locally becoming strongly concave (Pl. 2G).

Actinocyathus shows close affinity to *Cystolonsdaleia* and differs from it mainly by its typically well-defined continuous axial column composed of medial plate, radial lamellae and axial tabellae. In *Cystolonsdaleia*, axial structure ranges from axial plate to axial column, which, when fully developed, consists of medial plate, radial lamellae, lateral lamellae, discontinuous series of axial tabellae and periaxial cones (Fig. 1E) (Bamber & Fedorowski, 1998). Lateral lamellae, characteristic of *Cystolonsdaleia*, are lacking in *Actinocyathus*.

As suggested by presence of periaxial cones in both taxa, *Cystolonsdaleia* could have evolved from *Actinocyathus*, and evolution went in the direction of axial column becoming discontinuous and less regular, and lateral lamellae developing. Periaxial cones, developed within the limits of variability of the ancestral taxon, *Actinocyathus*, became characteristic structures in *Cystolonsdaleia* due to stabilizing selection.

Actinocyathus ranges in age from the uppermost Viséan (Brigantian) through the Serpukhovian, and *Cystolonsdaleia* from the Lower Pennsylvanian (Bashkirian) through the Lower Permian (Asselian). *Cystolonsdaleia* was originally described from the Moscovian (Pennsylvanian) of the Donets Basin, Ukraine (Fomichev, 1953). The earliest firmly dated occurrence of this genus is from the Bashkirian of the Voronezh area, Russia (Kozyreva, 1978); its presence in the Serpukhovian is not confirmed. *Cystolonsdaleia* has been found in the Pennsylvanian of Spain, Canada, USA and China; see Bamber & Fedorowski (1998) and Fedorowski et al., (2007) for details.

Six cerioid species from the Mississippian of the Western Interior Province, all showing periaxial cones, *Litostrotionella girtyi* Hayasaka, 1936 (Middle-Upper Viséan, Utah), *Lithostrotion pennsylvanicum* Shimer, 1926 (Middle Viséan, Alberta, British Columbia), *Lonsdaleia shimeri* Crickmay, 1955 (Middle-Upper Viséan, Alberta, British Columbia, Alaska, Arizona), *Lithostrotion (Lithostrotionella) berthiaumi* Merriam, 1942 (?Upper Viséan-Serpukhovian, Oregon), *Lithostrotionella peratrovichensis* Armstrong, 1970 (Upper Viséan, Alaska), *L. stelcki* Nelson, 1960 (uppermost Viséan-Serpukhovian, Alberta, British Columbia, Utah, Idaho, Wyoming), were assigned to *Cystolonsdaleia* by Bamber & Fedorowski (1998). All these species, however, most probably do not belong to *Cystolonsdaleia*, since they are lacking lateral lamellae and therefore do not completely fit the diagnosis of the genus given by Bamber & Fedorowski (1998) and Fedorowski et al. (2007).

4. Conclusions

Biform tabularia are expressed in many rugose species with minor septa long enough to penetrate tabularium; periaxial cones representing irregular, incomplete conical structures partly enclosing other structural elements of axial column develop less often. In *Lonsdaleia*, periaxial cones are composed of fused periaxial and axial tabellae. Biform tabularia are locally developed in ten species from the Brigantian-Serpukhovian (Mississippian) of the Moscow Basin, and periaxial cones in nine species.

Presence of biform tabularia and especially of periaxial cones in *Lonsdaleia* confirms and puts in evidence its close morphological similarity to *Cystolonsdaleia*. Periaxial cones, occasionally developed in *Lonsdaleia* within the limits of variability, became characteristic structures in *Cystolonsdaleia*. *Cystolonsdaleia* could have evolved from cerioid *Lonsdaleia* (*Actinocyathus*), and the evolution went in the direction of axial column becoming discontinuous and less regular with lateral lamellae and periaxial cones typically developed.

