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Discovery of trimerellide brachiopod *Gasconsia* from the Ordovician of Estonia

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ABSTRACT

In this study, the first trimerellide brachiopods from Estonia are described. They occur in the uppermost Katian (Upper Ordovician) shallow shelf environments and represent some of the largest Ordovician brachiopods. The trimerellides described are assigned to the genus *Gasconsia* Northrop, 1939, which disappears before the Hirnantian and reappears in the lowermost Wenlock after a long interregnum. In the Baltic Basin, the new data from Estonia expand the distribution area of *Gasconsia* from the Scandinavian facies belt in the west to the Estonian shallow shelf in the east. Despite poor preservation, the specimens studied revealed some structures in shell morphology important for species level identification. The stratigraphic position of *Gasconsia* is analyzed relative to the Katian-Hirnantian (Pirgu-Porkuni regional stages) boundary and the occurrence of the late Katian brachiopod *Holorhynchus* in Estonia. The improved data on the distribution of *Gasconsia* in time and space and a short discussion on brachiopod gigantism are presented.

Introduction

The trimerellides of the subphylum Craniiformea (Williams et al. 1996) form a separate evolutionary lineage of inarticulate brachiopods characterized by the early origination of articulation (Gorjansky and Popov 1986). In view of the stratigraphic range from the Sandbian (Upper Ordovician) to the Ludlow (Silurian), these brachiopods are known to inhabit warm water environments on both sides of the paleo-equator (Torsvik and Cocks 2017; Chen et al. 2023). Trimerellides form a minor part in the Ordovician benthic faunas on different paleocontinents from Laurentia to Gondwana (Rong et al. 2017; Chen et al. 2023). The aragonitic shells of trimerellide brachiopods (Jaanusson 1966; Hanken and Harper 1985) are usually poorly preserved, which complicates the understanding of their morphology and functional mechanisms. Most investigations on trimerellides concentrate on systematic paleontology (see references in Popov and Holmer 2000; Chen et al. 2023).

A recent overview by Chen et al. (2023) first subdivided the Ordovician and Silurian trimerellide brachiopods into four groups (A–D) based on the shell outline, varying from elongate with a high ventral pseudointerarea (group A) to a transversely oval shell with a low ventral pseudointerarea (group D). A second subdivision of trimerellides by Chen et al. (2023) into three types (I–III) is based on the features of shell interiors, particularly the expression of platforms and vaults (weak, moderate, high). These types characterize the taxa, which could belong to different groups based on the shell outline. The species diversity of Katian (Ordovician) trimerellides in South China (Rong et al. 2017) and Australia (Webby and Percival 1983) during the Middle Ordovician is replaced in the Silurian by higher diversity in Laurentia and Baltica (Chen et al. 2023).

The first appearance of trimerellide brachiopods in Baltica is associated with the second wave of faunal immigration from Kazakhstan during the mid-Katian. Before that, trimerellides appeared in the Sandbian in Gondwana and Laurentia (Popov et al. 1997). Some Silurian trimerellides (*Eodinobolus* and *Monomerella*) and their Ordovician relatives (*Eodinobolus*) have been recorded in Estonia (Popov and Holmer 2000). The list of Baltic Silurian brachiopods (Rubel et al. 1984) comprises the species *Trimerella* cf. *lindstroemi* and *Dinobolus* cf. *davidsoni* without data on exact

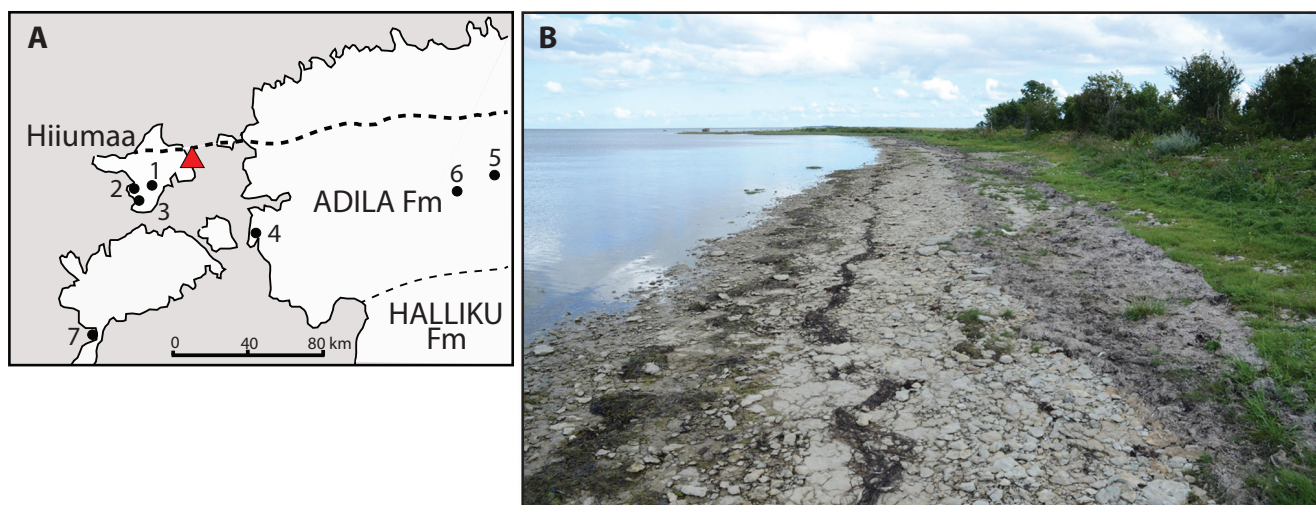


Fig. 1. **A** – sketch map of western Estonia with the localities mentioned in the text, showing the coastal outcrop in the eastern part of the Vohilaid Island (triangle) and the drill cores (dots): 1 – Männamaa F-367, 2 – Külaküla K-29, 3 – Lassi K-39, 4 – Virtsu 360, 5 – Põhjaka-Saare H-171, 6 – Äiamaa, 7 – Kaugatuma 509. The distribution areas of formations are separated by dashed lines. **B** – view of the outcrop on Vohilaid.

