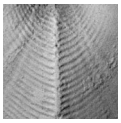
Silurian *Kenzieana* Liljedahl, 1989 (Bivalvia, Spanilidae) from Bohemia, Gotland and Sardinia

JIŘÍ KŘÍŽ



The genus *Kenzieana* Liljedahl, 1989 (Nepiomorphia Kříž, 2007) from Perunica, the European peri-Gondwana and Baltica is the oldest known, very long ranging Silurian (late Wenlock to late Přídolí) genus of Spanilidae Kříž, 2007, and was most probably the ancestor of the Gorstian *Algerina* Kříž, 2008, and the Ludfordian *Spanila* Barrande, 1881. *Kenzieana* is represented by *K. bellula* (Barrande, 1881) from the Homerian (late Wenlock), and *K. cardiopsis* (Barrande, 1881) from the late Wenlock to the late Přídolí. *K. angusta* Liljedahl, 1989, and *K. lata* Liljedahl, 1989 from Gotland are the junior synonyms. Distinctly inflated, foreshortened shells of *Kenzieana* with almost flat and circular frontal face show adaptive convergence with the Silurian *Slavinka plicata* (Barrande, 1881), Recent *Corculum* Röding, 1798, *Fragum* Röding, 1798, and *Hippopus* Lamarck, 1799. *Kenzieana* was very shallow and slow burrower resting in the sediment on its anterior, almost subcircular or widely elliptical and flat frontal face with a few byssal threads attached to loose detritus. • Key words: Bivalvia, Nepiomorphia, Silurian, systematics, palaeoecology, Perunica, European peri-Gondwana, Baltica.

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The family Spanilidae Kříž, 2007 was created for ecologically specialized genera of Antipleurida Kříž, 2007, adapted to the life in the Silurian (Homerian–late Přídolí cephalopod limestone biofacies of peri-Gondwana regions and late Wenlock of Gotland. *Kenzieana* Liljedahl, 1989 represents the oldest known genus of the family. The genus is probably the ancestor of *Spanila* Barrande, 1881 and *Tetinka* Barrande, 1881, and it is related to *Algerina* Kříž, 2008. Dorsoventrally elongated shells and prominent radial ribs of *Kenzieana* are characteristic of the Spanilidae. The enantiomorphous dimorfism of Antipleurida is suppressed in the family and in different species the shells are reclining slightly or to the left or to the right. The hinge with reduced number of pseudotaxodont teeth was observed in *Kenzieana* and *Spanila*. *Kenzieana* was erected by Liljedahl (1989) for *Kenzieana lata* Liljedahl, 1989 from the Silurian of Gotland, which is junior synonym of *Kenzieana cardiopsis* (Barrande, 1881) (= *Spanila cardiopsis* Barrande, 1881) from the Silurian of the Prague Basin, Bohemia.

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); JK 14 931–JK 15 114 (181 specimens) deposited in the 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

Genus *Kenzieana* Liljedahl, 1989

1881 *Spanila* Barrande, pp. 161–162 (partim).
1989 *Kenzieana* gen. nov., Liljedahl, pp. 230–232.

Type species. – *Kenzieana lata* Liljedahl, 1989 [= *Kenzieana cardiopsis* (Barrande, 1881), senior synonym], Sweden, Gotland, Silurian, early Homerian (*Cyrtograptus lundgreni* Biozone).

Diagnosis. – Spanilid characterized by small, obliquely obtriangular to broadly obtriangular in outline, dorso-ventrally elongated, foreshortened distinctly inflated shells.

