Paleontological Journal, Vol. 38, No. 3, 2004, pp. 285–293. Translated from Paleontologicheskii Zhurnal, No. 3, 2004, pp. 53–59.

A Revision of the Paleozoic Bryozoan Genera *Synocladia* and *Thamniscus*

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Received January 14, 2003

Abstract—New data on the morphology of the genera *Synocladia* and *Thamniscus* are presented, and the diagnoses and species composition of these genera are revised. A new genus, *Synocladiella* Lisitsyn, and a new species, *Thamniscus perplexus* Ernst, designated as the type species of the genus *Thamniscus* in place of *Th. dubius*, which was erroneously determined by King when establishing the genus *Thamniscus*, are described.

The shape of colonies has been long considered a basic criterion in designating the genera of fenestellid bryozoans. However, Harmelin (1974) has shown that the shape of colonies can be strongly affected by the environment. Thus, the classification of fenestellid bryozoans has begun to use the internal structure of autozooecium (the shape of the zooecial chamber and presence of hemisepta), the presence of heterozooecia (cyclo-, para-, and cavernozooecia, etc.), and the presence and type of ovicells. Based on these characters, Morozova (1974) revised the genus *Fenestella* and divided it into several genera that have the same colony shape but different internal structures (Morozova, 1974). The revision of the genus *Polypora* was performed in the same manner (Morozova and Lisitsyn, 1996).

The genus *Synocladia* was designated by King (1849) from the Zechstein of western Europe based on only external features of colonies, thus ignoring their internal structure. King (1849, p. 388) provided the genus *Synocladia* with the following diagnosis:

"A foliaceous or frondiferous infundibuliform Fenestellidia. Fronds consisting of numerous connected stems or ribs. Stems bifurcating; radiating from a small root; running parallel to, and at short distance from each other, on one plane; and giving off bilaterally numerous short, simple branches, of which opposite pairs conjoin midway between the stems arcuately or at an ascending angle. Branches occasionally modified into stems. Cellules on the inner or upper surface of the fronds; on both stems and branches; imbricated; and distributed in longitudinal series. Series of cellules separated from each other by a dividing ridge."

In his next paper, King (1850, p. 38) supplemented this diagnosis by the only phrase: "Gemmuliferous vesicles on the dividing ridges."

Subsequently, bryozoan species with this generic name were described from the Permian of Pakistan (Waagen and Pichl, 1885), the Urals (Stuckenberg, 1895), Australia (Crockford, 1944; 1957), China (Yang and Lu, 1962), Transcaucasia, and the Russian Far East (Morozova, 1965; 1970). Most of these species contained spherical cavities located within the secondary skeletal tissue that were referred to as cyclozooecia. It was believed that King described them as "gemmuliferous vesicles." At present, cyclozooecia are considered to be a diagnostic character of the family Septoporidae Morozova, 1962, to which the genus *Synocladia* has recently been assigned (Morozova, 1962, 1970; Gorjunova, 1996). However, recent data suggest that views on the morphology and taxonomic position of the genus *Synocladia* should be radically changed.

In 1995–1999, Ernst studied the bryozoan faunas of Permian basins from the Zechstein of Germany and England (Ernst and Schafer, 1999; Ernst, 2001). The emphasis was on type collections and new bryozoan collections from the type localities. This study has shown that the type species of the genus *Synocladia*—*S. virgulacea* (Sedgwick, 1829)—and all the other species of this genus that were described from the same basin lack cyclozooecia and possess ovicells. King described ovicells as "gemmuliferous vesicles." The Zechstein species differ from the other species of the genus *Synocladia* in autozooecial morphology. Thus, the distribution of the genus *Synocladia* King, 1849 is restricted to the Zechstein basin (the species *Thamniscus indubius* Morozova, 1970, in which no ovicells have been found, perhaps also belongs to this genus). This genus is assignable to the family Acanthocladiidae Zittel, 1880 based on the morphology of autozooecia, structure of colonies, and absence of cyclozooecia. All the other species that have cyclozooecia and have previously been assigned to the genus *Synocladia* belong to a new genus, *Synocladiella* Lisitsyn gen. nov. from the family Septoporidae (see Systematic Paleontology for description).

The genus *Thamniscus* was designated by King from the Zechstein of western Europe with the following diagnosis: "The typical Thamniscidia. Stems frequently and irregularly bifurcating more or less on one plane: celluliferous on the side overlooking the imaginary axis of the coral. Cellules imbricated and arranged in quincunx. Gemmuliferous vesicles overlying the cellule-apertures" (King, 1849, p. 389). King designated *Keratophytes dubius* Schlotheim, 1820 as the type species. Study of the type specimens of this species has shown that they belong to the species *Synocladia virgulacea* (Sedgwick, 1829). The error of King is due to the fact that, in *Synocladia*, colonies vary in shape from freely branching to fenestrate (dissepiments of fenestrate colonies are characteristic of this genus and bear autozooecia). Thus, *Synocladia virgulacea* (Sedgwick) is a junior synonym of *Keratophytes dubius* Schlotheim.

The description and figures of the species described by King suggest that it differs from *Keratophytes dubius* Schlotheim and does not belong to the genus *Synocladia*. King (1850) provided the description and figures of cyclozooecia found in *Thamniscus dubius*, referring to them as accessory vesicles.