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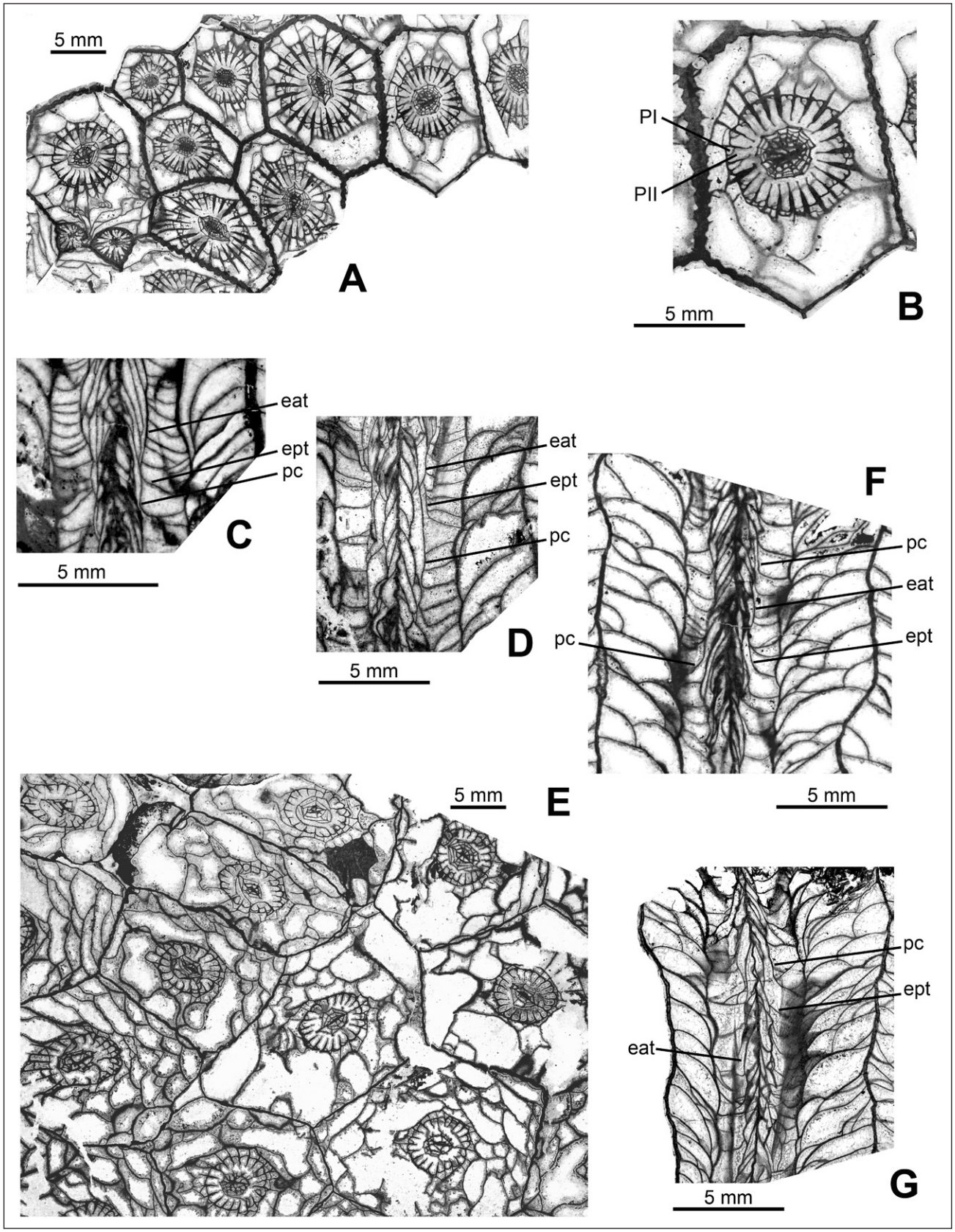