stratigraphic occurrences. These latter species are presumably represented by specimens (TUG 1091-62 and ELM 622:93:1, 622:93:2 from the Estonian geocollections database) from the Silurian of Gotland. A few specimens of *Dinobolus* (GIT 506-1347, TUG 39-644 from the Estonian geocollections database) are known from the Jaani Regional Stage (RS; Wenlock) on the Saaremaa Island (western Estonia). The occurrence of trimerellides has also been mentioned in the Slite Group (mid-Wenlock) in Gotland (Sweden), forming reef-like structures there (Budd et al. 2011). The trimerellide brachiopod *Gasconsia worsleyi* Hanken and Harper, 1985 occurs in the Bønsnes Formation (Fm; upper Katian) in Norway (Owen et al. 1990), just below the Hirnantian strata. In Estonia, the new finds of *Gasconsia* occur on a similar stratigraphic level, in the uppermost Katian (Pirgu RS). The Estonian data expand the distribution area of trimerellides in the Baltic Basin from the Scandinavian facies belt in the west (Hanken and Harper 1985) to the Estonian shelf in the east. The trimerellides described in this paper are assigned to the genus *Gasconsia* based on many fundamental characters, including the shell shape, articulation structure, and a muscle system with an impressed, solid platform.

The aim of this study is to explain the taxonomic affiliation of the Ordovician trimerellides first identified in Estonia, show their relationship with the Norwegian species, and highlight their stratigraphic occurrence relative to the boundary between the Pirgu and Porkuni RSs (Katian and Hirnantian), and age relationship with the brachiopod *Holorhynchus*. The latter genus is a nominal taxon of the latest Katian brachiopod fauna (Brenchley and Cocks 1982; Brenchley et al. 1997, Rong and Harper 1988, Hints 1993; Paškevičius 2000; Shiino et al. 2014), which is widely distributed on different paleocontinents (Rong and Boucot 1998; Rong et al. 2004).

Material and notes on associated fossils

The five specimens of large trimerellide brachiopods described here were collected in 2022 by Ursula Toom and

Björn Kröger from a small coastal outcrop in the eastern part of the Vohilaid Island (locality Vohilaid 8 by Stein 1937; Fig. 1). The small island of Vohilaid lies about 500 m east of the larger island of Hiiumaa in northwestern Estonia. Small old quarries and coastal outcrops on Vohilaid, up to about 1 m in total thickness, expose Katian–Hirnantian boundary strata (the Pirgu–Porkuni transitional beds; Stein 1937). In the northernmost part of the island, the carbonate grainstone presumably belongs, at least partly, to the topmost Ordovician Porkuni RS, lower Hirnantian. The skeletal limestone in the easternmost locality (Stein 1937, locality 8 in fig. 129; Fig. 2) belongs to the Adila Fm (upper Katian). This formation comprises a rich association of various fossil groups, including corals, bryozoans, cephalopods, gastropods, and others, many of which are considered index fossils for the Pirgu RS (Kaljo et al. 1963; Männil 1990). In addition, the Adila Fm is striking for the presence of numerous species of corals and stromatoporoids, such as *Proheliolites dubius*, *Sarcinula luhai*, *Catenipora parallela*, and *Clathrodictyon microundulatum*, shared with the Norwegian pre-Hirnantian unit 5a, previously known as the Gastropod Limestone (Kaljo et al. 1963; Owen et al. 1990; Liang et al. 2013). In the Vohilaid section, *Gasconsia* is associated with *Maclurites neritoides* (specimens TUG 1723-1–7, identified by Mare Isakar), the index gastropod for the Adila Fm of the Pirgu RS (Isakar 1997). In Baltica, the warm-water *Maclurites* has been considered to belong to the shallow-water Benthic Assemblage 1–2 (Boucot 1975; Ebbestad et al. 2013), which could also be extrapolated to the youngest Katian deposits bearing *Gasconsia*.

The brachiopods described in this paper were collected from the upper part of the coastal outcrop section on the Vohilaid Island (Fig. 1). In this section, the Pirgu RS is represented by the strata commonly included in the Adila Fm (Fig. 2). However, Stein (1937) suggested the occurrence of transitional strata across the Katian and Hirnantian (Pirgu and Porkuni RSs) boundary.

All five specimens of *Gasconsia* studied here are represented by molds of convex dorsal valves of about the same

Global stage	Regional stage	Graptolite zone	Chitinozoan zone	Estonian Shelf	Transitional zone	Livonian Basin
HIRNANTIAN	PORKUNI	<i>Normalograptus persculptus</i>	<i>Conochitina scabra</i>			KULDIGA Fm
		<i>Normalograptus extraordinarius</i>	<i>Spinachitina taugourdeai</i>			ÄRINA Fm
KATIAN	PIRGU	<i>Dicellograptus anceps</i>	<i>Belonechitina gamachiana</i>	H G Kabala Mb	HALLIKU Fm	KUILI Fm
			<i>Conochitina rugata</i>	ADILA Fm		PAROVEJA Fm
		<i>Dicellograptus complanatus</i>	<i>Tanuchitina bergstroemi</i>	MOE Fm	JONSTORP Fm	

Fig. 2. The upper Katian–Hirnantian stratigraphic units and their correlation with formations in Estonia (modified from Harris et al. 2004). The Kabala Mb (Nölvak 1997) is used also as a Fm (Meidla 1996; Hints et al. 2005); however, it is not used in stratigraphic correlation charts (Meidla et al. 2014, 2023). H and G mark the occurrence of brachiopods *Holorhynchus* and *Gasconsia*, respectively, in the upper part of the Pirgu RS.

size, showing some traces of partly preserved interior and exterior structures of shells. Only one ventral valve is partly preserved behind the dorsal valve. The measurements of shells and structures are, in some cases, approximate due to poor preservation.

