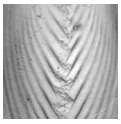
Silurian *Spanila* Barrande, 1881 (Bivalvia, Spanilidae) from European peri-Gondwana (Bohemia, Germany, France, and Austria)

JIŘÍ KŘÍŽ



Silurian *Spanila* Barrande, 1881 (Nepiomorphia Kříž, 2007) of Perunica and the European peri-Gondwana contains two species, *Spanila gracilis* (Münster *in* Goldfuss, 1837) and *Spanila discipulus* Barrande, 1881. It represents an important taxon-range-zone in the middle Ludfordian to the earliest Přídolí cephalopod limestone facies and may be correlated with the interval from the *Neocucullograptus kozlowskii* Biozone to the early *Monograptus parultimus* Biozone. Semi-infaunal *Tetinka* Barrande, 1881 from the Gorstian of Perunica was most probably the ancestor of *Spanila*, adapted to the specific semi-infaunal or infaunal mode of life. The assumption of semi-infaunal mode of life is supported by the cyrtiid brachiopod epibionts attached by their triangular ventral interarea to the posterior part of the shell, presumably above the level of the sediment. *Spanila* occupied narrow spaces between the crowded current-oriented cylindrical cephalopod shells and is commonly preserved with conjoined valves, often in the living position, *i.e.* with the frontal face down and parallel with bedding plane. • Key words: Bivalvia, Nepiomorphia, Silurian, systematics, evolution, palaeoecology, Perunica, European peri-Gondwana.

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The genus *Spanila* Barrande, 1881 (Spanilidae Kříž, 2007) was erected by Barrande (1881) for several species which he grouped in his sixth volume of "Systême Silurien" (planches 155–254) together with the genera *Lunulacardium* Münster, 1840, *Maminka* Barrande, 1881, *Mila* Barrande, 1881, *Tenka* Barrande, 1881, and *Tetinka* Barrande, 1881. Newell & LaRocque (1969) included all these genera together with *Stolidotus* Hede, 1915 in the ?Family Lunulacardiidae Fischer, 1887. Kříž (2007) formed the new family Spanilidae Kříž, 2007 for the genera *Kenzieana* Liljedahl, 1989, *Spanila* and *Tetinka* and reconstructed the family Stolidotidae Starobogatov, 1977 for the genera *Stolidotus* Hede, 1915, *Maminka*, *Mila* and *Tenka*. Later the genus *Algerina* Kříž, 2008 was included in the family Spanilidae. Barrande's original (1881) concept of *Spanila* comprised, beside the species *Spanila gracilis, Spanila culter,* and *Spanila discipulus*, also five other species I include preliminary here to the genera of Stolidotidae – *Tenka aspirans* (Barrande, 1881), *Tenka celer* (Barrande, 1881), *Tenka cuneus* (Barrande, 1881) and of Spanilidae – *Tetinka caesarea* (Barrande, 1881), and *Tetinka serva* (Barrande, 1881).

This paper is based on my collection from the Prague Basin (1953–2010), deposited in the Czech Geological Survey, Prague (JK). Abroad I collected in the Montagne Noire, France (1977 – the collection is deposited in the Département des Sciences de la Terre, Lyon, France) and in the Carnic Alps (1969, 1976, 1982, 1994, 1996, 1998 – the collection is deposited in the Geologische Bundesanstalt, Vienna, Austria).

Systematic palaeontology

Abbreviations. – V – valve, L – length of the shell, H – height of the shell, W – width of the shell, W/2 – width of one valve (Kříž 1969), S – stratigraphy: LL – lower Ludfordian, Ludlow, *Cardiola alata* Community (Kříž 1999a, c); ML – middle Ludfordian, Ludlow, *Cardiola conformis* Community (Kříž 1999a, c); UL – upper Ludfordian, Ludlow, *Cardiola conformis* Community (Kříž 1999a, c); PR – lowermost Přídolí, *Cardiolinka bohemica* Community (Kříž 1999a, c). BSPG – specimen deposited in the Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany, JK – specimens deposited in the

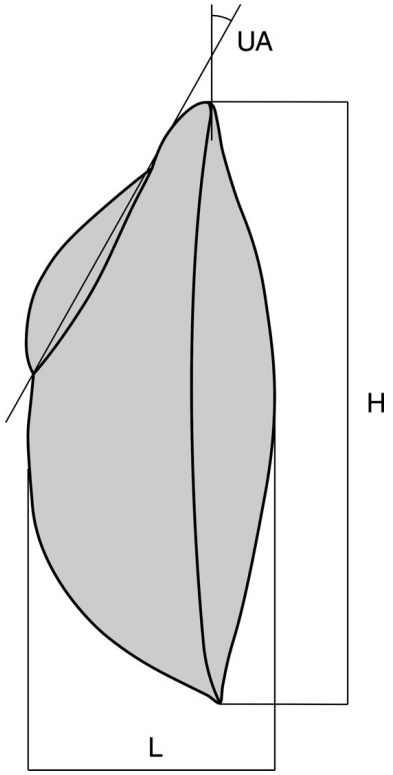

Figure 1. Schematic representation of basic morphology of the genus *Spanila*. H – height, L – length, UA – umbonal angle.

collection of Jiří Kříž in the Czech Geological Survey, Prague; NM bivalves deposited in the National Museum, Prague. All measurements are in millimetres.

