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Pentameroid brachiopod *Karlsorus* new genus from the upper Wenlock (Silurian) Slite Beds, Gotland, Sweden

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Abstract.—*Karlsorus* n. gen. is proposed in this study as a large, smooth-shelled pentameride brachiopod of the family Pentameridae, based on *Pentamerus gothlandicus* Lebedev, 1892, from the Wenlock (Silurian) Slite beds of Gotland, Sweden. This species is transferred from *Pentamerus* to the new genus because of the combination of a *Pentamerus*-like shell shape and the development of a brachiophorium through fusion of the outer hinge plates in the middle portion, like a dorso-ventrally inversed cruralium. The first appearance of brachiophorium in pentamerids is in the late Wenlock, known also in *Brooksina*, *Pentamerifera*, and other related pentamerid genera, marking a significant stage in morphological transformation of dorsal internal structures, as part of the Silurian pentameride diversification in both level-bottom and reefal depositional environments.

Introduction

Pentamerus Sowerby, 1813 is one of the most widely reported early Silurian pentameride brachiopods worldwide, often regarded as a good paleobiogeographic indicator for relatively cosmopolitan marine benthic shelly faunas in the early Silurian, in contrast to the strong endemism of Late Ordovician shelly benthos. True *Pentamerus*, however, occurs predominantly in middle–upper Llandovery strata, especially in Laurentia, Baltica, Avalonia, Siberia, and Kazakhstan. In South China, *Pentamerus* occurs only rarely in Aeronian rocks, whereas the common forms previously reported as *Pentamerus* have been assigned to a different genus, *Sulcipentamerus* Zeng, 1987 (see Rong et al., 2007). Thus, the occurrence of '*Pentamerus*' *gothlandicus* Lebedev, 1892 in the upper Wenlock Slite beds of Gotland (Bassett and Cocks, 1974; Bassett, 1977) has been one of the well-known exceptions outside the common stratigraphic range of the genus, and on Gotland this species forms a widely distributed marker bed known as the *Pentamerus gothlandicus* layer (e.g., Hede, 1927; Calner et al., 2004; Bassett, 2005)

Lebedev (1892) initially proposed the species *Pentamerus gothlandicus* based only on ventral valves from Gotland (see Bassett, 1977). Among the large number of genera of the family Pentameridae, the ventral valve usually has a rather conservative morphology, with a consistently developed median septum and spondylium. As a result, the differentiation of pentamerid genera often relies on the differences in internal structures of the dorsal valve, such as the various configurations of hinge plates and crura, skeletal structures that supported lophophores for suspension filter feeding and respiration. The lack of information from the original description of *P. gothlandicus*, in addition to its unusual stratigraphic position, cast some doubt on the affinity of this species to *Pentamerus*. In terms of shell shape and outline, relative convexity of the ventral and dorsal valves, and the configuration of ventral and dorsal umbo and beak, *P. gothlandicus* is nearly identical to the type species *Pentamerus oblongus* Sowerby, 1839, although the Gotland species generally has considerably larger shells than other known species of the genus on average (Fig. 1.1–1.5). In subsequent studies, Bassett and Cocks (1974) and Bassett (1977) provided two important clarifications on this species: first, *P. gothlandicus* is confined to the upper Wenlock Slite beds or its coeval strata on Gotland; second, the semi-transparent shell reveals two discrete inner hinge plates (i.e., outer brachial plates in old usage) at their junctions with the dorsal valve floor. The latter point, in particular, was used by Bassett (1977) as a convincing basis for confirming the identity of *P. gothlandicus* as *Pentamerus*.

After several recent revisions of *Pentamerus* (for a summary, see Boucot and Johnson, 1979; Sapelnikov, 1985; Jin and Copper, 2000), most species now seem to occur in strata from mid-Aeronian to Telychian; only a small number of species are found in the Wenlock–Ludlow, notably in the Ural Mountains and in the Racine Dolomite of North America. In many cases, the preservation of purported Wenlock–Ludlow species of *Pentamerus* is rather poor, with shells commonly showing distortion, disarticulation, or breakage. This is true also for *P. gothlandicus*, which occurs predominantly as disarticulated or broken valves in skeletal packstone or grainstone facies, although conjoined or even complete shells can be found. Such preservation bias has undoubtedly contributed to the difficulty of taxonomic identifications of these pentamerids. In this study, all the relatively well-preserved shells available from museum collections, supplemented by newly collected specimens, are assembled in an attempt to elucidate the morphology and taxonomic affinity of the Gotland species.

