Systematic position, distribution, and shell structure of the Devonian linguloid brachiopod *Bicarinatina bicarinata* (Kutorga, 1837)

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**Abstract.** The type species of the brachiopod genus *Bicarinatina* Batrukova was first described by Kutorga in 1837 (*Zweiter Beitrag zur Geognosie und Paläaontologie Dorpats und seiner nächsten Umgebeungen*. St.-Petersbourg, 51 pp.) as *Lingula bicarinata* from the Middle Devonian sandstone beds now assigned to the Aruküla Regional Stage in Tartu, Estonia. Gravitis (1981, in *Devon i karbon pribaltiki* (Brangulis et al., eds), pp. 455–462. Zinatne, Riga) described eight new species of the genus *Bicarinatina*. Revision of the collections in St Petersburg and Riga showed that four of these species names should be considered as subjective junior synonyms of the type species *Bicarinatina bicarinata* (Kutorga) and that the type specimens of the remaining four new species were either juvenile or too poorly preserved for species-level identifications. Therefore, *B. bicarinata* should be considered the only valid species of the genus *Bicarinatina* occurring in the Middle Devonian on the Baltic plate, known from Estonia, Latvia, and northwestern Russia. The shell structure of *B. bicarinata* is baculate symmetrical, with the finest baculate sets in the innermost parts of the valves and thicker and aggregated baculi in outer parts, due to stronger taphonomic changes in outer parts of the shell. In cross section, the valves are 70–100 µm thick.

**Key words:** Brachiopoda, *Bicarinatina*, shell structure, Middle Devonian, Estonia, Latvia, Russia.

**INTRODUCTION**

The type species of the genus *Bicarinatina* Batrukova, *Lingula bicarinata*, was first described by Kutorga (1837) from the Middle Devonian sandstones in the town of Tartu, Estonia, from the beds assigned today to the Aruküla Regional Stage. Later studies revealed other occurrences from the Middle Devonian of Estonia and northwestern Russia. Except for the Devonian of the East Baltic, the representatives of the genus *Bicarinatina* have been described from the Middle Devonian of Alaska (*B. kongakutensis* Popov, Blodgett & Anderson, 1994) and the Carboniferous of Scotland (*B. wisoni* Graham, 1970 and *B. indicis* Graham, 1970) (Popov et al. 1994).

Gravitis (1981) described eight new species of the genus *Bicarinatina* from the East Baltic. Due to poor quality of illustrations the systematic status of these species remained uncertain and they were neither recognized nor discussed in further studies of the genus *Bicarinatina* (e.g. Popov et al. 1994).

The aim of this study is to clarify the systematic status of *Bicarinatina bicarinata* (Kutorga) and related species reported from the East Baltic by revision of the original collection of Viktors Gravitis at the Latvian Museum of Natural History and to give the first description of the shell microstructure of this species.

**MATERIAL AND METHODS**

The topotypic collection of *Lingula bicarinata* Kutorga at St Petersburg State University (PSU), containing two specimens, was revised and the lectotype selected. The original collection of Devonian linguloids at the Latvian Museum of Natural History (Latvijas Dabas Muzejs, LDM), containing about 30 samples, was studied for the revision of *Bicarinatina bicarinata* and several species erected by Gravitis (1981). The material collected by Elga Mark-Kurik and others during several years from drill cores of Estonia (about 20 samples), stored in the collection of the Institute of Geology at Tallinn University of Technology (Geoloogia Instituut, Tehnikakool, GIT, collection 439, online catalogue www.gi.ee), was valuable for documenting the distribution of *B. bicarinata* in Estonia. In the course of field works in 2005 and 2006, the authors collected new material of *Bicarinatina* from the outcrops on the banks of the Poruni River (5–20 m upstream of the bridge on the Gorodenka–Poruni road) and the Gorodenka Stream (Fig. 1); the illustrated specimens from the Poruni River used for shell structure studies are deposited at the University of Tartu Museum of Natural History (Tartu Ülikooli Loodusmuuseum, TUG). For geological setting and stratigraphy, see Kleesment & Mark-Kurik (1997) and Sorokin et al. (1981).
Fig. 1. A sketch map showing the occurrences of Bicarinatina bicarinata in Estonia, Latvia, and NW Russia, confirmed by the revision of the collections. The stars mark locations of outcrops and the closed circles the following drill cores: Uulu-Leina (215), Kuningaküla (two cores, 6950 and 6951), Laeva (19), and Tsiistre (327) in Estonia; the Ludza-15 core in eastern Latvia; and the Petseri (Pechory) core in Russia. The exact locality of another specimen from Russia, illustrated in the Treatise (Holmer & Popov 2000) from the Luga River is unknown.