Class Bivalvia Linné, 1758
Superordo Nepiomorphia Kříž, 2007
Order Antipleurida Kříž, 2007
Superfamily Dualinoidea Conrath, 1887
Family Spanilidae Kříž, 2007

Spanila Barrande, 1881

1881 *Spanila* Barrande, pp. 161, 162.
1881 *Venusta* Barrande, p. 161.

Type species. – *Spanila discipulus* Barrande, 1881, Bohemia, Prague Basin, Silurian, Ludlow, latest Ludfordian and early Přídolí.

Diagnosis. – Spanilidae with small (length maximally 12.4 mm, height maximally 28.1 mm, and width maximally 14.2 mm), dorso-ventrally elongated, narrowly obtrullate, almost equivalve, strongly inequilateral, and obese shells. Slender umbos are in central terminal position, prosogyrate. Umbonal angle 22–54°. Inflated, lanceolate frontal face separated from less steep posterior part of the shell by narrow carina, slightly curved anteriorly. Ventral margin meets blunt ridge under sharp angle, the shell narrows and becomes pointed. Close to dorsal part of the shell short wing is developed. Enantiomorphous dimorphism suppressed (shells inclined a little to the left or not inclined). Outer surface generally smoother than inner surface, radial ribs in combination with irregular growth wrinkles. Frontal face of the shell is formed by 15–29 prominent radial ribs, posteriorly of the umbonal carina or narrow ridge by 31–47 radial ribs and behind the wing by 3–4 wide radial ribs. On the inner surface radial ribs are more prominent on frontal face. Both the radial ribs and radial gutters broaden ventrally. Cardinal area is amphidetic, triangular, and relatively high. Ligament probably monovincular. Hinge line short, straight. One long, spoon-like tooth split to two unequal parts developed on the right valve, curved dorsally and leaning against the supposed shallow sockets in the left valve. Relatively large posterior adductor muscle scar is developed close to the shell margin, in the sulcus and partly on the posterior wing. Shell thickness is 0.14–0.31 mm.

Remarks. – The genus *Spanila* may be derived from the Gorstian, semi-infaunal *Tetinka* Barrande, 1881. The frontal face became distinctly dorsoventrally elongated during adaptation to the endobyssate and semi-infaunal mode of life in the cephalopod limestone biofacies. The hinge of *Spanila* has one large split tooth into unequal parts developed in the right valve. The supposed teeth in the left valve are not preserved. In contrast to *Kenzieana* Liljedahl, 1989 the tooth in the right valve is split to two unequal parts, the posterior is larger. *Tetinka* differs from *Spanila* mainly by blunt umbos, less developed posterior wing, outer surface sculpture with dominant growth sculptures and enantiomorphous shells inclined mostly to the right. The earliest representative of *Spanila* [*Spanila gracilis* (Münster *in* Goldfuss, 1837)] occurs in the middle Ludfordian, Ludlow (*Neocucullograptus kozlowskii* Biozone) of Bohemia, Germany (Elbersreuth, Frankenwald) and in Austria (the Carnic Alps). In the early late Ludfordian (lowermost parts of the *Monograptus latilobus* Biozone) occurred the main radiation of the genus *Spanila*. The genus *Spanila* became extinct in the early Přídolí.

Mode of life. – The shells of *Spanila* are commonly found with conjoined valves in the late Ludlow and early Přídolí cephalopod limestone levels (Kříž 1998). The cephalopod limestone biofacies originated below wave base and was influenced by surface currents (*e.g.* Kříž 1979a, b, 1999a; Ferretti & Kříž 1995). Many *Spanila* shells are preserved in the living position with the lanceolate frontal face down, commonly parallel with the spaces between the current-oriented cephalopod shells (Fig. 2V, X), probably at least partly buried in the sediment. This is supported by the position

of attached cyrtiid brachiopod with ventral interarea in upright position on the posterior of the *Spanila gracilis* (Münster *in* Goldfuss, 1837), presumably occurring above the level of sediment (Fig. 2S–U). It is concluded that *Spanila* shells were attached during life by a single byssal threads to the cephalopod empty shells or biodetrital sediment. Shells of *Spanila* are enantiomorphous (Kříž 2001), mostly inclined slightly to the left. Like Recent *Pinna* Linné, 1758 they were able to move slowly in narrow spaces using contraction of the foot with byssus when necessary. They were suspension filterers, and occupied the spaces between the crowded cylindrical cephalopod shells. This conclusion is supported by the abundant occurrence of the shells with conjoined valves in the cephalopod limestones, commonly even in the living position, *i.e.* with the frontal face down and parallel with bedding plane.

Species and distribution. – *Spanila gracilis*: the middle Ludfordian, Ludlow (*Neocucullograptus kozlowskii* Biozone) of Bohemia (Prague Basin), Germany (Elbersreuth, Frankenwald and Giessen, Lindener Mark), France (the Montagne Noire, Mouthoumet Massif), and Austria (Dienten near Salzburg and the Carnic Alps), and the late Ludfordian and earliest Přídolí of Bohemia. *Spanila discipulus* Barrande, 1881: the late Ludfordian and earliest Přídolí of Bohemia.