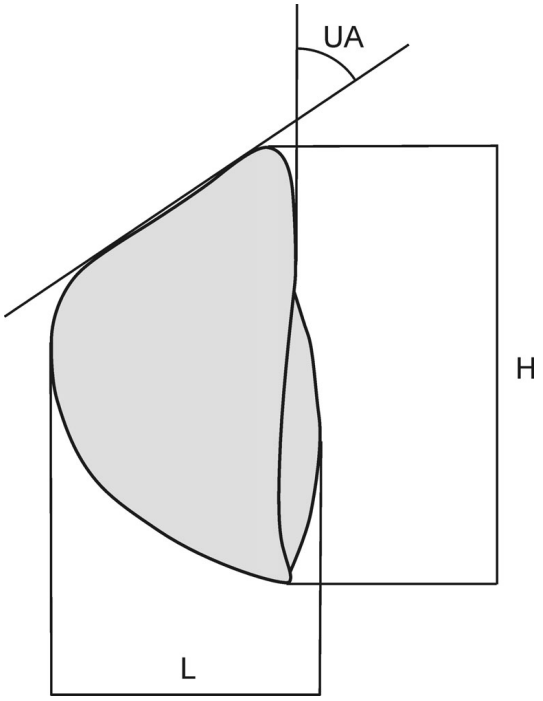


Figure 1. Schematic representation of basic morphology of the genus *Kenzieana*. L – length, H – height, UA – umbonal angle.

Outer surface with numerous radial ribs (more than 63–71) in combination with numerous growth bands of the same width. Very steep and very wide frontal face, carina between frontal face and the rest of shell, curved anteriorly. Enantiomorphous (shell is slightly inclined to the left or to the right). Hinge margin short, straight. Two blunt, spoon like and quite long, slightly dorsally curved teeth are developed on the left valve. Between two corresponding sockets on the right valve is developed one long, spoon like tooth curved dorsally and leaning against the inter-space between the teeth of the left valve. Relatively high, triangular ligamental area has radial ribs. Ligament is probably amphidetic. Posterior adductor muscle scar developed close to ventral margin, and dorsally of the posterior radial sulcus.

Remarks. – *Kenzieana* is very long ranging Silurian genus (late Wenlock to late Přídolí) and was most probably the ancestor of the Ludfordian genera *Spanila* and *Tetinka* from which it differs especially by less dorsoventrally elongated shells and by numerous narrow radial ribs.

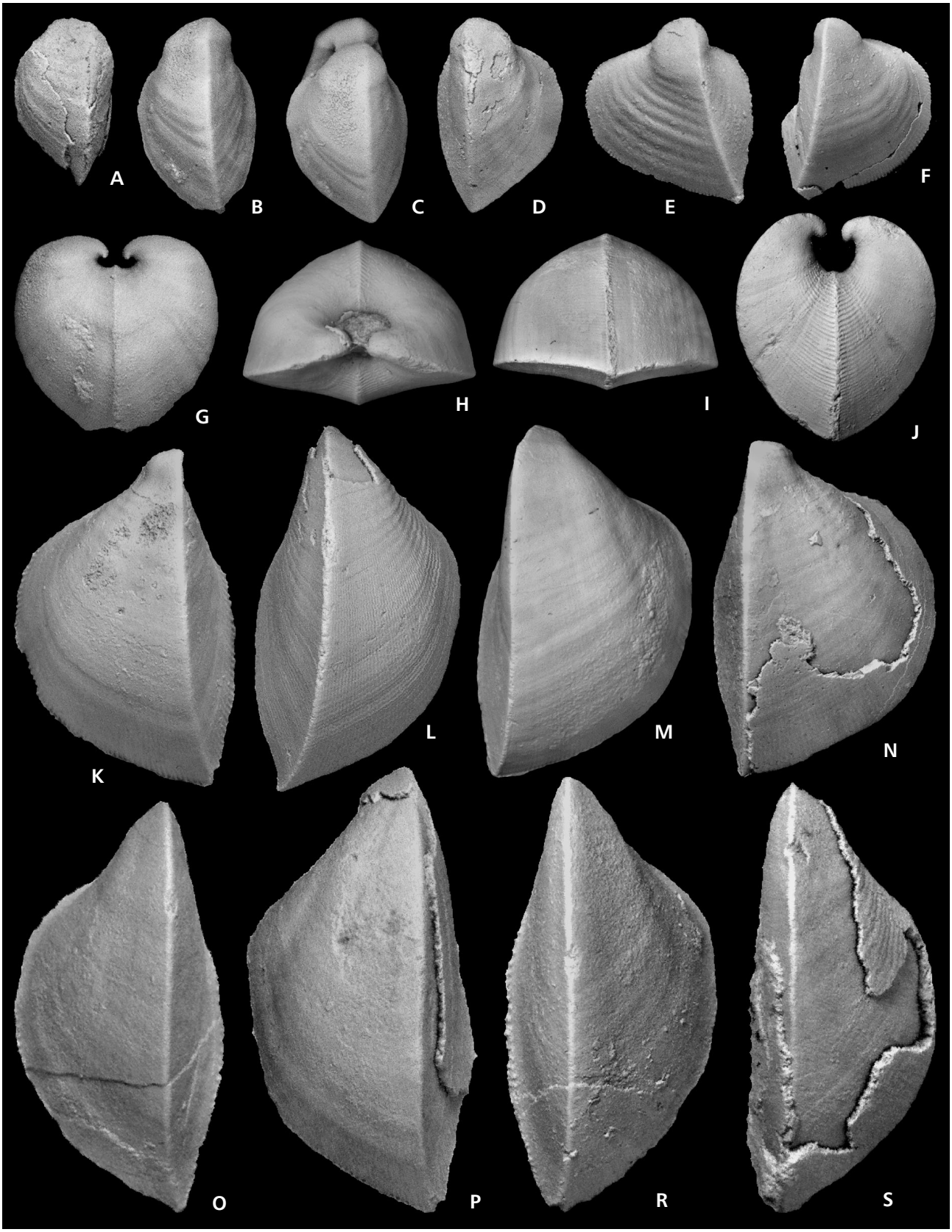
Mode of life. – Distinctly foreshortened, inflated shells with almost flat and circular frontal face representing a very specialised adaptation which shows adaptive convergence with the Silurian *Slavinka plicata* (Barrande, 1881) and Recent *Corculum* Röding, 1798, *Fragum* Röding, 1798, and *Hippopus* Lamarck, 1799 (Kříž 1985, Liljedahl 1989). It is possible to presume that *Kenzieana* had very similar mode of life, being a very shallow and slow burrower (H/W 0.8–1.4) reclining in the sediment on its anterior, almost subcircular and flat frontal face with a few byssal threads attached to loose detritus. In Recent bivalves radial ribs are largely restricted to shells of borers and shallow burrowers; they have stabilizing function (Stanley 1970).