Data on shelly fossils from the localities on Vohilaid are available in the Estonian geocollections database. The Estonian specimens of *Gasconsia* described here are housed at the Department of Geology, Tallinn University of Technology (institutional abbreviation GIT). The institutional abbreviations TUG and ELM mentioned above mark the specimens housed at the Museum of Geology of the University of Tartu and the Estonian Museum of Natural History, respectively.

On the taxonomy of Estonian trimerellides

The Estonian Upper Ordovician trimerellides described below are very large with a transversely oval outline, similar to the species of the genus *Gasconsia* (Northrop 1939; Hanken and Harper 1985; Mergl 1989; Watkins 2002). Given the shell outline, this genus belongs to group D (Chen et al. 2023), characterized by a relatively short pseudointerarea, and based on internal features, to type I (Chen et al. 2023). Specimens of type I have low platforms that are not vaulted and have feebly impressed or missing median ridges (Chen et al. 2023). The Estonian trimerellides, however, have a relatively high ventral pseudointerarea with an apical angle of about 120° (GIT 759-292b), and a two-partite, anteriorly trigonal platform that is vaulted with a strong wedge-like myophragm. The elements of the articulation mechanism could not be precisely observed in the studied specimens.

The updated description of *Gasconsia*, with its type species *Gasconsia schucherti* from the Silurian of Canada, and the description of *G. worsleyi* from the Upper Ordovician of Norway (Hanken and Harper 1985) represent a significant step towards a better understanding of trimerellide brachiopods. The similarity in the articulation and muscle systems of *Gasconsia* with the Ordovician genus *Eodinobolus* and the Silurian genus *Dinobolus* (Norford 1960) enabled the assignment of these three taxa to the subfamily Dinobolinae Li and Han, 1980. The Silurian species *Dinorthis bohemicus*

(Barrande) differs essentially from Estonian trimerellides in dorsal interior features, such as the outline of anterior muscle scars, their subcircular ribbing, and furrow-shaped septa. The Estonian specimens differ from the species of *Eodinobolus* from Canada (*E. magnifica*, *E. canadaensis*, *E. erectus*; Norford and Steele 1969) in having a much larger size, a transversely oval shell outline, and specific details of dorsal interiors. The large size, transversely oval outline, dorsal socket, two-partite platform, central and anterior muscle scars, and external ornamentation of Estonian trimerellides support their identification within the genus *Gasconsia*.

Systematic paleontology

Subphylum CRANIIFORMEA Popov, Bassett, Holmer and Laurie, 1993

Class CRANIATA Williams et al., 1996

Order TRIMERELLIDA Gorjansky and Popov, 1986

Superfamily TRIMERELLOIDEA Davidson and King, 1872

Family TRIMERELLIDAE Davidson and King, 1872

Genus *Gasconsia* Northrop, 1939

Type species. *Gasconsia schucherti* Northrop, 1939, p. 161, pl. 12, figs 6–8; pl. 13, fig. 7; Hanken and Harper (1985), p. 246, text-figs 4B–G; the Gascons and Bouleaux Fms (Ludlow), Gaspé Peninsula, Quebec, Canada.

Diagnosis. Large to very large (up to 120 mm in width), semi-elliptical, gently to strongly biconvex shell; cardinal margin wide and cardinal extremities round. Ornament of concentric growth lines and some stronger ribs. Ventral valve with muscle field platform. Dorsal interiors with rounded dorsal sockets, pair of central muscle scars, and two larger anterior muscle scars with well-developed anterior-lateral directed ridges.

Species assigned and their occurrences (Fig. 3):

- Gasconsia worsleyi* Hanken and Harper 1985, p. 246, figs 2A, B, 3A–H, 4A; the Bønsnes Fm (upper Katian, Upper Ordovician), Ringerike district, Oslo region, southern Norway.
- Gasconsia* in Sweden is yet undescribed (unpublished data by courtesy of Lars Holmer are used here).

3. *Gasconsia gigantea* sp. nov. (this paper).
4. *Gasconsia* cf. *worsleyi* Popov et al., 1997, p. 591, fig. 4.29; upper part of the Oroj Fm (*Climacograptus bicornis* Biozone, upper Katian, Upper Ordovician), western side of the Shiderti River, southwest of Lake Eskeldykol, central Kazakhstan.
5. The species name *Gasconsia transversa*, applied for the brachiopods from the Silurian Much Wenlock Limestone (Silurian), England, was considered as a *nomen nudum* in a note by Davidson (1853; see Cocks 1978, p. 21), but was recognized as a formal specific name by Mergl (1989). As pointed out by Holmer et al. (2014), *Gasconsia transversus* described by Watkins (2002) from the late Silurian (Ludlow) of the Welsh Borderland seemingly lacks all evidence of an umbonal perforation and colleplax; most likely it is not conspecific with *Trifissura transversa*. Thus, quotation marks are used for this species (see also the next below).
6. *Gasconsia transversa* (Salter); Mergl 1989, pl. 2, fig. 4; pl. 3, figs 1, 2; pl. 4, fig. 1; Kopanina Fm (Ludlow, Late Silurian), Bohemia, the Czech Republic.
7. *Gasconsia schucherti* Northrop, 1939, the type species of *Gasconsia*; see above.
8. *Gasconsia* sp.; Wenlock, Delphi, Indiana, USA (see Popov and Holmer 2000).