***Spanila gracilis* (Münster *in* Goldfuss, 1837)**
Figure 2A–X

1837 *Cardium gracile* Münster; Goldfuss, p. 215, pl. 142, figs 6a–e.
1840 *Cardium gracile*. – Münster, p. 61.
1881 *Spanila gracilis* Barr. – Barrande, pl. 214, figs I/1–8.
1925 *Amita gracilis* Mstr. sp. – Heller, pp. 220–227, pl. 7, figs a–c.
1929 *Amita (Spanila) cardiopsis* Barr. – Heritsch, pp. 9, 10, pl. 4, figs 342–349.
1953 *Spanila gracilis* Barr. – Kegel, p. 51, pl. 3, figs 7a, b.
1953 *Spanila aspirans* Barr. – Kegel, pp. 51, 52, pl. 3, figs 8a–c, 9a, b.
1953 *Spanila acuta* n. sp. – Kegel, p. 53, pl. 3, figs 11a, b.
1996 *Spanila gracilis* Barr. – Kříž, p. 53, pl. 6, figs 8, 9.
1999b *Spanila gracilis* Barr. – Kříž, p. 298, pl. 9, figs 8, 14.

Holotype. – (By monotypy) shell with conjoined valves figured by Münster *in* Goldfuss (1837) on pl. 142 as figs 6a–e, deposited in the Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany, AS VII 1758.

Type locality. – Germany, Frankenwald, Elbersreuth.

Type horizon. – Ludlow, Ludfordian.

Material. – 82 shells with conjoined valves, 104 left and 95 right valves.

Diagnosis. – Small, narrow *Spanila* with narrowly obtrulate or angular-obovate in outline, dorso-ventrally elongated (H/L = 1.5–2.4), strongly inflated shells. Umbonal angle 30–53°. Moderately inflated, lanceolate frontal face steeper than posterior part of the shell, with 22–29 well developed radial ribs, separated from the central part of the shell with 31–47 radial ribs by prominent narrow carina curved anteriorly and pointed ventrally. Enantiomorphous (mostly inclined slightly to the left).

Description. – Shell small (length maximally 12.4 mm, height maximally 28.1 mm, and width maximally 14.2 mm), slightly inequivalve, strongly inequilateral, prosocline, narrowly obtrullate or angular-obovate in outline. They are dorso-ventrally elongated, and strongly inflated. In adult shells the height/length relation (H/L) ranges from 1.5 to 2.4. Enantiomorphous dimorphism supressed (shells inclined mostly slightly to the left). Blunt umbos in central terminal position, formed by mesoconch, prosogyrate. Umbonal angle 37–53°. Slighty inflated, angular obovate frontal face very steep and wide, separated from the central part of the shell by prominent narrow carina, almost straight or curved anteriorly and pointed ventrally. Ventral margin meets blunt ridge under sharp angle, the shell here narrows and becomes pointed. The small and narrow posterior wing separated from the rest of shell by radial sulcus. Outer surface of frontal face is formed by 15–19 rounded radial ribs, posteriorly of the carina are 31–47 radial ribs. Posteriorly of the wing the shell is formed by 3–4 wide radial ribs. Both the radial ribs and radial gutters broaden ventrally and slightly increase in number during the life of individual. The ribs on the outer surface are less prominent than on the inner surface. Exceptionally the radial sculpture is almost supressed in the outer surface and only radial crenulations are developed on inner surface sculpture on the shell margin. Narrow growth bands regular in umbonal part narrows and become irregular and narrower ventrally. Relatively large posterior adductor scar developed close to the shell margin, in the sulcus and partly on the posterior wing. Cardinal area amphidetic, triangular, small and relatively high. Ligament probably monovincular. Shell thickness is 0.14–0.31 mm.

Ontogeny.– Prodissoconch not known. Mesoconch equivalve, inequilateral, obliquely obtriangular, prosogyrate, separated from adult shell by a distinct growth furrow caused by increase of the commissural angle (Kříž 1979a). Outer and inner surface smooth or with supressed radial ribs. In the small, juvenile shells the H/L ratio is usually small (1.5–1.6). During ontogeny the L/W and H/W ratio increases (L/W ratio from 0.6 to 1 and H/W ratio

from 1.4 to 2.2), shells become relatively higher, umbonal angle decreases as well as width in relation to height. The average height of adult shells varies from 10 to 15 mm. The shells with the height more than 20 mm are rare and occur in the late Ludlow. The maximum known height is 27.9 mm.