Species. – *Kenzieana bellula* (Barrande, 1881), late Wenlock, Bohemia and Gotland and *Kenzieana cardiopsis* (Barrande, 1881), late Wenlock to the late Přídolí, Bohemia, Sardinia and Gotland.

***Kenzieana cardiopsis* (Barrande, 1881)**
Figures 2A–N, 3A, B, D, E, J, N, O

1881 *Spanila cardiopsis* Barr.; Barrande, pl. 212, figs II/1–12, pl. 246, figs II/5–10.
1881 *Tetinka bellula* Barr.; Barrande, pl. 183, figs IV/1–3, pl. 215, figs II/1–5, pl. 244, figs II/1–4.
1881 *Hemicardium colonus* Barr.; Barrande, pl. 183, figs IV/4–11.
1881 *Goniophora phrygia* Barr.; Barrande, pl. 195, figs V/8–11.
1881 *Conocardium clypeus* Barr.; Barrande, pl. 203, figs I/1–2.
1881 *Hemicardium baro* Barr.; Barrande, pl. 244, fig. I/1.
1881 *Hemicardium noduliferum* Barr.; Barrande, pl. 246, figs V/1–6.
1989 *Kenzieana lata* sp. n.; Liljedahl, pp. 232–234, figs 2A–F, figs 3C, D, E, figs 4, 5, 8D and 9A.