No fossil record of *Gasconsia* has been documented in the Hirnantian (latest Ordovician) and early Llandovery (Silurian). These brachiopods reappear in the USA (Laurentia) and England (Avalonia) in the Wenlock (Silurian) (Popov and Holmer 2000; Mergl 1989), and then in the Ludlow

in Quebec, Canada (Laurentia) and Bohemia, the Czech Republic. The youngest Bohemian specimens occur in the Ludlow (Northrop 1939; Mergl 1989). It is assumed that *Gasconsia* may have become extinct in the interval of the Mid-Ludfordian extinction event (Kaljo and Martma 2006).

Gasconsia gigantea sp. nov.

Figs 4–6

Derivation of the name. In Greek “γίγαντιαία” (*giganteia*), *gigantea*. The Estonian shells may grow up to nearly 120 mm in width and thus represent the largest known shell width of Ordovician brachiopods in the world.

Holotype. Mold of dorsal valve GIT 759-293 (Fig. 5A1, A2), Vohilaid Island, NW Estonia, Adila Fm, Pirgu RS, uppermost Katian.

Diagnosis. Very large brachiopod with shell width up to 120 mm; outline transversely oval. Dorsal valve moderately convex, with thickness about half of valve length. Wedged depression marks a short median myophragm reaching up to middle of valve; laterally of that occur pair of large oval wing-shaped traces of anterior muscles and posteriorly pair of small, elongated teardrops central muscle scars (Figs 4 and 5A1, A2).

Ventral pseudointerarea (Fig. 5B1, B2) about 0.33 as high as long, with apical angle of about 120°. Radial ornament of large ribs (wave-length of about 10 mm) and up to 9 fine ribs between them. Low, fine, tightly spaced rugae may occur randomly.

Description. Large dorsi-biconvex shell up to 120 mm wide, with transversely oval to semicircular outline, about half as

Chronostratigraphy			Baltica			Chingiz	Avalonia	Bohemia	Laurentia		
System	Series	Stage	Norway	Sweden	Estonia	Kazakhstan	England	Czechia	Canada	USA	
			Hanken & Harper, 1985	Popov & Holmer, 2000	This paper	Popov et al., 1997	Watkins, 2002	Mergl, 1989	Northrop, 1939	Popov & Holmer, 2000	
SILURIAN	Pridoli										
		Ludlow	Ludfordian								
	Gorstian						<i>Gasconsia "transversa"</i> 5	<i>Gasconsia transversa</i> 6	<i>Gasconsia schucherti</i> 7	<i>Gasconsia</i> sp. 8	
	Wenlock	Homerian									
		Sheinwoodian									
	Llandovery	Telychian	No fossil record of <i>Gasconsia</i>								
Aeronian											
Rhuddanian											
ORDOVICIAN	Upper Ordovician	Hirnantian	Late Ordovician Mass Extinction								
		Katian	1 <i>Gasconsia worsleyi</i>	2 <i>Gasconsia</i> sp.	3 <i>Gasconsia gigantea</i> sp. nov.	4 <i>Gasconsia</i> cf. <i>worsleyi</i>					

Fig. 3. Stratigraphic occurrences (polygons) of eight taxa (1–8) of *Gasconsia* in five regions from Baltica to Laurentia in relation of the global stratigraphic units according to the authors referred. The blue area marks the stratigraphic interval where the brachiopods of *Gasconsia* are missing. The grey strip below the blue area marks the interval of the first phase of the Late Ordovician Mass Extinction (LOME).

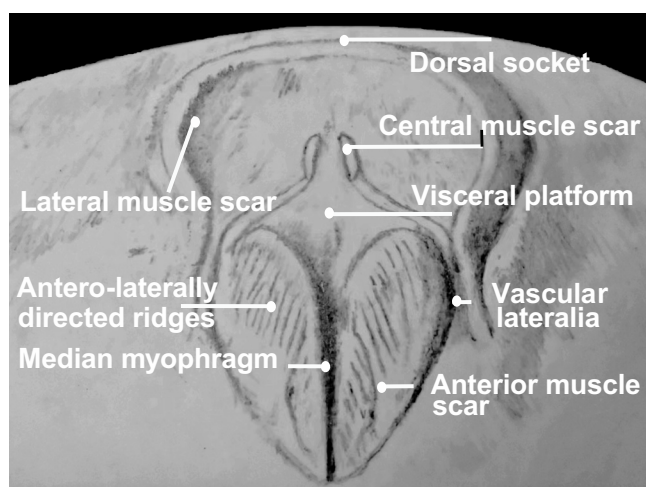


Fig. 4. Structures of the dorsal interior of *Gasconsia gigantea* sp. nov.

long as wide; length/width ratio 0.55–0.60; maximum width of dorsal valve in posterior part, at about 0.2 of valve length from posterior edge; highest convexity at about midlength of dorsal valve, thickness about half of valve length. Cardinal extremities rounded, hinge line straight, shorter than shell width, anterior commissure rectimarginate. Ventral valve with apical angle of about 120°. Ornamentation with variable sized radial costellae and rugae-like concentric growth lines; distance between stronger ribs is about 10 mm, with up to 9 finer costellae between them; growth lines partially as low densely spaced rugae.

Dorsal valve (Fig. 4, Fig. 5A1, A2, Fig. 6A1, A3, B1, B2) evenly convex, with slightly flattened lateral parts; thickness about half of valve length; highest point at mid-valve; length/width ratio 0.55–0.60. On lateral profile, posterior curvature steeper than that of anterior part (Fig. 6A2). Cardinal angles rounded. Curved dorsal socket delineating posteriorly; oval platform (Fig. 5A1, A2) about 30 mm in length and 24 mm in width, forming 0.25 of valve length and 0.16 of valve width. Dorsal bipartite platform extends to midline; two oblique nodes about 5 mm long in the middle of platform (Fig. 6B1, B2) mark deeply impressed central muscle scars. Anterior muscle scars (Fig. 5A1, A2) represented as oval wing-like structures, open backwards, 15 mm in length and width, extending for about 0.2 and 0.3 of valve length and width. Wedged septa reaching up to mid-valve separates anterior scars. Scars covered by sub-radial pattern.