Dimensions. –

Specimen	V	L	H	width/2	L/W	H/W	H/L	S
JK 11 141a	R	4.1	8.6	2.5	0.8	1.7	2.0	UL
JK 4837	R	4.1	9.6	3.0	0.6	1.6	2.3	UL
JK 8996	L	4.3	6.6	2.1	1.0	1.6	1.5	ML
NM L 21 758	L	4.3	11.2	3.6	0.6	1.6	2.6	UL
JK 2963	R	4.4	7.1	2.1	1.0	1.7	1.6	UL
JK 11 094	L	4.6	7.2	2.5	0.9	1.4	1.6	LL
JK 4836	R	4.7	10.0	3.0	0.8	1.7	2.1	UL
JK 8988	L	4.9	7.6	2.6	0.9	1.5	1.6	PR
JK 4931	R	5.0	11.0	3.3	0.8	1.7	2.2	UL
JK 4838	R	5.4	11.6	3.5	0.8	1.7	2.1	UL
JK 4970	L	5.5	10.8	3.6	0.8	1.5	2.0	ML
BSPG AS VII 1758	L	5.6	13.6	3.4	0.8	2.0	2.4	LL
JK 2985	L	5.7	11.4	3.6	0.8	1.6	2.0	UL
JK 8916	R	5.7	12.6	3.2	0.9	2.0	2.2	UL
JK 8993	L	5.7	12.5	4.6	0.6	1.4	2.2	UL
JK 4951	L	6.4	12.2	3.0	1.1	2.0	1.9	UL
JK 8980	R	6.4	13.0	3.7	0.9	1.8	2.0	UL
JK 8906	L	6.4	13.5	3.7	0.9	1.8	2.1	UL
JK 8923	L	6.4	13.9	3.6	0.9	1.9	2.2	UL
JK 4967	L	6.5	10.9	3.7	0.9	1.5	1.7	UL
JK 8985	R	7.1	14.1	3.8	0.9	1.9	2.0	PR
JK 8954	R	7.3	15.1	4.3	0.8	1.8	2.1	UL
JK 2977	R	7.5	15.5	4.8	0.8	1.6	2.1	PR
JK 2987	L	7.7	17.1	4.0	1.0	2.1	2.2	UL
JK 4978	L	8.1	16.3	4.6	0.9	1.8	2.0	UL
JK 8944	L	8.2	15.3	3.7	1.1	2.1	1.9	UL
JK 8933	R	8.3	15.5	4.0	1.0	1.9	1.9	UL
JK 8992	R	8.4	16.7	5.2	0.8	1.6	2.0	UL
JK 2986	L	8.4	17.5	4.6	0.9	1.9	2.1	UL
JK 4859	R	8.5	13.0	4.2	1.0	1.5	1.5	UL
JK 4957	L	8.5	17.4	4.5	0.9	1.9	2.0	UL
JK 8970	L	8.7	17.7	4.7	0.9	1.9	2.0	UL
JK 2983	R	8.8	17.1	4.8	0.9	1.8	1.9	UL
JK 4834	R	8.8	19.0	4.6	1.0	2.1	2.2	PR
JK 8932	L	9.1	18.2	4.5	1.0	2.0	2.0	UL
JK 8928	L	9.4	17.3	5.2	0.9	1.7	1.8	UL
JK 4706	R	9.6	20.4	5.0	1.0	2.0	2.1	UL
JK 8968	R	9.7	21.5	5.3	0.9	2.0	2.2	UL
JK 11 014	L	9.9	18.2	5.7	0.9	1.6	1.8	ML
JK 8952	L	10.2	21.0	4.8	1.1	2.2	2.1	UL
NM L 26 522	L	10.2	24.6	6.8	0.8	1.8	2.4	UL
JK 2989	L	10.3	21.2	5.1	1.1	2.1	2.1	UL
JK 8942	R	10.3	21.4	5.8	0.9	1.8	2.1	UL
JK 4843	L	10.6	20.7	5.1	1.0	2.0	2.0	UL
JK 4858a	R	10.7	21.2	6.5	0.8	1.6	2.0	UL
JK 8995	R	10.8	21.6	6.0	0.9	1.8	2.0	UL
JK 8849	R	12.0	27.9	7.1	0.8	2.0	2.3	UL

Remarks. – Ancestors of *Spanila gracilis* appearing in the lower Ludfordian of peri-Gondwana were most probably among the Gorstian representatives of the genus *Tetinka*. Most probably the direct descendant of *Spanila gracilis*