Figure 2. A–N – *Kenzieana cardiopsis* (Barrande, 1881). • A – juvenile right valve, mesoconch, JK 8851, lateral view; × 10. • B, C, G – juvenile shell with conjoined valves, JK 8827; B – right lateral view; × 9.1; C – dorso-lateral right view showing prodissoconch in umbonal part; × 9.6; G – posterior view; × 8.4. • D – juvenile shell with conjoined valves, JK 8840a, left dorso-lateral view showing mesoconch, × 7.2. • E – juvenile right valve with mesoconch, JK 8875, lateral view; × 7.2. • F – left valve, JK 8807, lateral view; × 5.5. • H–J, M – shell with conjoined valves, NM L 21416, lectotype; H – dorsal view, × 3.8; I – ventral view, × 3.7; J – anterior view, × 3.3; M – left lateral view, × 5.1. • K – right valve, JK 8848, lateral view; × 5.3. • L – left valve, NM L 21417, paralectotype, lateral view; × 5. • N – left valve, JK 8887, lateral view; × 5.5. • O–S – *Kenzieana bellula* (Barrande, 1881); O – right valve, JK 8838, lateral view; × 6.1; P – right valve, JK 8812, lateral view; × 6.6; R – left valve, JK 11236, lateral view; × 5.7; S – left valve, NM L 22424, lectotype, lateral view; × 6.7. • A, D–F, K, N – Na Břekvici locality near Praha-Butovice, lower Ludlow, *Neodiversograptus nilssoni* Biozone. • B–C, G, O, P – Arethusina Gorge locality near Praha-Řeporyje, Wenlock, *Testograptus testis* Biozone. • H–J, L, M – Kozel locality near Beroun-Lištice, lower Ludlow. • R – Vyskočilka locality near Praha-Malá Chuchle, Wenlock, *Testograptus testis* Biozone. • S – Kační Quarry near Praha-Butovice, Wenlock, *Testograptus testis* Biozone.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1993 *Spanila cardiopsis* Barrande, 1881; Kříž *in* Kříž & Serpagli, p. 332, pl. 8, figs 33, 35–38.

Lectotype (designated herein). – Shell with conjoined valves figured by Barrande (1881) on pl. 212, as figs II/1–5, NM L 21 416.

Paralectotypes. – Shell with conjoined valves figured by Barrande (1881) on pl. 212, as figs II/6–8 (NM L 21 418), and left valve figured on pl. 212, as figs II/9–12 (NM L 21 417).

Type locality. – Bohemia, Prague Basin, Kozel Rocks near Beroun-Lištice.

Type horizon. – Ludlow, early Gorstian.

Material. – 18 articulated shells, 34 left and 30 right valves.