Ventral valve (Fig. 5B1b, B2) partly preserved behind dorsal valve GIT 759-292a, from where it has shifted about half of width to right side. Pseudointerarea about 0.3 as long as wide and about 0.4 of valve length, with flat surface; apex of pseudointerarea (apical angle) forming an angle of about 120°; apical homeodeltidium narrow, slightly shorter than pseudointerarea length, forming an angle of about 45° on top.

Comparison. The new species *Gasconsia gigantea* is most similar to the Norwegian species *G. worsleyi* Hanken and Harper, 1985. However, it differs in having a transversely oval or subsemicircular outline, with the length/width ratio

of the dorsal valve about 0.8 instead of 0.6 in the Norwegian species; the dorsal valve of the Estonian species is half as high as long, whereas that of *G. worsleyi* is one quarter as high as long. The low ventral pseudointerarea in *G. worsleyi* is ca 0.1 as long as wide but 0.3 in the new species.

Estonian specimens of *Gasconsia*. Molds of dorsal valves, Vohilaid Island, locality 8 by Stein (1937), W Estonia (coordinates: 58.919734° N, 23.038809° E), Adila Fm, Pirgu–Porkuni transitional beds.

GIT 759-291 (Fig. 6A1–A3). **Outline.** Transversely oval, with length 61 mm, width over 100 mm, length/width ratio 0.60, thickness about 30 mm, thickness/length ratio 0.30. Highest convexity of valve at mid-valve; on lateral profile, curvature steeper in posterior than in anterior half. Hinge line shorter than maximum valve width; cardinal angles rounded.

Ornamentation. Some traces of ribbing and plication observed on surface of mold. A few concentric growth lines present close to margins. **Interior features.** Muscle scars occur laterally from trigonal myophragm, represented on mold as wedge-like depression. Two oval, open, backwards wing-like structures represent anterior muscle scars, occupying middle part of valve; reach anteriorly about 0.4 of valve length and form about 0.2 of valve width. Scars covered by sub-radial ridge-like pattern surrounded laterally by thickened border.

GIT 759-292a (Fig. 5B1a). Mold of an incomplete sub-circular convex dorsal valve, with length about 41 mm, width about 70 mm, length/width ratio 0.58. Hinge line shorter than maximum width of valve. Cardinal angles rounded.

GIT 759-292b (Fig. 5B1b, B2). Part of ventral valve preserved behind dorsal valve GIT 759-292a. Single specimen with ventral pseudointerarea. Ventral valve pseudointerarea with apical angle of 120°, pseudodeltidium with angle of 45°.

GIT 759-293 (Fig. 5A1, A2). **Holotype.** **Outline.** Transversely oval dorsal valve with length 56 mm, width about 96 mm, length/width ratio about 0.58. Cardinal angles rounded; on lateral profile, curvature steeper in posterior than in anterior part. **Radial ornament** with intercalation of stronger and finer ribs. **Interior features.** Oval wing-like muscle scars separated by narrow wedge-like depression, marking median myophragm. Poorly preserved sub-radial pattern on muscle scars similar to that on specimen GIT 759-291.

GIT 759-294 (Fig. 6B1, B2). Dorsal valve, poorly preserved convex mold with length 66 mm, width 116 mm, length/width ratio about 0.57, thickness about 30 mm, thickness/length ratio about 0.45. Mold bears groove, marking myophragm in middle part of valve, reaching up to middle of valve. Muscle scars poorly impressed. Two small subparallel knobs marking central muscle scars occur posteriorly of septum close to hinge line. Ornament likely consists of a few ribs.

GIT 759-298 (Fig. 6C). Poorly preserved mold of dorsal valve. Surface damaged by boring organisms and erosion. Largest specimen in the collection, with transversely oval