Figure 2. A–X – *Spanila gracilis* (Münster *in* Goldfuss, 1837). • A–C – shell with conjoined valves, internal mould, BSPG AS VII 1758, holotype, original Münster *in* Goldfuss (1837, pl. 142, fig. 6); A – left lateral view, × 3.1; B – right lateral view, × 3.1; C – anterior view, frontal face, × 3.1. • D – left valve, internal mould, JK 8937, lateral view, × 3.4. • E – juvenile right valve, JK 2963, lateral view, × 4.3. • F, G – shell with conjoined valves, recrystallized shell preserved, NM L 21758, original Barrande (1881, pl. 214, figs 6–8); F – right lateral view, × 3.6; G – anterior view, frontal face, × 3.6. • H, I, M – right valve, internal mould, JK 8942; H – posterior view, × 2.5; I – lateral view, × 2.5; M – dorsal view, × 3.5. • J – left valve, internal mould, JK 2986, lateral view, × 5.3. • K, L – right valve, internal mould, JK 8992a; K – lateral view, × 3; L – anterior view, frontal face, × 3. • N – shell with conjoined valves, internal mould, NM L 26 522, original Barrande (1881, pl. 214, figs I/1–5), ventral view, × 2.6. • O – left valve, internal mould, JK 8931, detail of the posterior adductor muscle scar, × 6.2. • P – right valve, internal mould, JK 8995, detail of cardinal area, × 5.6. • R – left valve, JK 8966, detail of the outer and inner surface sculpture in posterior part of the valve, × 4.7. • S – shell with conjoined valves, inner surface with shell pathology, JK 11141a, right lateral view, × 7.5. • T, U – left valve, inner surface with shell pathology, JK 2961; T – lateral view, x 4.8; U – posterolateral view, × 4.2. • V, X – shell with conjoined valves preserved in the living position on the upper bedding plane of the cephalopod limestone, JK 8918; V – posterior view, × 3.3; X – posterolateral view, × 8.6. • A–C – Elbersreuth locality, Frankenwald, Germany, *Neocucullograptus kozlowskii* Biozone, middle Ludfordian, Ludlow. • D, H, I, M, O, R, V, X – Praha-Pankrác, Sdružení Street locality, *Cardiola conformis* Community (Kříž 1999a, c), upper Ludfordian, Ludlow. • E–G, J, P, T, U – Praha-Lochkov, Cephalopod Quarry locality, *Cardiola conformis* Community (Kříž 1999a, c), upper Ludfordian, Ludlow. • K – Beroun, Kosov Quarry locality, uppermost *Cardiola conformis* Community (Kříž 1999a, c), upper Ludfordian, Ludlow. • N, S – Kosoř, Barrandes test pits, *Cardiola conformis* Community (Kříž 1999a, c), upper Ludfordian, Ludlow.


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(Münster *in* Goldfuss, 1837) is *Spanila discipulus* Barrande, 1881, occurring in the late Ludfordian cephalopod limestones of the Prague Basin. It differs in having a mesoconch with prominent radial ribs, in its generally slender, distinctly dorsoventrally elongated narrow adult shell with reduced number of radial ribs. In contrast to 31–47 ribs in *Spanila gracilis* in *Spanila discipulus* only 6–11 radial ribs are developed posteriorly of the carina.

Shell pathology. – On the interior of the shell with conjoined valves (Kosoř locality, upper Ludfordian, JK 11141a, fig. 2S) and on another single valve (Praha-Lochkov, Cephalopod Quarry locality, latest Ludfordian, JK 2961, Fig. 2T, U) is preserved an almost identical triangular impression caused most probably by some organism attached during the life of bivalve to its outer surface. Both specimens were found in two distant localities and in slightly different stratigraphic levels in the Prague Basin, Bohemia. The organism was most probably only attached to the shell wall and did cause only small deformations in the shell growth.

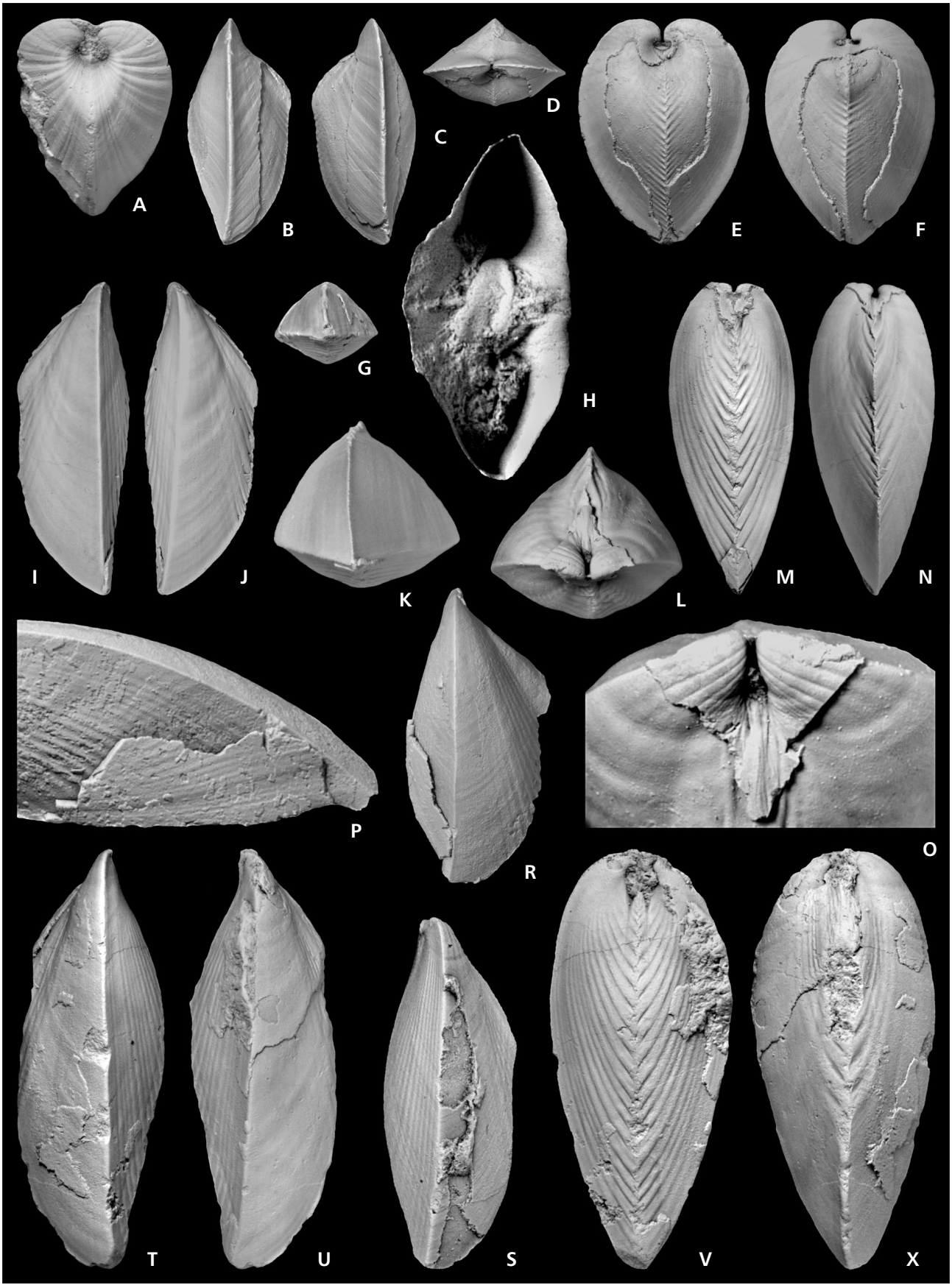
Spanila gracilis is supposed to be attached by byssal threads with the subhorizontal frontal face to the substrate. Triangular impressions on the shell are situated posteriorly of the carina (above), with the hypotenuse of the triangle up and the vertex down. Between vertex and centre of hypotenuse is a prominent narrow rounded gutter, increasing in width from vertex up.