Among bryozoans of the Zechstein, Ernst revealed dendroid forms with a morphology consistent with King's diagnosis of the genus *Thamniscus*. In internal structure, these bryozoans do not differ from the genus *Shulgapora* Termier et Termier, 1971. The shape of autozooecia and the presence of cyclozooecia indicate that these genera are closely related. However, there is a difference in the structure of colonies: the genus *Shulgapora* has colonies formed by straight branches that are connected by dissepiments devoid of autozooecia, whereas *Thamniscus* has colonies consisting of freely dichotomizing branches that, very occasionally, are connected by anastomoses or dissepiments. It is quite possible that further investigation will show that the genus *Shulgapora* is a junior synonym of *Thamniscus*.

In our opinion, the generic name *Thamniscus* King, 1849 should be retained, but the type species that was erroneously identified by King should be replaced, according to article 70.3.2 of the International Code of Zoological Nomenclature (*International*..., 1999).

Various bryozoans with dendroid colonies were placed in the genus *Thamniscus* (Waagen and Wentzel, 1886; Bassler 1929; Sakagami, 1961; and others). These bryozoans were described on the basis of external characters, not mentioning the presence of cyclozooecia. The question whether they belong to the genus *Thamniscus* can be answered only after studying the type material. The type material of the Zechstein species of this genus was restudied (Ernst, 2001). The species *Th. diffusus* Korn, 1930 was assigned to the genus *Acanthocladia*. The species *Th. geometricus* Korn, 1930 was assigned to the genus *Synocladia*. Since the type material of the species *Th. siccus* Dreyer, 1961 has not been found, it cannot be assigned to any genus.

The bryozoans were measured by the methods developed by Snyder (1991) and Hageman (1991). These authors proposed measuring a large set of characters to assess the difference between taxa statistically. Application of this method usually involves the calculation of such statistical characteristics of the characters as the number of measurements (N), arithmetic average (X), standard deviation (SD), coefficient of variation (CV), minimum value (MIN), and maximum value (MAX).

The following measurements have been made of the material under study: the diameter of the apertures of autozooecia (AW), distance between the centers of apertures in longitudinal series (ADB), distance between the centers of apertures in the neighboring longitudinal rows (AAB), distance between the centers of apertures on the neighboring branches (ABB), width of the branch (WB), width of the dissepiment (WD), length of the fenestrule (LF), width of the fenestrule (WF), diameter of nodes (DN), distance between the centers of nodes (SNB), minimum (MIW) and maximum (MAW) width of the zooecial chamber, length (CL) and height (CD) of the zooecial chamber, distance between the centers of dissepiments (DDC), distance between the centers of the neighboring branches (DBC), length of vestibule (VD), thickness of lateral wall (TLW), and the angle of budding of the proximal wall (RA). The specimens marked with (*) in the Material sections have been measured.

MATERIAL

The collections being studied are housed at the Paleontological Institute of the Russian Academy of Sciences, Moscow, PIN, nos. 4922, 4923, and 3229; Museum of Petroleum Geology of the All-Russia Research Institute of Petroleum Geology and Prospecting, St. Petersburg, VNIGRI, no. 134; Museum of Natural History of the Humboldt University in Berlin (Museum für Naturkunde, Humboldt-Universität zu Berlin) MNHU-B, K. 45; paleontological collections of the Institute of Geosciences at the Martin-Luther University in Halle (Institut für Geowissenschaften, Martin-Luther Universität, Halle), IGMLU-H, Korn collection (Korn, 1930); Federal Institute of Geosciences and Raw Materials, Berlin (Bundesanstalt für Geowissenschaften und Rohstoffe, Dienstbereich Berlin), BGR, X11875, X11894, and X11895; and Senckenberg Museum, Frankfurt am Main (Senckenberg-Museum) SMF, 1630–1637.

SYSTEMATIC PALEONTOLOGY

Order Fenestellida

Family Acanthocladiidae Zittel, 1880

Genus *Synocladia* King, 1849

(non *Synocladia* King, 1849: Crockford, 1944, p. 165; Yang and Lu, 1962, pp. 107–108; Morozova, 1970, p. 200; 2001, p. 74).

Retepora: Sedgwick, 1829, p. 120.

Fenestella: Howse, 1848, p. 44.

Synocladia: King, 1849, p. 388; 1850, pp. 38–39; Geinitz, 1861, p. 118; Korn, 1930, pp. 357–359; Dreyer, 1961, p. 24; ?Sakagami, 1961, p. 45.

Thamniscus: King, 1850, p. 44 [partim]; Korn, 1930, pp. 364–365 [partim]; Dreyer, 1961, p. 19 [partim]; Morozova, 1970, p. 237.

Type species. *Retepora virgulacea* Sedgwick, 1829 [=*Keratophytes dubius* Schlotheim, 1820]; Upper Permian, Magnesian Limestone; England.