Materials and methods

In a recent survey of available collections at the Gotland Museum (Visby), the Swedish Museum of Natural History (Stockholm), and the Natural History Museum (London), a fairly large number of specimens of *Pentamerus gothlandicus* were examined in order to clarify the phylogeny and evolutionary patterns of *Pentamerus* because this Silurian hallmark taxon can provide important information on the faunal evolution and paleobiogeography of the period. Examination of museum collections, as well as new collections from Tjeldersholm, one of the *P. gothlandicus* localities on Gotland, through naturally exposed dorsal interiors and transversely cut sections, immediately reveals that the dorsal internal structures of *P. gothlandicus* are distinctly different from those of the typical *Pentamerus*. Rather, the ventral sides of the outer hinge plates show various degrees of fusion to form a ventrally projecting plate, resembling a medially crested arch, usually around the mid-length of the hinge plates (Fig. 1.7–1.11). The inner hinge plates and the dorsal portions of the outer hinge plates, however, are clearly discrete, as is typical of *Pentamerus*. Such a tent-like structure, called a "closed brachiophorium" by Sapelnikov (1972), has been reported in several pentamerid genera of Wenlock–Ludlow age, such as *Pentamerifera* Khodalivich, 1939; *Capelliniella* Strand, 1928; and *Brooksina* Kirk, 1922, which are most common in the Ural Mountains, Alaska, and western North America (e.g., Kirk, 1922, 1925; Sapelnikov, 1972, 1985; Johnson et al., 1976; Boucot and Johnson, 1979; Rong and Zhang, 1988; Sheehan and Harris, 1997). Thus, it appears that this brachial structure was exclusively a post-Llandovery evolutionary trend among some genera of the Pentameroidea, since such a structure is unknown in Llandovery or older members of the superfamily. Sections of other well-preserved dorsal interiors of the Gotland species have also confirmed the presence of a brachiophorium with a fused crest, thus warranting the establishment of a new genus, to be called *Karlsorus* n. gen. in this study. The main purpose of this study, therefore, is to clarify the morphology of *Karlsorus gothlandicus* (n. comb.) and to discuss the implications of its revised taxonomy for pentamerid evolution and paleobiostratigraphy in the Silurian.

A recent summary and update of the geology of Gotland and the litho- and biostratigraphy of the Slite beds can be found in Calner et al. (2004). Details of the geology of the *Pentamerus gothlandicus*-bearing localities (Tjeldersholm 1, Stora and Lilla Karlsö, Valle 1, and Valle 2) can be found in Hede (1927), Laufeld (1974), Calner et al. (2004), and Bassett (2005). The *Karlsorus*-bearing upper Slite beds lie in the upper Wenlock *Cyrtograptus lundgreni* Biozone, where a minor extinction event has been recognized, but it affected mainly planktonic fossil groups (e.g., graptolites; see Jaeger, 1991; Lenz et al., 2006) rather than the shelly benthos (e.g., brachiopods; Copper, 2004).

Repositories and institutional abbreviations.—Specimens examined and cited in this study, including figured specimens, are from the following institutions: Gotland Museum (LMG), Visby, Gotland, Sweden; Swedish Museum of Natural History (Riksmuseum, Br), Stockholm, Sweden; Natural History Museum (B), London, UK; Paleontological Institute (VSEGEI), St. Petersburg, Russia.

Evolutionary and biostratigraphic significance

Historically, *Pentamerus* has been a taxonomic dump bag for a variety of smooth-shelled pentameride genera. This has greatly diminished the biostratigraphic utility of this globally widespread taxon and obscured its evolutionary trend during the early Silurian, although true *Pentamerus* has been thought largely as a middle Aeronian–late Llandovery genus.