Specimens were coated with Mg powder and photographed with a digital camera. The environmental scanning electron microscope (ESEM) LEO (currently Carl Zeiss) at the electron microscopy laboratory, Norwegian Geological Survey, was used to study fracture sections of untreated and uncoated specimens in the regime of back-scattered electron imaging. Energy dispersive spectroscopy (EDS) was used for point identification of minerals in taphonomically altered valves. These settings have proven to be most suitable for observing and photographing delicate structures, such as the thinnest baculi, in high magnifications.

SYSTEMATIC PALAEOONTOLOGY

Phylum BRACHIOPODA Duméril, 1806
Subphylum LINGULIFORMEA Williams et al., 1996
Class LINGULATA Gorjansky & Popov, 1985
Order LINGULIDA Waagen, 1885
Superfamily LINGULOIDEA Menke, 1828
Family PSEUDOLINGULIDAE Holmer, 1991
Genus Bicarinatina Batrukova, 1969

Type species. Lingula bicarinata Kutorga, 1837. From Narva and Aruküla regional stages (Eifelian Stage, Middle Devonian) of Estonia, Latvia, and NW Russia.


Remarks. Batrukova (1969) established a new genus Bicarinatina, with Lingula bicarinata Kutorga, 1837 as its type species. Popov et al. (1994) described a new species of this genus, Bicarinatina kongakutensis from the Eifelian Stage, Middle Devonian of the Arctic Alaska. They also included two species from the Mississippian Series, Carboniferous of Scotland, Liralingua indicis Graham, 1970 and Liralingua wilsoni Graham, 1970 to the genus Bicarinatina. These four species are accepted here as the valid representatives of the genus Bicarinatina.

Gravitis (1981) described Bicarinatina bicarinata and eight new species of the same genus. However, as discussed below, these new species names are either junior synonyms of B. bicarinata or nomina dubia, assigned to poorly preserved specimens that cannot be identified at species level.

Diagnosis (from Holmer & Popov 2000). Shell sub-rectangular to elongate subelliptical, ornamented by growth lines or concentric rugellae; both valves with two or three broad, radial plications, ventral pseudo-interarea short, with deep, narrow pedicle groove; ventral visceral area large, rhomboidal, extending to midvalve; dorsal visceral area bisected by long median ridge, with wide, semielliptical anterior projection extending anterior to mid-valve; central muscle scars large, situated close to anterior lateral muscle scars.

Distribution. Middle Devonian of Estonia, Latvia, NW Russia, and USA (Arctic Alaska); Lower Carboniferous of Scotland.

Bicarinatina bicarinata (Kutorga, 1837)
Figures 2A–D; 3A–F

1837 Lingula bicarinata Kutorga, p. 38, pl. VIII, fig. 4; pl. IX, fig. 2.
1846 Lingula bicarinata Kutorga, p. 116, pl. VII, fig. 1.
1981 Bicarinatina ugalana sp. nov.; Gravitis, p. 456, pl. XXII, figs 5, 6.
1981 Bicarinatina bicarinata (Kutorga); Gravitis, p. 455, pl. XXII, figs 1–4.
1981 Bicarinatina sakalana sp. nov.; Gravitis, p. 458, pl. XXII, figs 7, 8.
1981 Bicarinatina acuta sp. nov.; Gravitis, p. 459, pl. XXII, fig. 10.
Fig. 2. *Bicarinatina bicarinata* (Kutorga, 1837), Middle Devonian Narva Regional Stage, Estonia. A, GIT 439-24-1, ventral exterior, from the outcrop at the Poruni River, 10 m downstream of the bridge on the Gorodenka–Poruni road. B, GIT 439-10-1, ventral valve exterior, from the Kuningaküla core No. 6950 (NE Estonia), interval 9.3–13.0 m. C, LDM G50/4a, dorsal interior, outcrop on the Gorodenka Stream, NE Estonia, coll. Viktors Gravitis (photo: Ivars Zupins). D, GIT 439-11-1, ventral interior of *B. bicarinata* from the Kuningaküla core No. 6950, NE Estonia, interval 9.3–13.0 m. All scale bars 1 cm.
Fig. 3. The shell structure of *Bicarinatina bicarinata* (Kutorga, 1837), all specimens from the Middle Devonian Narva Regional Stage in the Poruni outcrop, 5–20 m downstream of the bridge on the Gorodenka–Poruni road, collected by Liisa Lang in 2005–2006. A–C, TUG 1323-1, ventral valve. A, B, General views of a ventral valve cross section in different magnification. Scale bars 100 µm and 10 µm, respectively. C, Close-up of the fracture section of the valve showing the alternation of baculate (Bl) and compact laminae (Cl). Note the baculate sets with the fine baculi in the inner part of the valve and transition of fine baculi to the aggregated baculi in outward direction. Scale bar 2 µm. D, TUG 1323-2: alternation of baculate and compact laminae in the inner part of the valve. Scale bar 2 µm. E, TUG 1323-1, close-up of slightly recrystallized baculate sets. Scale bar 1 µm. F, TUG 1323-3, baculate sets of the secondary layer with fine well-preserved baculi. Scale bar 1 µm.
?1981 Bicarinatina scaphulata sp. nov.; Gravitis, p. 458, pl. XXII, fig. 9.
1994 Bicarinatina bicarinata (Kutorga); Popov, Blodgett & Anderson, fig. 4.
2000 Bicarinatina bicarinata (Kutorga); Holmer & Popov, p. 39, fig. 11, 2a–2d.