Plate 1. A-D: *Lonsdaleia (Actinocyathus) borealis* (Dobrolyubova, 1958). A-C: Specimen PIN 1562/2514. A: Transverse section. B: Transverse section showing biform morphology of tabularium. C: Longitudinal section showing axial column with elongated axial tabellae and periaxial cone on right side of axial column; Lower Serpukhovian, Steshevo horizon, north-western part of the Moscow Basin, village of Podbor'e, 7 km NW of the town of Borovichi. D: Specimen PIN 705/644, longitudinal section showing variously spaced and declined periaxial tabellae, axial column with elongated axial tabellae and periaxial cone on right side of axial column, x4; Lower Serpukhovian, Steshevo horizon, north-western part of the Moscow Basin, Sukhaya Poneretka Brook, 12 km SW of the town of Borovichi. E-G: *Lonsdaleia (Actinocyathus) rossicus* (Stuckenberg, 1904). E-F: Specimen PIN 703/33. E: Transverse section. F: Longitudinal section showing variously spaced and declined periaxial tabellae, axial column with irregular axial tabellae and periaxial cones on both sides of axial column; Lower Serpukhovian, Steshevo horizon, southern part of the Moscow Basin, left bank of the Oka River at the village of Luzhki, 12 km SE of the town of Serpukhov. G: Specimen PIN 703/40, longitudinal section showing irregularly spaced and variously declined periaxial tabellae, axial column with irregular loosely spaced axial tabellae and periaxial cones on both sides of axial column; Lower Serpukhovian, Steshevo horizon, southern part of the Moscow Basin, left bank of the Oka River at the village of Luzhki, 12 km SE of the town of Serpukhov. Legend: PI: periaxial tabella in Position I; PII: periaxial tabella in Position II; eat: elongated axial tabella; ept: elevated periaxial tabella; pc: periaxial cone; cpt : concave periaxial tabella.