Diagnosis. Colonies funnel-shaped. Slender secondary branches frequently separated from main branches and forming regular meshwork. Branches frequently fused. Zooecia arranged in three to five rows on main branch and in one to three rows on secondary branches. Apertures of zooecia on interior part of funnel-shaped colony. One acanthostyle frequently present in peristomes of apertures. Zooecia relatively long, with expanded middle part, slightly flattened, with well-developed vestibule. Shape of zooecia hexagonal in median section and tetragonal in other sections. Angle between reverse and basal walls of zooecium (RA) 30°–55° (X = 42.35). Upper hemiseptum poorly developed; lower hemiseptum absent. Ovicells spherical, restricted to proximal wall of vestibule, of frequent occurrence.

Comparison. In the structure of the zooecia and ovicells, the genus *Synocladia* is close to the genus *Acanthocladia* King, as well as to *Penniretepora* and *Kalvariella* from the Zechstein (Ernst, 2001), but differs from them in having fenestrate and dendroid colonies and in the presence of a single node in the aperture of zooecium.

Species composition. *S. dubia* (Schlotheim, 1820) and *S. geometrica* (Korn, 1930).

Occurrence. Upper Permian, Zechstein, lower Werra Carbonate (reef facies); Germany, England, Poland.

Synocladia dubia (Schlotheim, 1820)

Plate 8, figs. 2, 3, and 6

Keratophytes dubius: Schlotheim, 1820, pp. 340–341 [partim].

Retepora virgulacea: Sedgwick, 1829, p. 120, pl. 12, fig. 6.

Fenestella virgulacea: Howse, 1848, p. 44.

Synocladia virgulacea: King, 1849, p. 388; King, 1850, pp. 38–40, pl. 3, fig. 14, pl. 4, figs. 1–8; Geinitz, 1861, p. 118, pl. 22, figs. 3 and 4; Korn, 1930, pp. 357–359, pl. 32, fig. 7, pl. 33, figs. 2–4, text-fig. 3.

Thamniscus dubius: King, 1850, pp. 44–47 [partim], pl. 5, fig. 10 (non figs. 11, 12).

Synocladia weigelthi: Korn, 1930, pp. 359–360, pl. 32, figs. 10 and 11, pl. 33, fig. 1.

Synocladia dux: Korn, 1930, pp. 357–359, pl. 2, figs. 5 and 6.

Lectotype. MNHU-B, K. 45-1; Gluecksbrunn, Thuringia, Upper Permian, Zechstein reef dolomite.

Description. The branches are wide, form a funnel-shaped colony, are connected by regularly spaced dissepiments bearing zooecia, frequently merge, and bifurcate at an angle of 17°–48°. The zooecia are arranged in three to five rows on the branches and in one to three rows on the dissepiments. In the proximal part of the colony, the branches are thicker and usually bear four rows of zooecia. In the distal parts of the colony, the branches are thinner and usually bear three rows of zooecia. Before the bifurcation, the branches usually form one or two additional rows of zooecia. After the bifurcation, the number of rows diminishes down to two or three. New branches can quite often be formed through a transformation of a lateral secondary branch. The apertures of zooecia are located on the interior part of the funnel-shaped colony. The peristomes of apertures have a single acanthostyle, located distally. The zooecia are relatively long, with an expanded middle part, and slightly flattened, with a well-developed vestibule. The angle between the reverse and basal walls of zooecium (RA) is 30°–55° (X = 44.75). The zooecia are hexagonal in the median section. The upper hemiseptum is poorly developed, and the lower hemiseptum is absent. Heterozooecia, in the form of circular ovicells, are common on the proximal wall of the vestibule. The ovicells are 0.13–0.15 mm in diameter. The carinas are straight, bear regularly arranged small nodes 0.02–0.04 mm in diameter, and are located between the longitudinal rows of zooecia.

Measurements in mm (by A. Ernst):