Lectotype. Selected here, Museum of St Petersburg State University, ventral valve exterior, PSU 161/6, from Kütimägi (Jägerberg), 12 Jaama Street, Tartu, Estonia. Illustrated as Lingula bicarinata Kutorga in Kutorga (1837, p. 38, pl. VIII, fig. 4; pl. IX, fig. 2).

Topotype. Ventral valve interior, PSU 161/7, from Kütimägi (Jägerberg), 12 Jaama Street, Tartu, Estonia. Illustrated as Bicarinatina ugalana by Gravitis (1981, p. 456, pl. XXII, figs 5, 6).

Diagnosis. As for genus.

Description of shell structure. Earlier investigations have revealed that the genus Bicarinatina has baculate shell structure, but it has not been studied in greater detail. The only known published illustration of the shell structure of Bicarinatina is an oblique view of a fracture section of Bicarinatina wilsoni Graham from the Carboniferous of Scotland showing baculate shell structure, but not in great detail (Cusack et al. 1999, text-fig. 3, photo G, p. 807).

According to our ESEM observations, the shell structure of Bicarinatina bicarinata can be classified as baculate symmetrical, with alternating baculate and compact laminae (Fig. 3A–F). In the context of phylogeny, this structure of the secondary shells of linguloid brachiopods is considered to be one of the oldest, known already from the Early Cambrian times (Cusack et al. 1999; Williams & Cusack 1999, 2007).

The baculate structure is similar to that of Obolus apollinis Eichwald, with the exception that the baculi of Bicarinatina bicarinata are thinner. The studied shells of B. bicarinata were mostly well preserved, although some evidence of recrystallization can be observed. The valve is about 70–100 µm thick and appears to be very even in its thickness. The studied valves have homogeneous outer layers (Fig. 3A, B), consisting of closely packed apatitic spherules or mosaics grading inwardly into the baculate zone. At a closer look, some aggregated and packed-together baculi can be recognized. The baculi in the outer part of the shell appear to be larger in size (approximately 0.25–0.5 µm in cross section) than in the inner layers where the baculi are very fine (Fig. 3F). The baculate sets are well defined in middle parts of the vertical sections of the valves.

The size of compact laminae is varying from 0.5 to 2.5 µm in thickness (Fig. 3C, D). Compact laminae are better developed in the inner part of the valves and appear to be thicker than baculate laminae.

The cross-sections of the shells show gradual increase in the size of baculi from the internal parts towards the exterior, due to higher extent of recrystallization closer to shell surface. The finest baculi can be observed in inner parts of the valves, where they usually form trellised baculate sets (Fig. 3C). In some cases the transition from the fine baculi to thicker, aggregated baculi can be observed: the apatitic spherules cover the fine baculi and form their granular surface (Fig. 3C). Williams & Cusack (2007) consider this type of preservation of baculi the most common one. In contrast, the very fine needle-like baculi of the size observed here appear to be rare, being found in cases of exceptional preservation.

Distribution. Narva and Aruküla regional stages (Eifelian, Middle Devonian) of Estonia, Latvia, and NW Russia.

Discussion. In his study of the geology of the Estonian town of Tartu and its environs, Kutorga (1835) described some layers with brachiopods. Two years later he described and illustrated the species Lingula bicarinata Kutorga, 1837 from Jägerberg in Tartu. This outcrop is today called Kütimägi and is exposed in the backyard of house 12, Jaama Street. Unfortunately, the lower part of the outcrop which yielded the brachiopods is inaccessible today, because it is covered by geotextile.