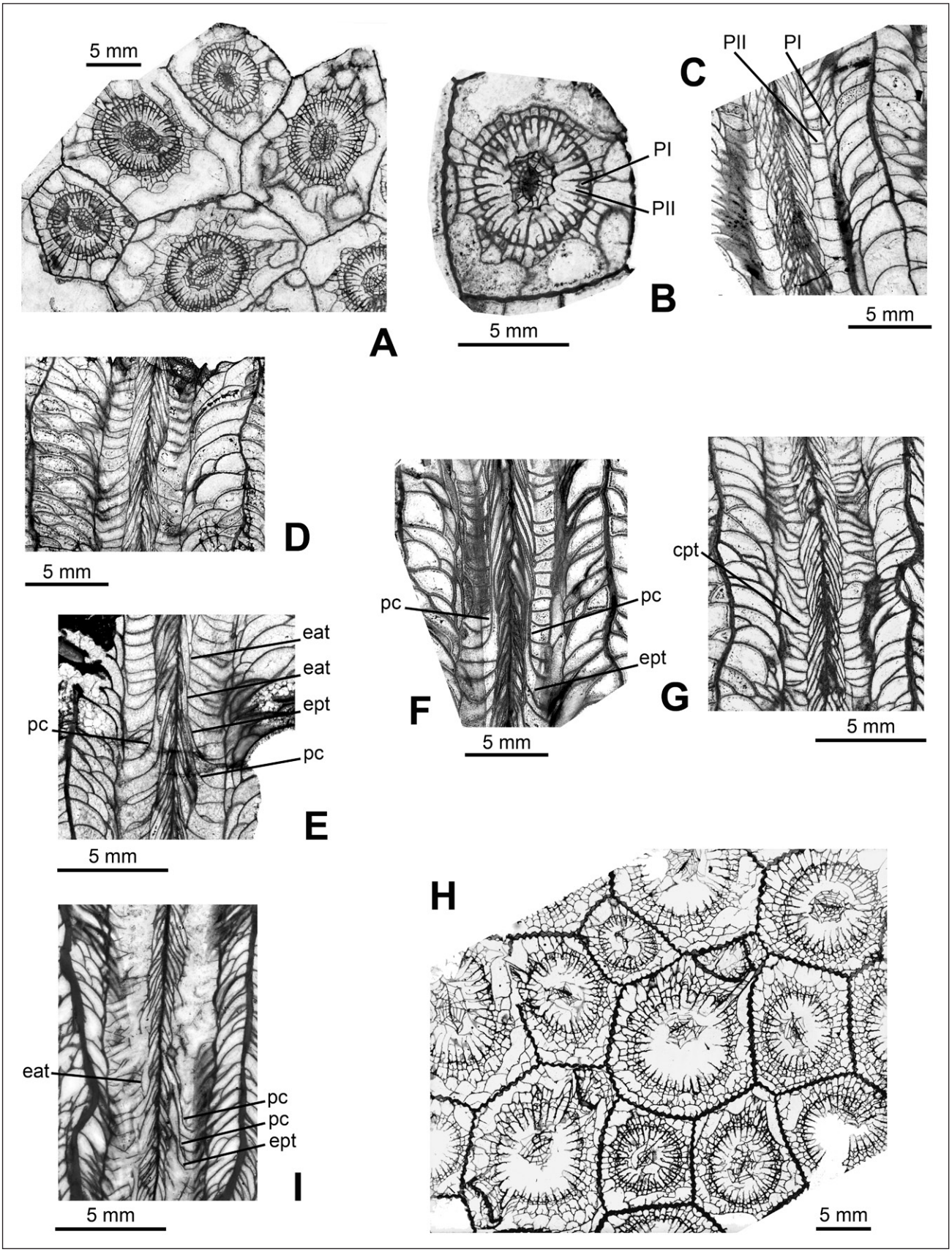

Plate 2. A-G: *Lonsdaleia (Actinocyathus) subtilis* (Dobrolyubova, 1958). A-C: Specimen PIN 705/646. A: Transverse section. B: Transverse section showing biform morphology of tabularium. C: Longitudinal section showing biform morphology of tabularium; Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Retesha River 60 km NE of the town of Boksitogorsk. D-E: Specimen PIN 705/184. D: Longitudinal section showing axial column with regularly conical steeply elevated axial tabellae. E: Longitudinal section showing axial column with variable axial tabellae and periaxial cones on both sides of axial column; Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Tutoka River 60 km NE of the town of Boksitogorsk. F: Specimen PIN 707/332A, longitudinal section showing axial column with regularly conical axial tabellae and long periaxial cones on both sides of axial column; Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Tutoka River 60 km NE of the town of Boksitogorsk. G: Specimen PIN 705/187, longitudinal section showing variously declined, including deeply concave, periaxial tabellae; Lower Serpukhovian, Tarusa horizon, north-western part of the Moscow Basin, Tutoka River 60 km NE of the town of Boksitogorsk. H-I: *Lonsdaleia (Actinocyathus) gorskyi* (Dobrolyubova, 1958); specimen PIN 705/133, holotype. H: Transverse section. I: Longitudinal section showing axial column with variable axial tabellae and periaxial cones on both sides of axial column; Lower Serpukhovian, Steshevo horizon, north-western part of the Moscow Basin, Sukhaya Poneretka Brook, 12 km SW of the town of Borovichi. Legend: see Plate 1.