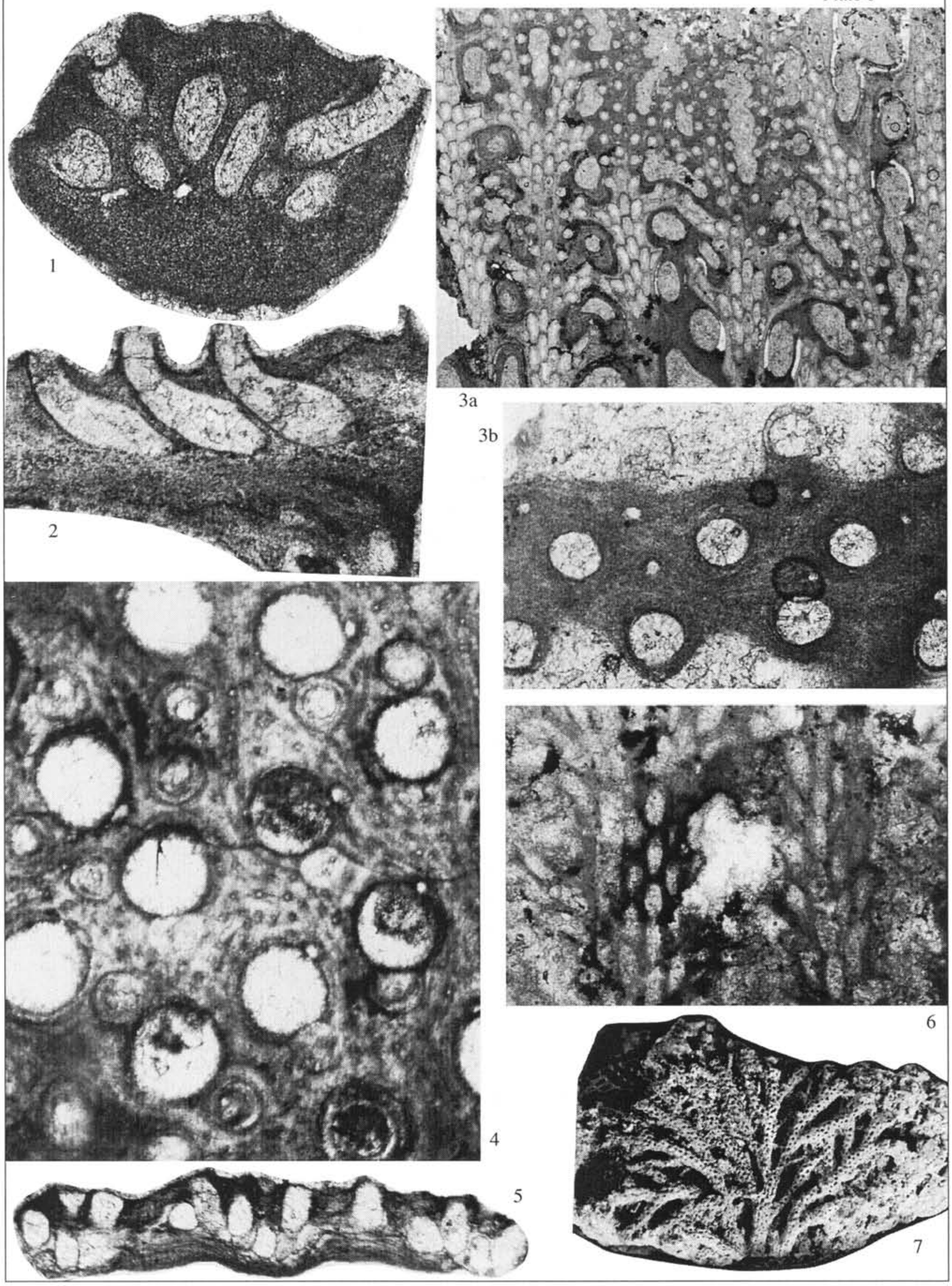
	N	X	SD	CV	MIN	MAX
AW	152	0.09	0.0093	9.8324	0.07	0.12
ADB	150	0.30	0.0397	13.1661	0.20	0.41
AAB	133	0.24	0.0280	11.8593	0.17	0.30
ABB	11	0.44	0.0975	21.9220	0.31	0.58
WB	74	0.65	0.1037	16.0564	0.46	0.95
WD	48	0.42	0.0865	20.7863	0.26	0.60
WF	9	0.70	0.2253	31.9618	0.35	1.14
LF	7	1.16	0.2370	20.4874	0.74	1.39
DN	32	0.05	0.0212	46.0372	0.02	0.09
SND	21	0.27	0.0442	16.3939	0.19	0.37
MIW	42	0.08	0.0116	14.7492	0.05	0.11
MAW	49	0.12	0.0136	11.3189	0.10	0.15
DBC	4	1.27	0.2965	23.3865	0.86	1.56
DDC	6	1.49	0.2559	17.1289	1.02	1.72
CL	48	0.28	0.0268	9.7588	0.20	0.35
CD	3	0.16	0.0083	5.2486	0.15	0.17
VD	2	0.17	0.0000	0.0000	0.17	0.17
TLW	6	0.03	0.0058	19.1220	0.02	0.04
RA	12	44.75	9.2552	20.6821	30.00	55.00

Comparison. *S. dubia* differs from *S. geometrica* Korn, 1930 in having regular fenestrate colonies and acuter angles of bifurcation.

Occurrence. Upper Permian, Zechstein, lower Werra Carbonate (reef facies); Germany, England.

Material. In addition to the lectotype, ten paralectotypes: MNHU-B, K. 17, K. 18, K. 19, K. 20, K. 23, K. 27, K. 28, K. 29, K. 38, K. 45; IGMLU-H, originals of Korn (1930) to the species *Synocladia virgulacea*,

Plate 8



holotypes of *S. dux* and *S. weigelthi* (Korn, 1930, pl. I, figs. 9*, 10*; pl. II, figs. 1*, 9*); collections taken by A. Ernst: specimen SMF 1630 (three colonies*), Tunstall Hills, England; SMF 1631 (two colonies*), Altenburg near Pößneck, Germany; SMF 1632 (two colonies*), Hylton Castle, England; SMF 1633, Hasselberg near Pößneck, Germany; SMF 1634, Gamsenberg near Oppurg, Germany; SMF 1635 (one colony*), Drommberg near Neunhof, Germany; SMF 1681, Streitberg near Neunhof, Germany. Upper Permian, Zechstein, lower Werra Carbonate (reef facies).

Synocladia geometrica (Korn, 1930)

Plate 8, figs. 1 and 7

Thamniscus dubius: King, 1850, pp. 44–47 [partim], pl. 5, fig. 12 (non figs. 10, 11).

Thamniscus geometricus: Korn, 1930, pp. 366–367, pl. 33, figs. 17 and 18, pl. 34, figs. 2–5, text-fig. 8; Dreyer, 1961, p. 20, pl. 8, figs. 5 and 6.