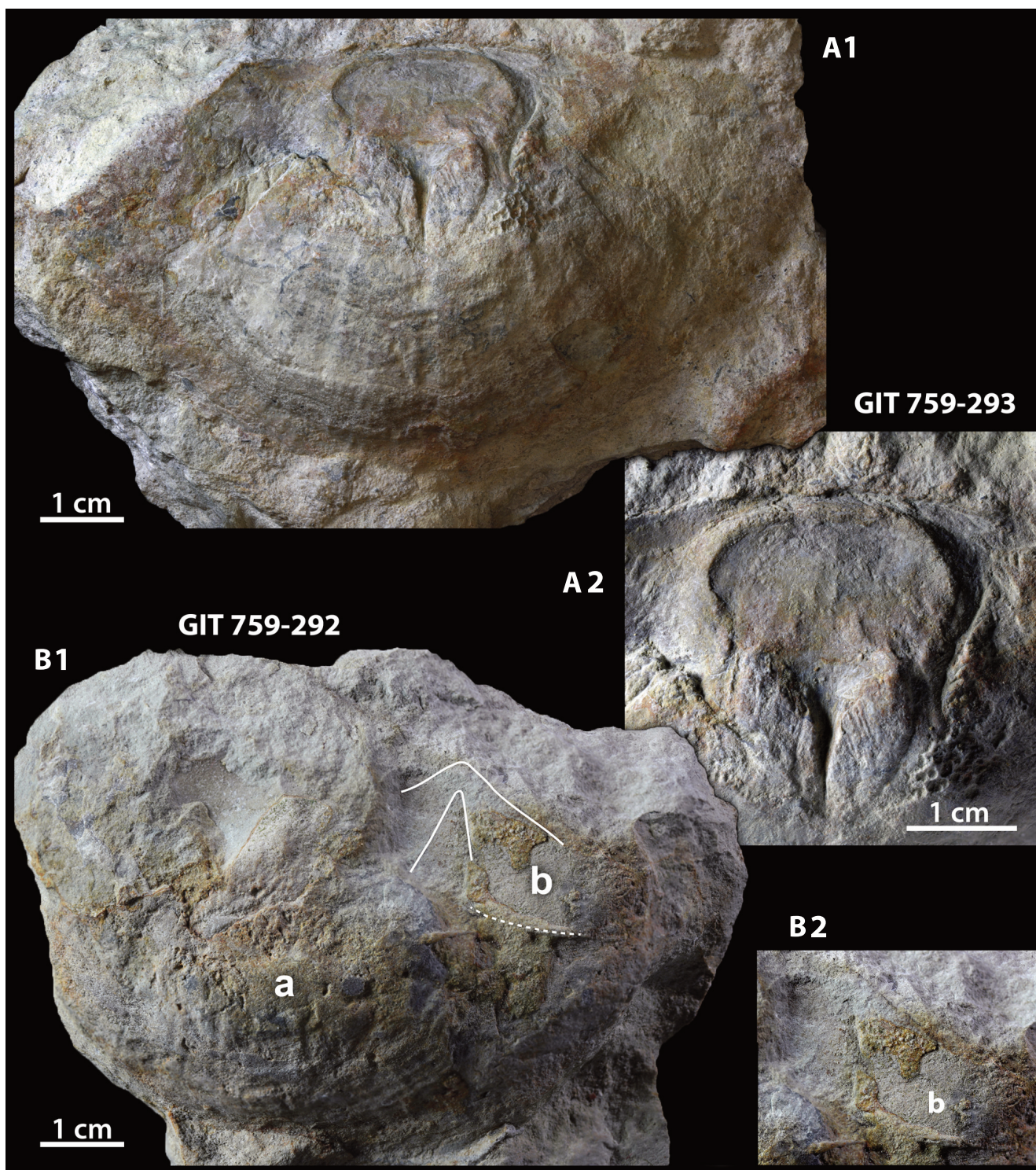


Fig. 5. *Gasconsia gigantea* sp. nov., eastern part of Vohilaid, Adila Fm (upper Katian, i.e., Pirgu RS). A1–A2 – holotype, GIT 759-293, mold of dorsal valve and interior structures. B1–B2 – GIT 759-192, incompletely preserved molds of dorsal (a) and ventral (b) valves; solid and dashed white lines on B1b mark the outline of ventral pseudointerarea, which is also shown in natural view in B2b.

outline, valve width over 120 mm, length 68 mm, length/width ratio about 0.6, thickness about 38 mm, length/ thickness ratio about 0.6; hinge line shorter than valve width.

Distribution of *Gasconsia* in Estonia

In the late Katian, *Gasconsia* has been known to occur in two regions: Baltica (Norway, Sweden, and Estonia) (Hanken and Harper 1985; Popov and Holmer 2000; this paper) and central Kazakhstan (Popov et al. 1997; Fig. 3).

In Estonia, the new species *Gasconsia gigantea* occurs in the upper Katian, as does *Gasconsia* in southern Norway (Hanken and Harper 1985). *Gasconsia gigantea* is found in the Adila Fm of the Pirgu RS, which comprises two chitinozoan zones: *Conochitina rugata* below and *Belonechitina gamachiana* above (Harris et al. 2004; Kaljo et al. 2017; Fig. 2). Exceptionally, the rock sample containing a specimen of *Gasconsia* (GIT 759-292) comprises the zonal chitinozoan *Spinachitina taugourdeau* (identified by J. Nölvak) of the Porkuni RS. This may indicate a high stratigraphic position