The triangular impression very much recalls the imprint of the ventral interarea of the juvenile cyrtiid brachiopods, which served for attachment to the substratum, commonly to other shells on the bottom. According to Ivanova (1962) and Havlíček *in* Havlíček & Štorch (1990), on the triangular area is the delthyrium completely covered by a convex plate, which corresponds to the narrow gutter in the impression. The cyrtiids were only attached, not incrustated by their ventral interarea to the substratum (Ivanova 1962, p. 31). This is most probably the reason why mantle was not so irritated to produce a malformed shell below the attachment (Boschoff 1968), so the shell exhibits the normal growth on the posterior margin with radial ribs produced posteriorly (above) of the impression. The impression intervened slightly to the shell interior.

The living position of cyrtiids is with the dorsal valve up. It corresponds exactly with the shape and orientation of the impressions of the ventral interarea of juvenile cyrtiids on the surface of the valve but it is impossible to determine the exact species. In the late Ludfordian of the Prague Basin several species of cyrtiids occurs having a similar ventral interarea: *Cyrtia humilis* Bouček, 1941, *Cyrtia postera* Bouček, 1941, and *Cyrtia maior ludlowensis* Bouček, 1941.

Occurrence. – Bohemia, Prague Basin – middle Ludfordian, *Cardiola alata* Community: Praha-Řeporyje – Požáry section, Beroun – Kosov Quarry. Upper Ludfordian, early *Cardiola conformis* Community: Beroun – Kosov Quarry, Praha-Pankrác – Sdružení Street locality, Praha-Butovice. Upper Ludfordian: Praha-Velká Chuchle, Praha-Lochkov – Barrande's test-pits, Praha-Slivenec, Kosoř, Praha-Radotín Valley – Hvížďalka section. Uppermost Ludfordian, *Cardiola conformis* Community: Praha-Malá Chuchle – Vyskočilka locality, Praha-Pankrác – temporary outcrop for the TV Studio and Sdružení Street locality, Praha-Butovice, Praha-Lochkov – Cephalopod Quarry, Praha-Zadní Kopanina, Praha-Radotín Valley, U topolů section, Beroun – Kosov Quarry. Lowermost Přídolí: Praha-Lochkov – Cephalopod Quarry, Praha-Radotín Valley, U topolů section. The middle Ludfordian, Ludlow (*Neocucullograptus kozlowskii* Biozone) of Germany – Elbersreuth, Frankenwald (Greiling 1962, Heller 1925, Münster in Goldfuss 1837, Münster 1840), and Alfredscacht near Giessen, Lindener Mark (Kegel 1953), France – Vigne de M. Sourgnes, north of Félines-Termenés, Mouthoumet Massif, the Montagne Noire (Kříž 1996), and Austria – Nagelschmiedpalfen near Dienten, Salzburg (Heritsch 1929, Kříž 1979a) and the Base of Seewarte, Carnic Alps (Kříž 1999b).