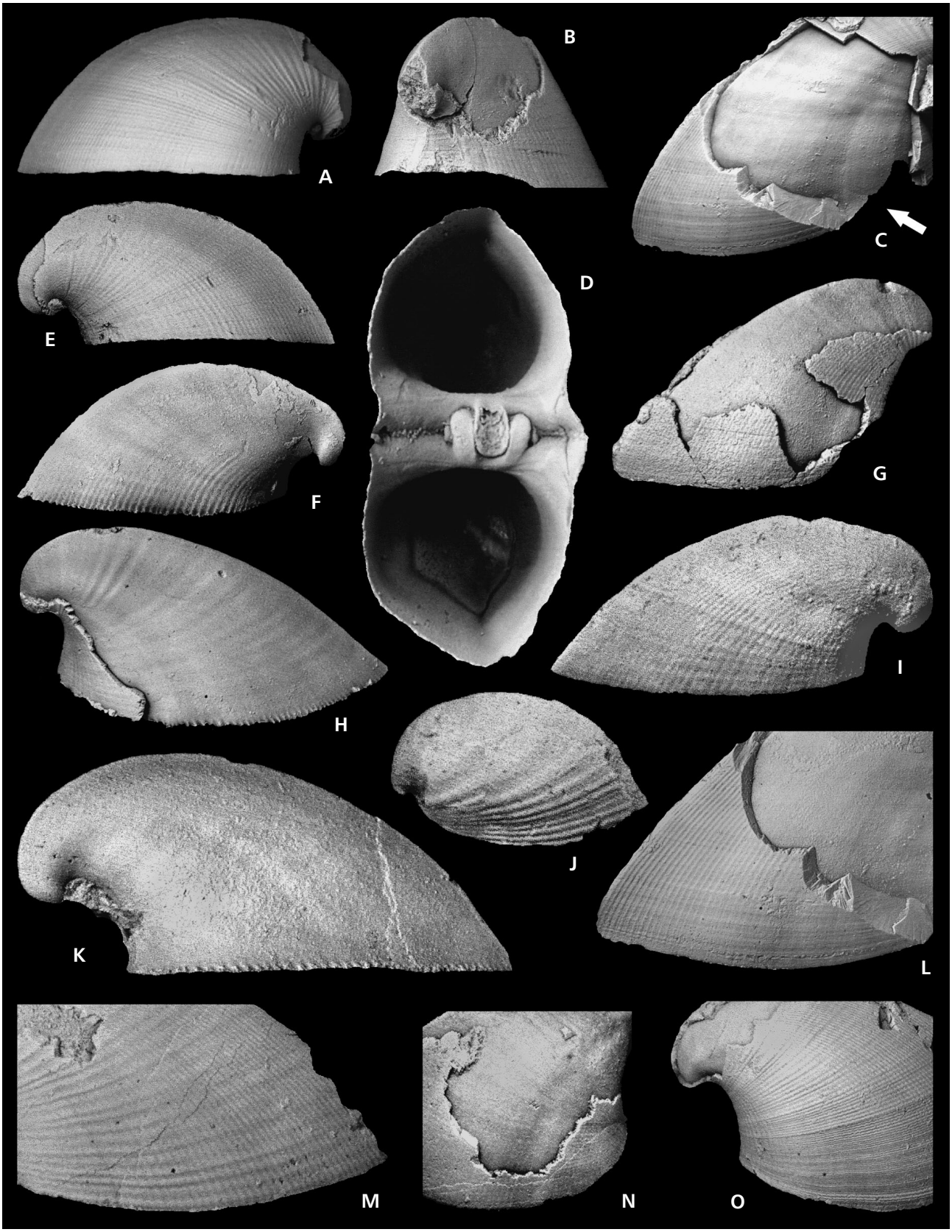
Diagnosis. – In adult shells the length/width relation (L/W) ranges from 1.1 to 0.5 (average 0.8), height/width relation (H/W) ranges from 0.8–1.3 (average 1.1). Umbonal angle 44–89° (average 66°). The shells are longer than in *Kenzieana bellula* from the late Wenlock (early Homerian), have more numerous radial ribs posteriorly of carina (> 71 in number) and thinner shell wall. Two blunt, possibly spoon like and quite long, slightly dorsally curved teeth are developed on the left valve. Between two corresponding sockets on the right valve is developed one long, spoon like tooth curved dorsally and leaning against the interspace between the teeth of the left valve.

Description. – Small, equivalve, inequilateral, prosocline, obliquely broadly obtriangular in outline, dorso-ventrally elongated, foreshortened, strongly inflated shells. In adult shells the high/length relation (H/L) ranges from 1.1 to 2.3 (average 1.5), length/width relation (L/W) ranges from 0.5 to 1.1 (average 0.8), height/width relation (H/W) ranges from 0.8–1.3 (average 1.1). Umbonal angle 44–89° (average 66°). Enantiomorphous (mostly equivalve but some specimens slightly inclined to the left or to the right). Prominent umbones in anterior terminal position, prosogyrate, with relatively large circular inflated opistogyrate prodissoconch preserved commonly on the beaks. Slighty inflated, subcircular or widely elliptical lanceolate frontal face very steep and wide, separated from the central part of the shell by carina curved anteriorly. Posterior sulcus indicates the presence of siphons. Outer surface with numerous rounded radial ribs (> 71 in number posteriorly of carina) and radial gutters in combination with numerous growth bands of approximately the same width. Both, the radial ribs and radial gutters broaden ventrally. In some specimens regular wide growth bands and furrows developed in umbonal part. Inner surface smooth, crenulations developed along the margin. Hinge margin short, straight. Two blunt, possibly spoon like and quite long, slightly dorsally curved teeth are developed on the left valve. Between two corresponding sockets on the right valve is developed one long, spoon like tooth curved dorsally and leaning against the interspace between the teeth of the left valve. Relatively high, triangular ligamental area with radial ribs. Shell thickness 0.14–0.28 mm.