L e c t o t y p e. IGMLU-H, specimen of Korn presented in pl. 33, fig. 17 (Korn, 1930); Altenburg near Pößneck, Thuringia; Zechstein, lower Werra Carbonate (reef facies).

D e s c r i p t i o n. The branches freely bifurcate to form a funnel-shaped colony. The main branches bifurcate frequently, 1–3 mm apart, at an angle of 45°–60°. The zooecial apertures are arranged on branches in three to five rows. The rounded apertures have a well-defined peristome. The peristome has one small acanthostyle. The small nodes are randomly arranged on the surface of the colony. The branches are connected by either sterile (frequently) or zooecia-bearing dissepiments, especially in the basal parts of the colony. Carinas are absent. The zooecia are hexagonal in the median section. The vestibule is well developed, often being quite long owing to the deposits of skeletal material on the frontal surface of the colony. The upper hemiseptum is poorly developed, and the lower hemiseptum is absent. The ovicells are circular and quite common, being located on the proximal wall of the vestibule. The diameter of the ovicells is 0.13–0.15 mm.

M e a s u r e m e n t s in mm (by A. Ernst):

	N	X	SD	CV	MIN	MAX
AL	52	0.11	0.0150	13.1970	0.08	0.15
AW	97	0.09	0.0117	12.7458	0.07	0.12
BW	39	0.70	0.1367	19.4261	0.52	0.96
ADB	76	0.30	0.0343	11.3127	0.24	0.36
AAB	76	0.25	0.0279	11.1534	0.20	0.32
MAW	2	0.13	0.0136	10.4757	0.12	0.14
CL	2	0.23	0.0354	15.7135	0.20	0.25
CD	4	0.12	0.0117	9.8587	0.11	0.14
DN	12	0.07	0.0302	42.3306	0.04	0.12
SND	6	0.32	0.0628	19.6771	0.25	0.38
VD	3	0.07	0.0133	18.4778	0.06	0.09
TLW	2	0.02	0.0071	35.3553	0.02	0.03
TB	3	0.55	0.1136	20.6506	0.42	0.63

C o m p a r i s o n. *S. geometrica* differs from *S. virgulacea* in having a dendroid colony with irregular fusion of branches, rare dissepiments, and absence of carinas.

O c c u r r e n c e. Upper Permian, Zechstein, lower Werra Carbonate (reef facies); Germany, England, Poland.

M a t e r i a l. In addition to the lectotype*, two paralectotypes, i.e., IGMLU-H, specimens of Korn (Korn, 1930) presented in pl. 34, fig. 4* and pl. 34, fig. 5*, and six colonies from the collections taken by A. Ernst in 1996 and 1997, i.e., SMF 1636 (three colonies*), Altenburg near Pößneck, Germany; SMF 1637 (one colony*); and SMF 1681 (two colonies*), Gamsenberg near Oppurg, Germany. Upper Permian, Zechstein, lower Werra Carbonate (reef facies).

Family Septoporidae Morozova, 1962

Genus *Synocladiella* Lisitsyn gen. nov.

Synocladia: Simpson, 1897, p. 513; Zittel, 1876–1880, p. 602; Ulrich, 1890, p. 398; Nickles and Bassler, 1900, pp. 41, 424; Crockford, 1944, p. 165; Bassler, 1953, p. G128; Schulga-Nesterenko *et al.*, 1960, p. 82; Dreyer, 1961, p. 24; Sakagami, 1961, p. 45; Morozova, 1970, p. 200; 2001, p. 74.

Phyllopora: Trizna and Klaucen, 1961, p. 447.

E x p l a n a t i o n of P l a t e 8

Fig. 1. *Synocladia geometrica* (Korn); specimen SMF 1637; Gamsenberg near Oppurg, Thuringia, Germany; Upper Permian, Zechstein, lower Werra Carbonate (reef facies); cross section, ×81.

Fig. 2. *Synocladia dubia* (Schlotheim); specimen SMF 1631; Altenburg, Thuringia, Germany; Upper Permian, Zechstein, lower Werra Carbonate (reef facies); longitudinal section of branch, ×81.

Fig. 3. *Synocladia dubia* (Schlotheim); specimen SMF 1630; Tunstall Hills, England; Upper Permian, Zechstein reef; (3a) tangential section, ×11; (3b) tangential section, ×80.