The original collection of Stepan Kutorga, deposited at the Museum of Geology of St Petersburg University includes two specimens. The dorsal valve PSU 161/6, illustrated as Lingula bicarinata in Kutorga (1837, p. 38, pl. VIII, fig. 4; pl. IX, fig. 2), is selected here as the lectotype. Another specimen, the ventral valve PSU 161/7, is a toptype (illustrated by Gravitis 1981, p. 456, pl. XXII, figs 5, 6). Gravitis (1981) regarded these two totypic specimens as different species and referred to the dorsal valve PSU 161/7 as the holotype of his new species Bicarinatina ugalana. As this would restrict the size of the type collection of B. bicarinata to one, Gravitis considered PSU 161/6 the holotype of B. bicarinata (Kutorga) by monotypy. However, we consider that Gravitis (1981) placed a ventral and a dorsal valve to different species. Therefore, B. ugalana is a subjective junior synonym of B. bicarinata (Kutorga).

Orviku (1948) illustrated B. bicarinata as Lingula bicarinata from the localities of the Narva Regional Stage in northeastern Estonia (Gorodenka and Poruni) and reported it from the environs of Viljandi.

The approach of Gravitis (1981) to the systematics of the genus Bicarinatina apparently underestimated the infraspecific variability, which led him to erecting eight new species of this genus. The case of Bicarinatina...
ugalana was discussed above. The revision of the collection at the Latvian Museum of Natural History in Riga revealed the following aspects of the systematic position of the original specimens in the collection of Viktors Gravitis.

(1) A well-preserved dorsal interior (Fig. 2C) of a specimen from the Gorodenka Stream, Estonia, in the collection of Gravitis, LDM G50/4a, assigned to *Bicarinatina sakalana* is closely similar to the dorsal interior of *B. bicarinata* described by Popov et al. (1994). This specimen and associated specimens from the same rock slab, including a ventral valve of *B. sakalana* illustrated by Gravitis (1981, p. 458, pl. XXII, fig. 8) and labelled as ‘paratype’ in the collection, come from the locality from where *B. bicarinata* is well known. It is concluded that *B. sakalana* Gravitis, 1981 is a subjective junior synonym of *B. bicarinata* (Kutorga).

(2) The ventral valve exterior illustrated by Gravitis as the holotype of *Bicarinatina acuta* Gravitis, 1981 (Gravitis 1981, pl. XXII, fig. 10) from the Ludza (15) core (depth 382 m), eastern Latvia, is identical to the ventral valve exterior of *B. bicarinata* (Kutorga). It is concluded that *B. acuta* is a subjective junior synonym of *B. bicarinata* (Kutorga). According to this interpretation, *B. bicarinata* occurs in the subsurface of eastern Latvia.

(3) A partly preserved dorsal exterior, illustrated by Gravitis (1981, pl. XXII, fig. 9) as the holotype of *Bicarinatina scaphulata*, is closely similar to *B. bicarinata*. It also occurs in the Ludza (15) core (depth 389 m). Considering these circumstances, it is concluded that *B. scaphulata* is a subjective junior synonym of *B. bicarinata*.

(4) The specimens, illustrated by Gravitis (1981, pl. XXIII, figs 12, 13) as the holotype and a paratype of *Bicarinatina rozenshteini*, are poorly preserved linguloids that cannot be identified at the species level.

(5) The specimens, illustrated by Gravitis (1981, pl. XXIII, figs 15, 16) as the holotype of *Bicarinatina gulbenensis*, is a poorly preserved linguloid valve fragment that cannot be identified at the species level.

In conclusion, the study of the original material in the collection of Viktors Gravitis in the Latvian Museum of Natural History has shown that four of his species names – *Bicarinatina ugalana*, *B. sakalana*, *B. acuta*, and possibly also *B. scaphulata* can be considered as subjective junior synonyms of *B. bicarinata* (Kutorga). The specimens, which Gravitis (1981) chose as holotypes or paratypes of the four remaining new species, cannot be identified at the species level because they are fragmentary, poorly preserved, or juvenile. Thus, *Bicarinatina livica*, *B. borchii*, *B. rozenshteini*, and *B. gulbenensis* should be considered as nomina dubia, invalid names for taxonomic purposes.

Therefore, no new species of *Bicarinatina*, erected by Gravitis (1981), can be considered as valid. In view of these considerations, *Bicarinatina bicarinata* (Kutorga) should be considered the only known valid species of this genus *Bicarinatina* occurring in the Middle Devonian on the Baltic plate.