Dimensions. –

	V	L	H	width/2	L/W	H/W
JK 10987	A	1.4	2.1	0.9	0.7	1.2
JK 8851	R	1.9	3.0	1.3	0.7	1.2
JK 8874	L	1.9	2.5	1.2	0.8	1.0
JK 8837	A	2.0	2.8	1.4	0.7	1.0
JK 8852	R	2.0	4.6	2.2	0.5	1.0
JK 8877	R	2.3	4.4	1.8	0.6	1.2
JK 8827	A	2.7	4.2	2.2	0.6	1.0
JK 8854	R	2.9	3.8	1.6	0.9	1.2
JK 8840a	A	3.2	6.1	2.9	0.6	1.1
JK 8855	R	3.8	4.8	1.8	1.1	1.3
JK 8878	R	3.9	5.1	–	–	–
JK 8873	R	4.0	4.4	1.9	1.1	1.2
JK 8808	L	4.2	5.4	2.1	1.0	1.3
JK 8875	R	4.3	4.8	2.0	1.1	1.2
JK 8883	L	4.5	7.7	3.6	0.6	1.1
JK 8879	L	4.6	5.8	2.2	1.1	1.3
JK 8807	L	4.6	6.0	2.6	0.9	1.2

Figure 3. A, B, D, E, J, N, O – *Kenzieana cardiopsis* (Barrande, 1881). • A, E – left valve with outer surface sculpture, NM L 21417, paralectotype; A – posterior view, × 5.1; E – anterior view, × 4.5. • B – left valve with outer surface sculpture, NM L 22452, dorsal view, × 5.5. • D – shell with conjoined valves, JK 8827, right valve up, latex mould, ventral view of hinge, × 19. • J – right valve, JK 8851, posterior view, outer surface sculpture, × 15.3. • N – left valve, JK 8887, posterior view, detail of the outer and inner surface sculpture. × 5.5. • O – right valve, JK 11154a, posterior view, detail of the outer surface sculpture; × 4.4. • C, L, G, H, I, K, M – *Kenzieana bellula* (Barrande, 1881). • C, L – JK 8832, left valve; C – posterior view, posterior adductor muscle scar (arrow); × 4.7; L – posterior view, detail of outer and inner surface sculptures; × 6.8. • G – left valve, NM L 22424, lectotype, postero-lateral view, outer and inner surface sculpture; × 6.1. • H – right valve, JK 8833, posterior view, inner surface sculpture and fragment of shell; × 6. • I – right valve, JK 8828, anterior view, outer surface sculpture; × 9.9. • K – left valve, JK 11236, anterior view, inner surface sculpture; × 7. • M – right valve, JK 8869, posterior view, outer surface sculpture; × 8.9. • A, E – Kozel Rocks near Beroun-Lištice, lower Ludlow. • B – Praha-Lochkov, Ludlow. • C, D, J, N – Na Břekvici locality near Praha-Butovice, lower Ludlow, *Neodiversograptus nilssoni* Biozone. • G, H, L – Kační Quarry near Praha-Butovice, Wenlock, *Testograptus testis* Biozone. • I, M – Arethusina Gorge locality near Praha-Řeporyje, Wenlock, *Testograptus testis* Biozone. • K, O – Vyskočilka locality near Praha-Malá Chuchle, Wenlock, *Testograptus testis* Biozone.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JK 8818	R	4.8	7.7	3.4	0.7	1.1
JK 8821	R	5.0	6.0	2.5	1.0	1.0
JK 8876	L	5.0	6.6	2.9	0.9	0.9
JK 8849	L	5.3	7.0	3.3	0.8	0.8
NM L 21418	L	5.6	7.3	3.3	0.8	1.1
NM L 21418	R	5.6	7.3	3.7	0.8	1.1
JK 11238	A	5.6	10.4	4.7	0.6	1.1
JK 8850	L	5.8	7.3	3.1	0.9	1.2
JK 8882	L	5.8	8.8	3.7	0.8	1.2
JK 8880	R	6.0	9.6	3.9	0.8	1.2
JK 8887	L	7.1	11.0	4.8	0.7	1.1
NM L 21416	R	7.3	12.0	5.3	0.7	1.1
NM L 21416	L	7.3	12.0	5.1	0.7	1.1
NM L 21417	L	7.3	12.0	6.2	0.6	1.0
NM L 22452	L	7.4	13.0	5.8	0.6	1.1
JK 8848	R	7.5	11.4	4.8	0.8	1.2
JK 8881	R	7.9	12.8	5.9	0.7	1.1

Remarks. – *Kenzieana cardiopsis,* known already from the early Homerian (*Cyrtograptus lundgreni* Biozone) of Gotland represents long ranging form of *Kenzieana* (up to the Přídolí). *Kenzieana bellula* (Barrande, 1881) from the early Homerian (*Testograptus testis* Biozone) differs from *Kenzieana cardiopsis* (Barrande, 1881) mainly in the higher shells (average H/L relation is 1.9) and smaller umbonal angle 36–62° (average 43°).