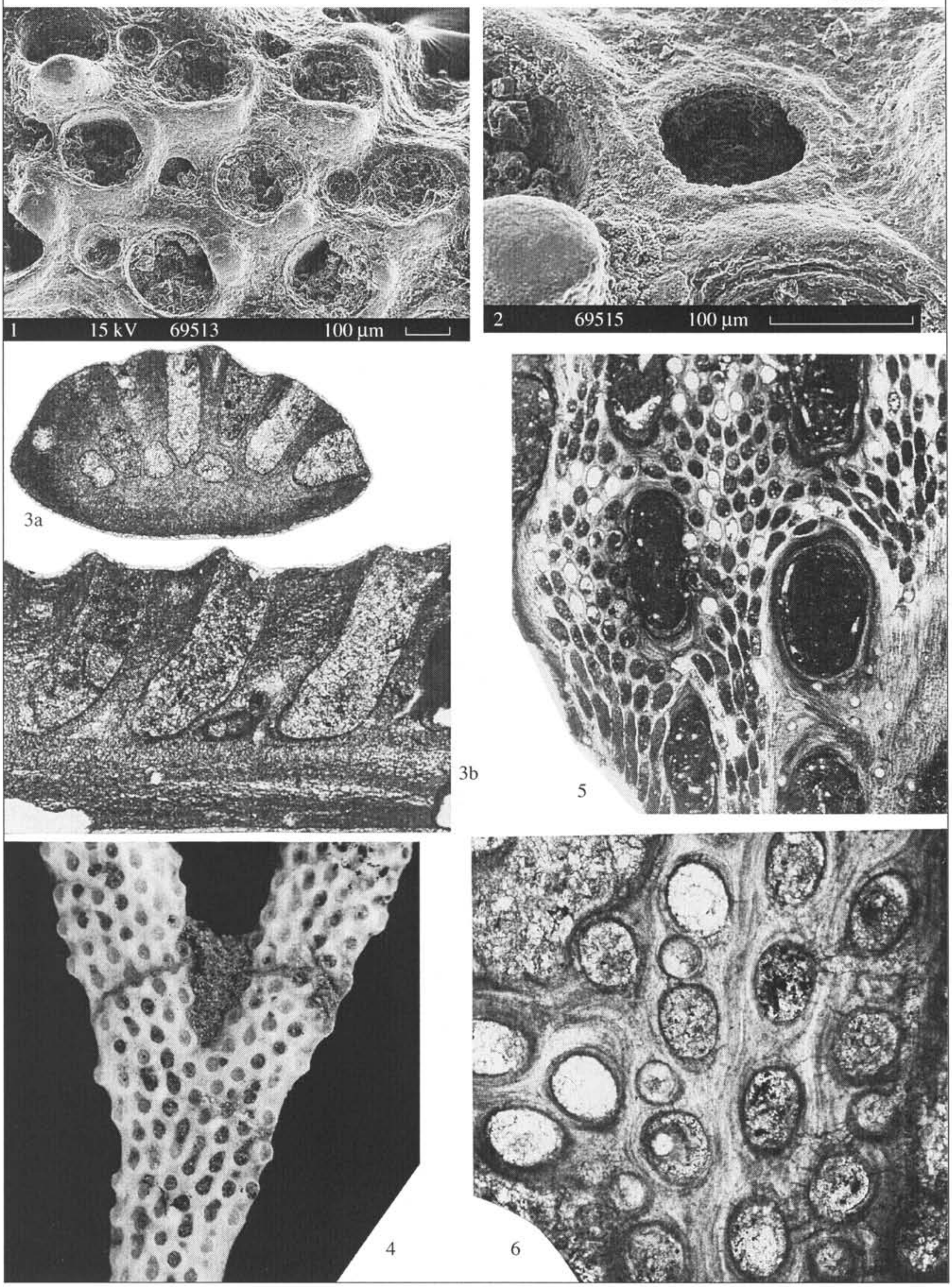
Fig. 4. *Synocladiella georgii* (Trizna et Clauсen); specimen PIN, no. 4922/028; northern Cisuralia, Inta River, outcrop 71; Lower Permian, Artinskian Stage; tangential section, ×90.

Fig. 5. *Synocladiella georgii* (Trizna et Clаucen); specimen PIN, no. 3229/243s; central Cisuralia, near the town of Krasnoufimsk, Borehole 33, depth 136.1–136.6 m; Lower Permian, Artinskian Stage; cross section, ×30.

Fig. 6. *Synocladia dubia* (Schlotheim); lectotype MNHU-B, K. 45-1; Gluecksbrunn, Germany; Upper Permian, Zechstein, reef dolomite; tangential section, ×44.

Fig. 7. *Synocladia geometrica* (Korn); holotype IGMLU-H, presented by Korn (1930) in pl. 33, fig. 17; Altenburg near Pößneck, Thuringia, Germany; Upper Permian, Zechstein, Werra Carbonate; outward appearance of the colony.

Plate 9



Etymology. From the genus *Synocladia* King, 1849.

Type species. *Phyllopora georgii* Trizna et Klaucen, 1961; Lower Permian, Artinskian Stage of the central Urals.

Diagnosis. Colonies formed by parallel bifurcating branches, consisting of three and more rows of zooecia. Secondary branches consisting of two or three rows of zooecia diverge from main branches to connect at an angle with similar processes of neighboring branches. Autozooecia tetragonal-hexagonal in tangential section. Zooecia tubular in shape, always overlapping the following zooecia, hemisepta not found. Apertures of zooecia round. Ridges separating longitudinal rows of zooecia absent. Cyclozooecia shaped like spherical cavities and always present in layer of secondary skeletal material at surface of colony. On frontal side of colony, cyclozooecia located among apertures of autozooecia, usually one cyclozooecium per aperture. On reverse surface of branches, cyclozooecia arranged at random, including those on secondary processes connecting branches.

Species composition. *S. georgii* (Trizna et Klaucen, 1961) Lower Permian, Artinskian Stage of the Fore-Urals; *S. pyriformis* (Yang et Lu, 1962) Upper Permian of China and Primorye.