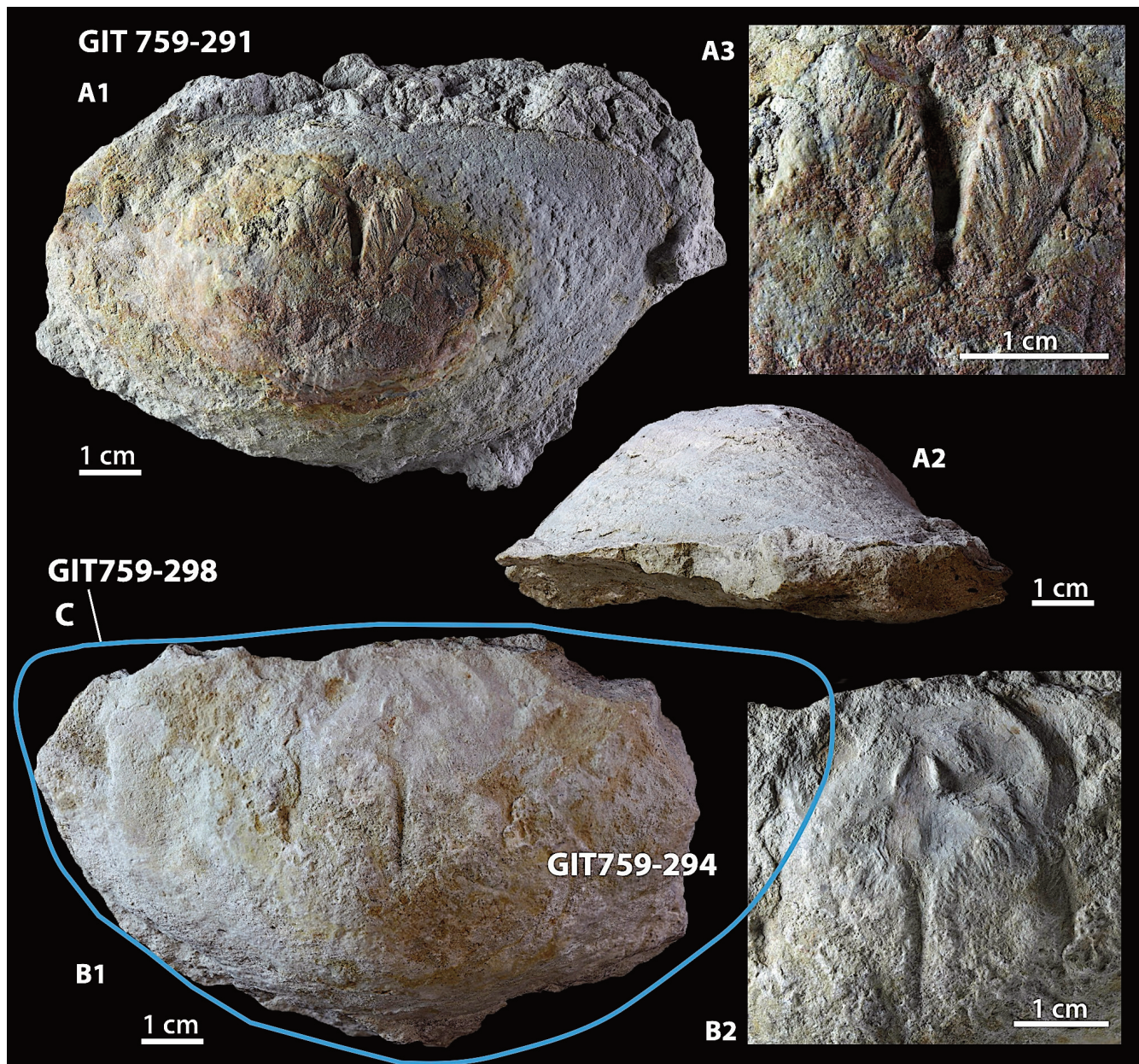


Fig. 6. *Gasconsia gigantea* sp. nov., eastern part of Vohilaid, Adila Fm (upper Katian, i.e., Pirgu RS). A1–A3 – GIT 759-291, mold of dorsal valve, lateral view (A2) and a view of anterior muscle scars (A3). B1–B2 – GIT 759-294, mold of dorsal valve and view on interior structures. C – blue line marks the outline of the poorly preserved dorsal valve GIT 759-298.

and the occurrence of transitional beds between the Pirgu and Porkuni stages, as suggested by Stein (1937). The occurrence of Porkuni zonal species *S. taugourdeau* together with the Pirguan species *Belonechitina gamachiana* has been noted in some other sections (Äiamaa, Hints et al. 2005; Kaugatuma, Brenchley et al. 2003, Kaljo et al. 2008). In addition, the unusual mixed Pirguan ostracode fauna (*Steusloffina cuneata*, *Daleiella rotundata*, and others), together with species commonly found in the Porkuni RS (*Apatochilina falacata* and *Gryphiswaldensia plicata*; Meidla 1996), has also been identified in the uppermost part of the Adila Fm, distinguished as the Kabala Member (Mb; in Kaugatuma, mentioned as F1c-F2kb, Põhjaka-Saare H-171, Virtsu-360 sections; Meidla 1996). The Kabala Mb has yielded the pentameride brachiopod *Holorhynchus*, known in Estonia only in a few sections on the Hiiumaa Island (Lassi K-39, Hints 1993; Tamme K-38, Brenchley et al. 2003; Männamaa F-367, Nõlvak

2008). *Holorhynchus* is a widely distributed brachiopod in the eastern and southern East Baltic (Brenchley et al. 1997; Paškevičius 1997). The occurrences of *Holorhynchus* and *Gasconsia* are valuable for understanding the latest Katian faunas and environments.

In Lithuania and Latvia, the *Holorhynchus giganteus* community in the Taučionys Fm characterizes the lagoonal facies of Benthic Assemblage 1 (Paškevičius 1997, 2000). The trimerellide brachiopod *Gasconsia*, based on the associated gastropod *Maclurites*, could also belong to shallow-water Benthic Assemblages 1–2 (Ebbestad et al. 2013).

In Norway, *Holorhynchus* and *Gasconsia* occur in different lithologies of the Oslo Region: the former in the Herøya Fm of the Eiker-Sandsvær district and the latter in the Bønnes Fm of the Ringerike district (Owen et al. 1990). Both *Gasconsia* and *Holorhynchus* are found in environments ranging from peritidal flats to the inner shallow subtidal facies, which have

patchy preservation in the geological record. The age of these brachiopods could be somewhat different, which needs to be clarified by future studies of time-related microfossils, especially those from the Kabala Fm with mixed faunas.

Gasconsia as a Lazarus taxon and gigantic brachiopod

In macroevolution, Lazarus taxa are assumed to be special taxa that disappear from the stratigraphic record for some time, particularly during a mass extinction, and re-appear after the event without any significant morphological changes. Lazarus taxa have been treated as extreme examples of a declining group (Rong et al. 2006). The trimerellide genus *Gasconsia* can be considered one of these taxa (Watkins 2002). In the stratigraphic range, it originates in the late Katian, just before the Late Ordovician Mass Extinction (LOME; Fig. 6). The order Trimerellida is recognized as a group of typical Lazarus taxa through the latest Ordovician and early Silurian (Chen et al. 2023). The disappearance of trimerellides, as well as the rarity of pentamerides and atrypides in the early–middle Hirnantian, not only in terms of richness and abundance but also in biodiversity, show the nature and effects of the LOME (Sheehan 2001; Rong et al. 2020). The dramatic temperature decrease (Finnegan et al. 2011) in tropical oceans during the LOME in the early–middle Hirnantian caused the disappearance of trimerellides and the establishment of the cold/cool water *Hirnantia* Fauna.