Mode of life. – *Kenzieana cardiopsis* was most probably a very shallow and slow burrower resting or reclining in the sediment on its anterior, widely elliptical to subcircular and relatively flat frontal face with a few byssal threads attached to loose detrital sediment. It is known from the Prague Basin *Cardiola gibbosa* Community, Praha-Butovice, *Neodiversograptus nilssoni* Biozone, early Gorstian (Kříž 1999a), *Cardiola donigala-Slava cubicula* Community, Loděnice-Sedlec, and Cromus Hillslope near Řeporyje, late *Saetograptus chimaera* Biozone, late Gorstian (Kříž 1999b), and from Sardinia *Cardiola agna figusi* Community, Wenlock-Ludlow boundary, Xea S'Antonio (Kříž *in* Kříž & Serpagli 1993).

Occurrence. – Bohemia, Prague Basin, Praha-Butovice, Praha-Braník, Praha-Velká Chuchle, Beroun-Lištice (early Gorstian, *Neodiversograptus nilssoni* Biozone), Praha-Řeporyje, Cromus Hillslope near Mušlovka Quarry, Loděnice-Bubovice (latest Gorstian, *Saetograptus chimaera* Biozone), Koledník near Beroun and Praha-Lochkov (early Ludfordian, *Saetograptus linearis* Biozone), Radotín Valley near U topolů Section (early Přídolí, *Monograptus ultimus* Biozone), Praha-Řeporyje, Lobolite Hillslope (late Přídolí, *Monograptus transgrediens* Biozone). Gotland (late Wenlock, Slite Beds, unit g, *Cyrtograptus lundgreni* Biozone), Italy, Sardinia (early Ludlow, early Gorstian).

***Kenzieana bellula* (Barrande, 1881)**
Figures 2O–S, 3C, L, G, H, I, K, M

1881 *Tetinka bellula* Barr.; Barrande, pl. 244, figs II/5–8.
1881 *Hemicardium debile* Barr.; Barrande, pl. 183, figs V/1–8.
1989 *Kenzieana angusta* sp. n.; Liljedahl, pp. 234–236, figs 3 B, 6 A–F, 7, 8 D, 9 B.

Lectotype (designated herein). – Left valve figured by Barrande (1881) on pl. 244, as figs II/5-8, NM L 22 424.

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

Type horizon. – Wenlock, early Homerian, *Testograptus testis* Biozone.

Material. – Two shells with conjoined valves, 25 left and 24 right valves.

Diagnosis. – In adult shells the height/length relation (H/L) ranging from 1.4 to 2.2 (average 1.9), length/width relation (L/W) ranging from 0.5 to 0.7 (average 0.6), height/width relation (H/W) ranging from 0.9–1.5 (average 1.2). Umbonal angle is 36–62° (average 43°). The shells are distinctly higher than in *Kenzieana cardiopsis* from the early Ludlow and have less numerous radial ribs posteriorly of carina (> 63 in number). Hinge unknown. Posterior adductor muscle scar developed close to ventral margin, and above the posterior radial sulcus.