Figure 3. A–X – *Spanila discipulus* Barrande, 1881. • A – shell with conjoined valves, outer surface, JK 8761, posterior view, × 5.1. • B–F – shell with conjoined valves, internal mould with fragments of recrystallized shell, JK 8993; B – left lateral view, × 3; C – right lateral view, × 3; D – dorsal view, × 2.8; E – anterior view, frontal face, × 3; F – posterior view, × 3. • H – shell with conjoined valves, inner surface, JK 8981, detail of the hinge, right valve up, latex mould, × 11.3. • I–O – shell with conjoined valves, internal mould, JK 11142a; I – right lateral view, × 2.8; J – left lateral view, × 2.8; K – ventral view, × 4.2; L – dorsal view, × 4.3; M – anterior view, frontal face, × 2.8; N – posterior view, × 2.8; O – posterodorsal view, detail of mesoconchs with recrystalized shell partly preserved, × 10.1. • P–R – left valve, internal mould with fragment of recrystallized shell on the frontal face, JK 11031; P – detail of inner and outer surface sculpture, × 7.7; R – lateral view, × 2.7. • S – shell with conjoined valves, internal mould with most of the recrystallized shell preserved, NM L 26521, original Barrande (1881, pl. 213, figs III/5–8), paralectotype, left lateral view, × 3.4. • T–X – shell with conjoined valves, internal mould, original Barrande (1881, pl. 213, figs III/1–4), lectotype, NM L 26519; T – right lateral view, × 3.1; U – left lateral view, × 3.1; V – anterior view, frontal face, × 3.1; X – posterior view, × 3.1. • A, S – Praha-Lochkov, Barrande's test pits, *Cardiola conformis* Community (Kříž 1999a, c), upper Ludfordian, Ludlow. • B–F, H, P–R – Praha-Lochkov, Cephalopod Quarry locality, uppermost *Cardiola conformis* Community (Kříž 1999a, c), uppermost Ludfordian, Ludlow. • I–O – Kosoř, *Cardiola conformis* Community (Kříž 1999a, c), upper Ludfordian, Ludlow. Ludlow. • G, T–X – Praha-Dvorce quarry, uppermost *Cardiola conformis* Community (Kříž 1999a, c), uppermost Ludfordian, Ludlow.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***Spanila discipulus* Barrande, 1881**
Figure 3A–X

1881 *Spanila discipulus* Barr.; Barrande, pl. 212, figs III/1–8.
1881 *Spanila culter* Barr.; Barrande, pl. 212, figs I/1–6.
1881 *Goniophora phrygia* Barr.; Barrande, pl. 195, figs V/1–4.

Lectotype. – (SD Růžička & Prantl, 1960, p. 54) Internal mould of the shell with conjoined valves and with fragments of the recrystalized shell figured by Barrande (1881) on pl. 213 as figs III/1–4, NM L 26 519 and refigured herein on Fig. 3T–X.

Paralectotype. – The other specimen figured by Barrande (1881) on pl. 213, figs III/5–8, NM L 26521 and refigured herein on Fig. 3S.

Type locality. – Bohemia, Prague Basin, Praha-Dvorce.

Type horizon. – Ludlow, latest Ludfordian.

Material. – 13 shells with conjoined valves, 7 left and 3 right valves.

Diagnosis. – Small *Spanila* with dorso-ventrally elongated (H/L = up to 3.1), narrowly obtrulate, slightly inequivalve, inequilateral, inflated shells. Close to dorsal part of the shell elongated, short, obtuse wing is developed. Umbonal part is slender, umbos in central terminal position, prosogyrate. Umbonal angle is 22–47°. Moderately inflated, lanceolate frontal face steeper than posterior part of the shell, with 9–15 well developed radial ribs, separated from the central part of the shell with 6–11 radial ribs by prominent narrow carina curved anteriorly. Enantiomorphous shells inclined mostly a little to the left. Hinge line short, straight. One long, spoon-like tooth split to unequal parts developed on the right valve, curved dorsally and leaning against the supposed shallow sockets in the left valve.

Description. – Shell small (length maximally 8.6 mm, height maximally 24 mm, and width maximally 10.6 mm), narrowly obtrulate, slightly inequivalve, inequilateral, dorso-ventrally elongated (H/L = 1.9–3.1), inflated. Close to dorsal part of the shell short wing is developed. Enantiomorphous shells inclined mostly a little to the left or not inclined. Inflated, lanceolate frontal face separated from less steep posterior part of the shell by prominent narrow carina, slightly curved anteriorly and pointed ventrally. Prominent, slender umbos are in central terminal position, formed by mesoconch with radial ribs, prosogyrate. Umbonal angle is 22–47°. Ventral margin meets blunt ridge under sharp angle, the shell here narrows and becomes pointed. Posterior wing elongated, short, obtuse. Outer surface generally smoother than inner surface, radial ribs in combination with irregular growth wrinkles. On the frontal face of the shell 15–19 prominent radial ribs are developed. Posteriorly of carina the shell is first almost smooth, than 6–11 radial ribs are developed close to the wing; posteriorly of wing the shell is formed by 3–4 less prominent radial ribs. On the inner surface radial ribs are more prominent on frontal face, regularly spaced, separated by radial gutters. Both the radial ribs and radial gutters broaden ventrally. Hinge line short, straight. One long, spoon-like tooth split to two unequal parts developed on the right valve, curved dorsally and leaning against the supposed shallow sockets in the left valve. Posterior adductor muscle scar is developed on the posterior wing close to the shell margin. Shell thickness is 0.14–0.28 mm.