Comparison. It differs from the genus *Septopora* Prout, 1859 in the larger number of rows of zooecia on branches (six to eight instead of two in *Septopora*). From the genus *Shulgapora*, it differs in the branches being connected by fused processes rather than dissepiments devoid of zooecia.

Synocladiella georgii (Trizna et Klaucen, 1961)

Plate 8, figs. 4 and 5; Plate 9, figs. 5 and 6

Phyllopora georgii: Trizna and Klaucen, 1961, pp. 447–449, pl. 15, fig. 4; pl. 16, figs. 1–3; text-figs. 35 and 36.

Holotype. VNIGRI, no. 67/134; central Urals, near the town of Krasnoufimsk, locality of Peshchernyi Log; Lower Permian, Artinskian Stage, Sarga Horizon.

Description. The colonies are formed by bifurcating branches, consisting most commonly of three or four rows of zooecia. The number of rows of zooecia increases before bifurcation (eight to ten) and diminishes after the bifurcation (two or three). Processes consisting of two or three rows of zooecia diverge from the main branches to connect at an angle with similar processes of the neighboring branches. Occasionally, these processes of the second order may be very short (as long as one or two zooecia), with their merging closely resembling anastomose. The zooecia are tetragonal-hexagonal in the tangential median section. The cyclozooecia are shaped like spherical cavities with a diameter of 0.0805–0.1495 mm and are always present in the layer of secondary skeletal material at the surface of the colony. On the frontal side of the colony, cyclozooecia are located among the apertures of autozooecia, usually one cyclozooecium per aperture. On the reverse surface of the branches, cyclozooecia are arranged at random, including those on the anastomizing processes connecting the branches.

Measurements in mm (by Lisitsyn):

	N	X	SD	CV	MIN	MAX
WB	36	1.02	0.3368	33.1338	0.40	1.76
DBC	41	1.81	0.3959	21.8900	1.07	3.00
WD	47	0.65	0.1987	30.3583	0.27	1.23
LF	62	1.47	0.2090	14.2400	1.00	2.00
WF	37	0.75	0.2481	33.2191	0.43	1.67
AF	29	6.31	0.6603	10.4633	5	8
AW	60	0.15	0.0127	8.2647	0.13	0.20
DSO	22	0.0108	0.0022	20.1948	0.0069	0.0138
RSL	15	0.0120	0.0022	18.0985	0.0069	0.0161
RSS	16	0.0029	0.0010	35.7771	0.0023	0.0046
CD	2	0.27	0.0942	35.3553	0.20	0.33
TB	2	0.58	0.0235	4.0406	0.57	0.60
CD + VD	4	0.67	0.2966	44.5346	0.40	1.00
CD	62	0.10	0.0145	13.9851	0.08	0.15

Comparison. From the species *S. pyriformis* (Yang et Lu, 1962) from the Upper Permian of China and Primorye, it differs in the larger diameter of the apertures of autozooecia (0.13–0.20 mm instead of 0.11–0.14 mm in *S. pyriformis*) and wider branches (0.40–1.76 mm instead of 0.33–1.27 mm in *S. pyriformis*).

Explanation of Plate 9

Fig. 1. *Thamniscus perplexus* Ernst, sp. nov.; specimen BGR 69513; Beekerwert mine near Duisburg, Germany; Upper Permian, Zechstein, Werra Carbonate (interreef facies); surface of the colony showing cyclozooecia and apertures of autozooecia.

Fig. 2. *Thamniscus perplexus* Ernst, sp. nov.; specimen BGR 69515; Beekerwert mine near Duisburg, Germany; Upper Permian, Zechstein, Werra Carbonate (interreef facies); cyclozooecium.

Fig. 3. *Thamniscus perplexus* Ernst, sp. nov.; holotype BGR X11875; Beekerwert mine near Duisburg, Germany; Upper Permian, Zechstein, Werra Carbonate (interreef facies); (3a) cross section, ×48.5; (3b) outward appearance of the colony, ×17.

Fig. 4. *Thamniscus perplexus* Ernst, sp. nov.; specimen BGR X11895; Beekerwert mine near Duisburg, Germany; Upper Permian, Zechstein, Werra Carbonate (interreef facies); longitudinal section, ×55.

Fig. 5. *Synocladiella georgii* (Trizna et Claucen); specimen PIN, no. 3229/148a; central Cisuralia, near the city of Krasnoufimsk, Borehole 2s, depth 100.7–104.2 m; Lower Permian, Artinskian Stage, Irga Formation; tangential section, ×16.

Fig. 6. *Synocladiella georgii* (Trizna et Claucen); specimen PIN, no. 4923/356; southern Cisuralia, Kuz'minovskii Massif, Borehole 13/21, depth 539–597 m; Lower Permian, Artinskian Stage; tangential section, ×70.

The other characters based on the measurements of autozooecia also show larger values than in *S. pyriformis*.

Occurrence. Cisuralia, Lower Permian, Artinskian Stage.

Material. In addition to the holotype and paratypes, fragments of six colonies from the collection PIN: southern Cisuralia, Kuz'minovskii Massif, Borehole 13/21, depth 593–597 m, nos. 4923/356*, 4923/360*, and 4923/431*; central Cisuralia, near the town of Krasnoufimsk, Borehole 33, depth 136.1–136.6 m, no. 3229/243* and Borehole 2s, depth 100.7–104.2 m, Irga Formation, 1971, no. 3229/148*; and northern Cisuralia, Inta River, outcrop 71 after A.A. Chernov, no. 4922/028.