Description. – Small, equivalve, inequilateral, prosocline, obliquelly obtriangular in outline, dorso-ventrally elongated, strongly inflated shells. In adult shells the height/length relation (H/L) ranging from 1.4 to 2.2 (average 1.9), length/width relation (L/W) ranging from 0.5 to 0.7 (average 0.6), height/width relation (H/W) ranging from 0.9–1.4 (average 1.2). Umbonal angle 36–62° (average 43°). The shells of *Kenzieana bellula* are distinctly higher than in *Kenzieana cardiopsis* from the early Ludlow. Enantiomorphous (mostly equivalve but some specimens are slightly inclined to the left or to the right). Prominent umbones are in anterior terminal position, prosogyrate, with relatively large circular inflated opistogyrate prodissoconch on the beaks. Slightly inflated, subcircular or widely elliptical lanceolate frontal face very steep and wide, separated from the central part of the shell by carina curved anteriorly. Posterior sulcus indicates the presence of siphons. Outer surface with numerous rounded radial ribs (> 63 in number posteriorly of carina) and radial gutters in combination with numerous growth bands of approximately the same width. Both, the radial ribs and radial gutters broaden ventrally. Inner surface smooth, crenulations developed along the margin. Hinge

margin short, straight. Hinge unknown. Posterior adductor muscle scar developed close to ventral margin, and above the posterior radial sulcus. Shell thickness 0.18–0.4 mm.

Dimensions. –

	V	L	H	width/2	L/W	H/W
JK 8828	R	4.0	7.0	2.9	0.7	1.3
JK 8869	R	4.8	9.2	3.9	0.6	1.2
JK 8860	L	4.9	11.0	4.6	0.5	1.2
JK 8825	L	5.1	11.0	4.3	0.6	1.3
NM L 22424	L	5.1	11.7	4.2	0.6	1.4
JK 11146	L	5.2	9.4	4.1	0.6	1.1
JK 8830	L	5.3	10.6	4.8	0.6	1.1
JK 8814	R	5.6	9.5	4.1	0.7	1.2
JK 8813	L	5.7	10.9	5.1	0.6	1.1
JK 8861	L	5.8	10.2	4.5	0.6	1.1
JK 8838	R	5.8	12.1	4.8	0.6	1.3
JK 8826	R	5.9	10.3	4.1	0.7	1.3
JK 8872	R	5.9	11.2	4.9	0.6	1.1
JK 8829	L	6.0	11.1	4.9	0.6	1.1
JK 11236	L	6.2	12.8	5.3	0.6	1.2
JK 8812	R	6.5	12.1	5.4	0.6	1.1
JK 8845	R	6.5	12.4	5.1	0.6	1.2
JK 8816	L	7.3	16.4	6.1	0.6	1.3
JK 11152	R	7.8	13.5	7.3	0.53	0.9

Mode of life. – *Kenzieana bellula* was most probably a very shallow and slow burrower, resting or reclining in the sediment on its anterior, widely elliptical and flatter frontal face with a few byssal threads attached to loose detrital sediment. It is known from the Prague Basin *Cardiola agna* Community, Arethusina Gorge near Praha-Řeporyje, late Wenlock, early Homerian, *Testograptus testis* Biozone (Kříž 1999a).

Occurrence. – Bohemia, Prague Basin, Praha-Řeporyje, Arethusina Gorge, Praha-Malá Chuchle, Vyskočilka Section above the road, and in the Malá Chuchle Valley, Praha-Pankrác, Praha-Motol, Beroun-Lištice, Kozel, Praha-Butovice, Tachlovice (late Wenlock, early Homerian, *Testograptus testis* Biozone). Gotland (late Wenlock, Slite Beds, unit g, *Cyrtograptus lundgreni* Biozone).

Conclusions

1. *Kenzieana* Liljedahl, 1989 from the late Wenlock (early Homerian) represents the oldest known genus of the family Spanilidae Kříž, 2007, most probably derived from the late Llandovery Stolidotidae Starobogatov, 1977.

2. *Kenzieana* is very long ranging Silurian genus (late Wenlock to late Přídolí) and was most probably the ancestor of the Gorstian *Algerina* Kříž, 2008, and the Ludfordian *Spanila* Barrande, 1881.

3. Distinctly inflated, foreshortened shells with almost flat and circular frontal face represent in *Kenzieana* adaptive convergence with the Silurian *Slavinka plicata* (Barrande, 1881), and Recent *Corculum* Röding, 1798, *Fragum* Röding, 1798.

4. *Kenzieana* was very shallow and slow burrower resting or reclining in the sediment on its anterior, almost subcircular or widely elliptical and flat frontal face with a few byssal threads attached to loose detritus.

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