However, little is known about the reasons why the fossil record of *Gasconsia* has not been documented (Fig. 6) in the Llandovery when climate warmed up. It should be emphasized that the Lazarus taxa were usually represented by extremely rare species (Watkins 2002), and their population size drastically decreased during the crisis (Rong et al. 2006).

Another characteristic feature of *Gasconsia* is gigantism – described shells are up to 120 mm wide. The gigantism of ancient organisms in the geological record is an interesting topic (Vermeij 2016). Even a size of 10 mm can be considered gigantic, such as in the scolecodont of Devonian polychaetes (Eriksson et al. 2017); however, some Middle Ordovician endoceratid cephalopods reach up to 8–9 m in length (Vermeij 2016). Studies on gigantism in the geological record (e.g., Verberk and Adkinson 2013; Vermeij 2016) have highlighted the importance of this phenomenon in analyzing different ecosystem characteristics: temperature, planktic productivity, food quantity, and water chemistry, with special attention paid to the availability of oxygen.

From both global and regional perspectives, early Paleozoic brachiopods, particularly those from the Cambrian and Ordovician periods, are of medium and small sizes, based on data from China (Rong et al. 2017). Shells larger than 100 mm in width or length are rare. Large Ordovician brachiopods, such as *Belubulla* Percival, 1995 (*Zhuzhaia*, Xu and Li 2002), recorded in China, have a shell width of up to about 75 mm. However, the biggest known shells of Silurian stricklandiid brachiopods, *Sinokulumbella*, have a maximum shell width of about 100 mm (Rong et al. 2004). In the

Baltic Ordovician, the largest brachiopod reaching 143 mm in width (Strophomenina) was recorded in the Porkuni RS (Rõõmusoks 2004) and supposedly belongs to the subfamily Strophomeninae. The Silurian trimerellide brachiopods of the genus *Keteiodoros* from Australia are of comparable size (width >145 mm; Strusz et al. 1998). Late Katian *Gasconsia* from Baltica and Kazakhstan might be linked to global climatic warming and increased nutrient supply (Brezinski and Kollar 2012). The temporal distribution of *Gasconsia* implies that its disappearance was caused by a dramatic temperature drop during the first phase of the LOME.

Conclusions

1. Based on distinctive characteristics, such as shell size, convexity, dorsal interiors, and a relatively high ventral pseudointerarea, the Ordovician trimerellides from Estonia are identified as a new species, *Gasconsia gigantea*. The new taxon is most similar to the Norwegian species *Gasconsia worsleyi*. Both occur in the upper Katian strata, just before the LOME.
2. *Gasconsia gigantea* sp. nov. occurs in biotrital limestones, where it is associated with the gastropod *Maclurites neritoides*. In Sweden, the latter is considered a characteristic fossil of Benthic Assemblages 1–2.
3. The strata containing *G. gigantea* could be younger than those containing *Holorhynchus* in the Kabala Mb of the Adila Fm or more or less contemporaneous.
4. The trimerellide brachiopod *Gasconsia* represents a Lazarus taxon, whose descendants reappear in the Silurian. With a shell width of up to 120 mm, *Gasconsia* represents the largest Craniata and one of the largest brachiopods in Estonia, somewhat smaller than the large strophomenids in the Porkuni RS (lowermost Hirnantian).

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Trimerelliidse brahhiopoodi *Gasconsia* esmaleiud Eesti ordoviitsiumist

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Artiklis kirjeldatakse seltsi Trimerellida (klass Craniata) brahhiopoodide esmaleide, mis kuuluvad perekonda *Gasconsia* ja esindavad uut liiki *Gasconsia gigantea*. Need Vohilau saare paljandist leitud brahhiopoodid tor-kavad silma erakordselt suurte mõõtmetega (koja laius kuni 120 mm), mis ületavad valdava osa ordoviitsiumi brahhiopoodide mõõtmeid. *G. gigantea* esineb ülemordoviitsiumi Pirgu lademe Adila kihistu kõige ülemises osas, mis mõningate paleontoloogiliste andmete põhjal võiks esindada ka üleminekulisi kihte ordoviitsiumi kõige ülemisse Porkuni lademesse. Kirjeldatud liik on sarnane Norras kirjeldatud liigiga *G. worsleyi*, mis esineb seal peaaegu samal stratigraafilisel tasemel kui Eesti liik. Võimalik, et *G. gigantea* nagu ka Pirgu lademe ülemise osa brahhiopoodid perekonnast *Holorhynchus* esindavad Pirgu lademe noorimat madalveelisele keskkonnale iseloomulikku kooslust. Samast Vohilau paljandist on pärit mitu gastropood *Maclurites neritoides* leidu, mida Rootsi teadlased peavad rannalähedase keskkonna indikaatoriks.

Perekond *Gasconsia* evolutsiooni üks eripära on esindajate puudumine alates ordoviitsiumi lõpus toimunud massilise väljasuremise perioodist jäätumisega kaasnenud temperatuurilanguse ja keskkonnatingimuste muutuste tagajärjel. *Gasconsia* ilmus uuesti välja peale pikka perioodi siluri teisel poolel. Sellise levikuga taksoneid, mis taastilmuvad peale lühemat või pikemat perioodi, nimetatakse Lazaruse taksoneiteks.

Trimerelliidsete brahhiopoodide hulgas on mitmeid taksoneid, mis on mõõtmete poolest erakordselt suured. Iidsete eluvormide gigantism on oluline ka keskkonna mõjutegurite (temperatuur, vee keemiline koostis, hapnikusaldus jm) hindamisel.