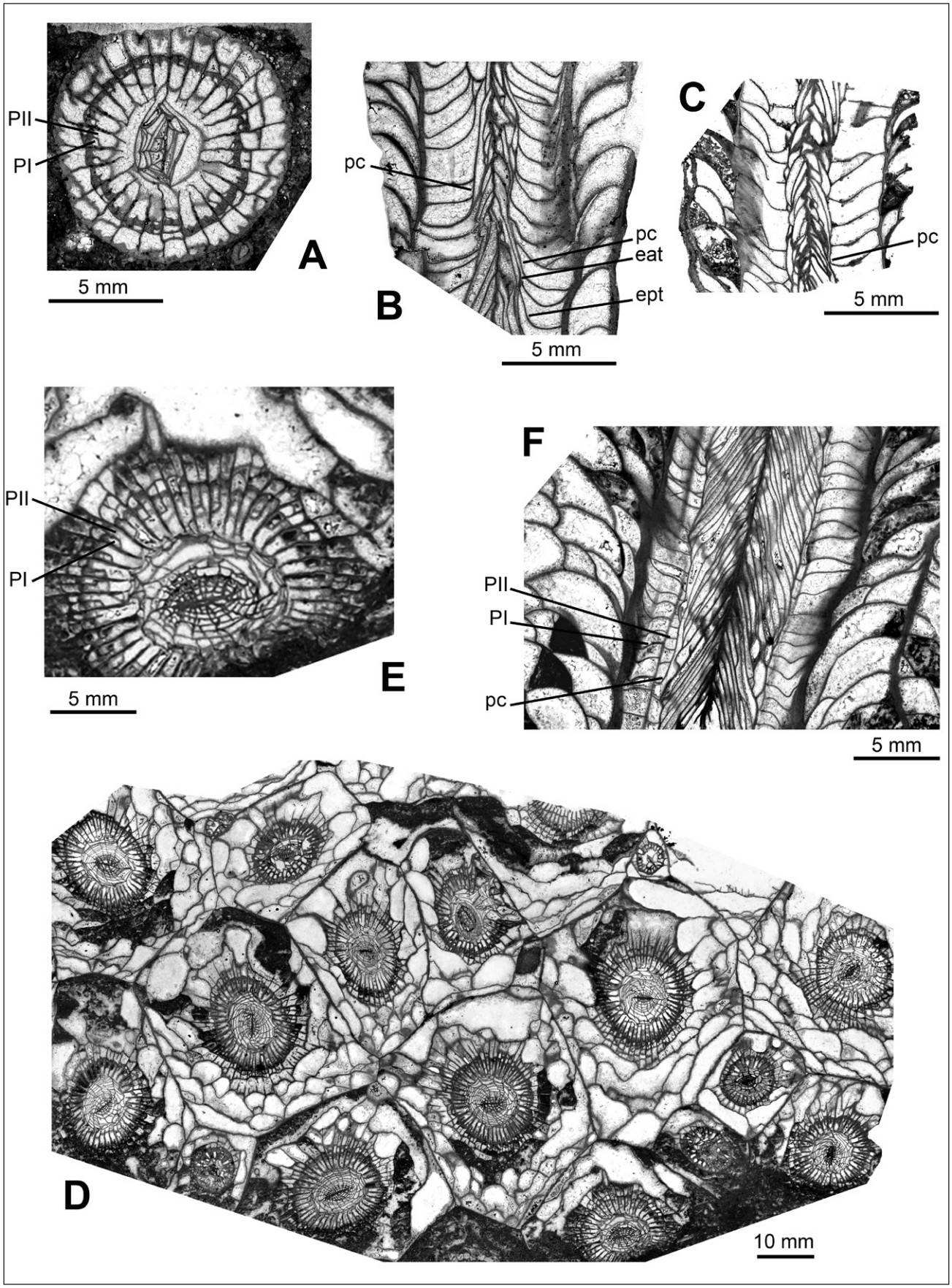

Plate 3. A-C: *Lonsdaleia (Lonsdaleia) duplicata* (Martin, 1809). A-B: Specimen PIN 705/200. A: Transverse section showing biform morphology of tabularium. B: Longitudinal section showing axial column with irregular axial tabellae and periaxial cones on both sides of axial column; Upper Serpukhovian, Protva horizon, north-western part of the Moscow Basin, 25 km SE of the town of Borovichi. C: Specimen PIN 703/2675, longitudinal section showing axial column with regular axial tabellae and periaxial cone on right side of axial column; Upper Viséan, Brigantian, Mikhailov horizon, southern part of the Moscow Basin, Kumova Gora Quarry, 8 km SW of the town of Mikhailov. D-F: *Lonsdaleia* (*Actinocyathus*) *sarytschevae* (Dobrolyubova, 1958); specimen PIN 703/2732, holotype. D: Transverse section. E: Transverse section showing biform morphology of tabularium. F: Longitudinal section showing axial column with regularly conical crowded axial tabellae and periaxial cone on left side of axial column; Lower Serpukhovian, Tarusa horizon, southern part of the Moscow Basin, Kievka River near the city of Kaluga. Legend: see Plate 1.