Ontogeny. – Prodissoconch not known. Mesoconch equivalve, obliquelly obtriangular, inflated (H/W = 1.2–1.5), inequilateral (H/L = 2–2.6). Blunt umbos are prosogyrate. The height of known shells varies from 3–4.4 mm. The frontal face is much steeper than posterior part of the shell. The anteriorly curved blunt edge separates frontal face from the posterior part of the shell. Outer surface sculpture with several regularly spaced, relatively wide growth bands in combination with prominent radial ribs (8 wide ribs developed on anterior face, posterior with 5 wide ribs plus 3 narrow radial ribs developed just before wing plus 3 narrow ribs posterodorsally of the wing). The prominent radial ribs practically disappear in the last growth furrow of mesoconch. On inner surface the ribs are just slightly developed and continue to adult stage. During further growth the shell becomes distinctly slender, dorsoventrally elongated (H/L = 1.9–3.1) with length and width equal (L/W = 0.4–1.1). H/W ratio increases (1.1–3.4). The umbonal angle decreases from 47° to 22°. Blunt edge between frontal face and the shell posterior turns to carina. Number of radial ribs increase. Frontal face of the shell is formed by15–19 prominent radial ribs. Posterior of the shell is first almost smooth, with 6–11 radial ribs close to the wing; posteriorly of wing 3–4 less prominent radial ribs are developed. The maximum known height is 24 mm.

Dimensions. –

Specimen	V	L	H	width/2	L/W	H/W	H/L	S
JK 11 142a	R	1.5	3.0	1.3	0.6	1.2	2.0	UL
JK 8770	L	1.7	4.4	1.5	0.6	1.5	2.6	UL
JK 8761	R	3.3	7.1	2.5	0.7	1.4	2.2	UL
JK 11 126	R	5.3	11.0	3.2	0.8	1.7	2.1	UL
JK 11 246	R	5.6	10.9	3.3	0.8	1.7	1.9	UL
JK 11 246	L	5.6	10.9	3.8	0.7	1.4	2.0	UL
JK 8993	R	5.8	12.7	4.1	0.7	1.6	2.2	UL

NM L 21 415	R	5.8	17.3	3.3	0.9	2.6	3.0	UL
NM L 26 521	L	6.9	18.2	4.1	0.8	2.2	2.6	UL
JK 2982	L	6.9	19.0	3.5	1.0	2.7	2.8	PR
JK 11 000	R	7.0	18.8	4.5	0.8	2.1	2.7	UL
JK 8770	L	7.0	21.2	4.3	0.8	2.4	3.0	UL
JK 11 142a	L	7.1	19.7	3.3	1.1	3.0	2.8	UL
JK 11 142a	R	7.1	19.7	4.2	0.8	2.3	2.8	UL
JK 8752	L	7.3	19.8	3.7	1.0	2.7	2.7	UL
JK 8999	R	7.4	21.5	3.7	1.0	2.9	2.9	UL
JK 3543	L	7.7	23.5	3.5	1.1	3.4	3.1	UL
JK 4993	L	8.1	21.2	4.2	1.0	2.5	2.6	UL
NM L 26 519	L	8.6	24.0	5.3	0.8	2.3	2.8	UL

Remarks. – Ancestral *Spanila gracilis* differs from *Spanila discipulus* mainly in its generally bulkier and less dorsoventrally elongated shells, by larger umbonal angle and blunt umbos, and by more numerous radial ribs on frontal face (22–29) and posteriorly of carina (31–47).

Occurrence. – Bohemia, Prague Basin – upper Ludfordian: Praha-Velká Chuchle, Praha-Lochkov – Barrande's testpits, Praha-Slivenec, Kosoř. Uppermost Ludfordian, *Cardiola conformis* Community: Praha-Lochkov – Cephalopod Quarry, Praha-Pankrác – temporary outcrop for the TV Studio and Sdružení Street locality, Praha-Radotín Valley – U topolů section. Lowermost Přídolí: Praha-Radotín Valley – U topolů section.

Conclusions

1. Late Silurian *Spanila* Barrande, 1881 originated most probably from the Gorstian representatives of *Tetinka* Barrande, 1881.

2. *Spanila* is represented by two species, *Spanila gracilis* (Münster *in* Goldfuss, 1837) and *Spanila discipulus* Barrande, 1881. *Spanila gracilis* appears in the middle Ludfordian, *Neocucullograptus kozlowskii* Biozone of Bohemia (Prague Basin), Austria (Dienten near Salzburg and the Carnic Alps), France (Montagne Noire, Mouthoumet Massif), and Germany (Frankenwald and Lindener Mark) and is most probably the direct ancestor of *Spanila discipulus,* which occurs together with *Spanila gracilis* in the late Ludfordian and earliest Přídolí of the Prague Basin.

3. *Spanila* is restricted to the middle and late Ludfordian and earliest Přídolí and was adapted to the specific semi-infaunal to infaunal mode of life in the cephalopod limestone biofacies of Perunica and European peri-Gondwana. The assumption of semi-infaunal mode of life is supported by the impressions on the shells caused by cyrtiid brachiopods, attached by their triangular ventral interarea above the level of the sediment. Later infaunal mode of life is supported by the abundant occurrence of the shells with conjoined valves in the living position with the frontal face down and parallel with bedding plane.

4. The middle and late Ludfordian and early Přídolí occurrence of *Spanila* represents an important taxon-range-zone in the cephalopod limestone facies and may be correlated with the interval from late *Neocucullograptus kozlowskii* Biozone (middle Lufordian) to the early *Monograptus parultimus* Biozone (early Přídolí).

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