**Occurrence.** The type locality of *Bicarinatina bicarinata* is 12 Jaama Street in the town of Tartu, Estonia (see Fig. 1), from where Stepan Kutorga in 1837 described and illustrated the shells of *Lingula bicarinata* (PSU 161/6, 161/7). The shells were found from the reddish-coloured clay that Kutorga called Leimen, stratigraphically belonging to the Aruküla Regional Stage (Middle Devonian, Eifelian). Another locality of the Aruküla Stage where *B. bicarinata* has been found is Tarvastu, a section near the watermill on the Tarvastu River (GIT 439-2).

Orviku (1948) documented the shells of *B. bicarinata* from several outcrops of the Narva Regional Stage (Middle Devonian, Eifelian) on the banks of the Gorodenka Stream and the Poruni River (Fig. 1) in northeastern Estonia and in the Pelda and Vardja outcrops in the environs of the town of Viljandi. The occurrences in the Gorodenka and Poruni localities are confirmed with our studies and new collections, including a specimen from Poruni collected by Anne Kleesament in 2004 (GIT 439-24-1, Fig. 2A) and a well-preserved dorsal interior from Gorodenka collected by Viktors Gravitis before 1981 (LDM G50/4a, Fig. 2C). The material of *Bicarinatina* from the Pelda outcrop has been mentioned and illustrated by Gravitis (1981) as *B. sakalana*, while the material from the Vardja outcrop is not available in the preserved collections and needs to be verified by future studies.

The specimens identified as *Bicarinatina bicarinata* (Kutorga) in the collection of Elga Kurik at the Institute of Geology, Tallinn University of Technology, originate from the Narva Regional Stage in the Uulu-Leina (215) core, depth 6.20 m (samples GIT 439-3, 439-4, 439-5, 439-6), Laeva (19) core, depth 8.50 m (sample GIT 439-1), two cores in northeastern Estonia: Kuningaküla (6950), depth 9.30–13.00 m (samples GIT 439-7, 439-8, 439-9, 439-10-1, 439-11-1), including a well-preserved ventral interior (Fig. 2D) and Kuningaküla (6951), depth
The genus Bicarinatina includes four species: Bicarinatina bicarinata (Kutorga, 1837), Liralingua indicis Graham, 1970; Liralingua wilsoni Graham, 1970, and Bicarinatina kongakutensis Popov, Blodgett & Anderson, 1994. None of the eight new species of the genus Bicarinatina described by Gravitis (1981) can be considered as valid: part of them must be considered as junior synonyms of the type species Bicarinatina bicarinata (Kutorga) and part of them were represented by poorly preserved holotypes or paratypes that cannot be identified at the species level. According to these results, it is likely that the genus Bicarinatina (Batrukova) is represented on the Baltica plate only by the type species, B. bicarinata (Kutorga), previously known to occur in Estonia and northwestern Russia. According to the re-interpretation of the systematic position of some specimens in the collection of Viktors Gravitis at the Latvian Museum of Natural History, this species occurs also in Latvia.

The shell of B. bicarinata (Kutorga) is almost three times thinner than the shell of Obolus apollinis Eichwald (comp. Cusack et al. 1999; Nemliher et al. 2004). Bicarinatina bicarinata has the structure of secondary shell composed of rhythmically alternating compact and baculate laminae. The baculate sets in the inner part of the shell are very fine. In the outer part of the shell the baculi are aggregated together, forming slightly thicker baculi that are occasionally cemented together by secondary apatite, forming in some places almost homogeneous structures. Thus, B. bicarinata is a quite typical representative of a linguloid with baculate structure. The very fine baculi observed in B. bicarinata give evidence of exclusive preservation.

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Bicarinatina livica Ülejäänud uued nimed Gravitise töös (kollektsiooni revisjon näitas, et vähemalt nelja Gravitise püstitatud liigi (Bicarinatina ugalana Brahhiopoodiperekonna Bicarinatina eksemplaridele, mis ei ole säilivuse tõttu liigi tasemel kirjeldatud. 
Eichwald. Tõenäoliselt peamiselt mattumisjärgsete tafonoomi liste muutuste tõttu on kojapoolmete siseosas jälgitada-kojapoolmete paksus vaid 70–100 µm, st need on ligi kolm korda õhemad kui Kambriumi perekonnal 
B. scaphulata lünguloidse käsijalgse Bicarinatina bicarinata (Kutorga, 1837) süsteematiik, levik ja koja struktuur 
Liisa Lang ja Ivar Puura 
Ülejäänud uued Gravitise tõös (Bicarinatina livica, B. borchii, B. rozenshteini ja B. gulbenensis) on omistatud eksemplaridele, mis ei ole säilivuse tõttu liigi tasemel kirjeldatavad. 