Genus *Thamniscus* King, 1949

Thamniscus: King, 1849, p. 389; King, 1850, p. 44 [partim]; Korn, 1930, pp. 364–365 [partim].

Type species. *Thamniscus perplexus* Ernst, sp. nov., Upper Permian, Zechstein, Germany, England.

Diagnosis. Large branches with four to six (up to seven) alternating rows of zooecia. Branches usually freely bifurcating, anastomoses or dissepiments of rare occurrence. Apertures of zooecia round or slightly oval, with high peristome, usually containing one large node. Large nodes randomly arranged over surface of colony. Rows of zooecia separated by low sinuous ridges. Reverse surface of branches covered with straight coarse striae. Zooecia rhombic or, more rarely, hexagonal in median section. Varying numbers of cyclozooecia present on frontal surface of colony, frequently one cyclozooecium against one aperture. On reverse side of colony, cyclozooecia occur sporadically. Spines and radiciform processes occur rarely.

Comparison. Although identical in branch structure, it differs from the genus *Schulgapora* Termier et Termier, 1971 in having dendroid colonies consisting of dichotomizing branches occasionally connected by anastomoses, instead of the regular fenestrate colonies with sterile dissepiments characteristic of *Schulgapora*.

Remark. Since the type species of this genus was erroneously designated by King as *Keratophytes dubius* Schlotheim (King, 1949), *Thamniscus perplexus* Ernst, sp. nov. is designated here (see Description section below) as the type species of the genus *Thamniscus* according to article 70.3.2. of the International Code of Zoological Nomenclature (*International...*, 1999).

Species composition. Type species.

Thamniscus perplexus Ernst, sp. nov.

Plate 9, figs. 1–4

Thamniscus dubius: King, 1850, pp. 44–47 [partim], pl. 5, fig. 11 (non figs. 10, 12); Korn, 1930, p. 366, pl. 2, figs. 8, 7?, 9–11?

Etymology. From Latin *perplexus* (intricate).

Holotype. BGR, X11875; Beekerwert mine near Duisburg, Germany; Upper Permian, Zechstein, Werra Carbonate (stratified facies).

Description. The branches freely bifurcate or anastomize and are rounded or slightly flattened in cross section. The zooecia are arranged in four to six rows (near the bifurcation, up to seven). The apertures are rounded or slightly oval, with a high and wide peristome containing a node 0.06–0.1 mm in diameter. A 5-mm long stretch of the branch contains 9.69–15 (X = 11.53) apertures. Apertures covered by terminal diaphragms are rather common. Low sinuous ridges occur between apertures. High nodes are arranged at random on the frontal surface of the colony. The reverse side of the colony is covered by coarse striae. Varying numbers of cyclozooecia occur between apertures of the frontal surface and on the reverse surface. The cyclozooecia have their own walls, are 0.08–0.096 mm in diameter and 0.096–0.125 mm in depth, and do not come into contact with the zooecia. The zooecia are large, tubular, and not expanded in the middle part. The vestibule is poorly defined. Hemisepta are absent. The zooecia are rhombic in the median section and first oval and then circular in shallower sections. The merging of zooecia with the formation of double zooecia is common.

Measurements in mm (by A. Ernst):

	N	X	SD	CV	MIN	MAX
AL	55	0.21	0.0284	13.6868	0.15	0.27
AW	83	0.16	0.0187	11.9376	0.13	0.21
ADB	75	0.45	0.0487	10.8673	0.36	0.55
AAB	75	0.29	0.0322	11.0058	0.22	0.35
BW	11	1.21	0.2494	20.5815	0.80	1.54
MIW	35	0.07	0.0089	13.5586	0.05	0.09
MAW	35	0.14	0.0128	9.1855	0.11	0.16
DN	14	0.09	0.0227	26.3865	0.05	0.13
CL	10	0.28	0.0224	7.9266	0.25	0.32
TB	5	0.76	0.1514	19.8018	0.59	0.92
LA	4	36.00	3.3665	9.3514	34.00	41.00
RA	2	45.00	4.2426	9.4281	42.00	48.00

Remark. Patrick Wyse Jackson (Dublin) has drawn our attention to the fact that King's material is now in the James Mitchell Museum, National University of Ireland, Galway (JMM). Examination of these specimens has revealed that a number belong to *Synocladia*, while JMM F B92a-d are conspecific with *Thamniscus perplexus*. King's material will be discussed further and illustrated in a short future communication.

Occurrence. Upper Permian, Zechstein, lower Werra Carbonate (interreef and reef facies); Germany, England, Poland?

Material: BGR, X11894*, X11896*, X11895*, X11875*, X69571, X69572, X69542, X9513, Beekerwert mine near Duisburg; Upper Permian, Zechstein, lower Werra Carbonate (interreef facies); MNHU-B, MB Br. 38*, Gamsenberg; Upper Permian, Zechstein, lower Werra Carbonate (reef facies).

ACKNOWLEDGMENTS

This work was supported by the German Research Society (Deutsche Forschungsgemeinschaft, DFG) (project no. Scha 355/1 u. 2).

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