The first appearance of *Pentamerus* during the middle Aeronian has been widely recorded in Laurentia, Baltica, Avalonia, Siberia, and some of their adjacent small terranes (see summaries of Boucot and Johnson, 1979; Sapelnikov, 1985; Jin and Copper, 2000). The early forms of *Pentamerus* developed a nearly equibiconvex shell, were most abundant from high tropical to subtropical regions, and adapted to a vertical life position on a muddy, level-bottom substrate in tightly packed clusters (Jin, 2008). By the late Aeronian, *Pentamerus* diversified into the paleoequatorial regions to give rise to *Sulcipentamerus*, a strongly ventribiconvex shell with an arched ventral valve and a flattened and reduced dorsal valve. This has been interpreted as an adaption for a recumbent life position in the generally low-energy paleoequatorial environment devoid of frequent severe storms, with the large and deep ventral valve partly embedded in the sediments, and the reduced dorsal valve behaving like a mobile lid (Rong et al., 2007; Gushulak et al., 2016).

By the middle Telychian, *Pentamerus* went through a major speciation event and gave rise to *Pentameroides* Schuchert and Cooper, 1931, which became a common pentameroid in Laurentia and Baltica during the late Telychian (Johnson, 1979; Baarli and Johnson, 1988; Jin and Copper, 2000). This cladogenetic event was marked by the formation of a cruralium, through the convergence of inner hinge plates onto a low median septum in the dorsal valve. The *Pentamerus*-*Pentameroides* transition has been regarded as a reliable biostratigraphic marker for a middle Telychian age for Laurentia and Baltica (Baarli and Johnson, 1988).

The post-Llandovery evolution of *Pentamerus* has been confusing because the taxonomic validity of many smooth-shelled pentamerids has been a matter of debate. In North America, some large-shelled forms of late Telychian–Wenlock age, such as *Apopentamerus* and *Pentamerus* (*Supertrilobus*) proposed by Boucot and Johnson (1979), have not been studied in detail regarding their internal structures. *Apopentamerus*, for example, was regarded by Sapelnikov (1985) as a junior synonym of *Harpidium*. The relationship between the smooth-shelled *Harpidium* Kirk, 1925 and *Pentamerus* also remains to be investigated. The strongly ventribiconvex shells of *Harpidium*, ranging from late Llandovery to Ludlow, may be similar to the evolution of *Sulcipentamerus* that adapted to low-energy level bottom or sheltered reefal depositional environments (Gushulak et al., 2016).

Pentamerus and *Karlsorus* n. gen., as well as many other genera of the family Pentameridae showed various diversifications in shell morphology during the Wenlock and Ludlow:

(1) Drastic increase in shell size, sometimes with highly arched ventral umbo to give the ventral valve a somewhat conical appearance (e.g., *Harpidium*; see Boucot et al., 2002). Large shells of *Rhipidium* Schuchert and Cooper, 1931 from Gotland may exceed 135 mm in length (e.g., specimen B5578 in the NHM collection), and large forms of *Karlsorus* n. gen. are nearly 130 mm long.
(2) Inversed biconvexity, with a flattened ventral valve and reduced ventral beak, in contrast to a strongly convex dorsal valve with its umbo and beak arched over the ventral posterior, as is typical of *Brooksina* and *Capelliniella*, which are common in North America and the Ural Mountains.
(3) Increased length of the spondylium and hinge plates, sometimes extending very close to the anterior margin (e.g., *Brooksina*; *Harpidium*; *Kirkidium* Amsden, Boucot, and Johnson, 1967; and *Pentamerifera*). These extravagant internal structures are rarely seen in the pentamerids of Llandovery age.
(4) Development of the brachiophorium, as discussed earlier in this study, can be viewed as a dorso-ventrally inversed cruralium, which seems to have first appeared in late Wenlock time, corresponding to the *Cyrtograptus lundgreni* graptolite Biozone.

The great range of morphological diversifications of large-shelled Pentameridae is a reflection of the success of this family in their ecological expansion in the level-bottom regime, as well as their invasion into the reefal environments during the Silurian. Pentamerid shells with a reversed biconvexity, a flattened ventral valve, and an orthocline ventral beak/palintrope had the delthyrium well exposed, and thus may have retained a functional pedicle to attach to a variety of hard surfaces (e.g., walls of large cavities or other sheltered areas) in reefal environments.

Systematic paleontology

Order Pentamerida Schuchert and Cooper, 1931
Suborder Pentameridina Schuchert and Cooper, 1931
Superfamily Pentameroidea M'Coy, 1844
Family Pentameridae M'Coy, 1844
Genus *Karlsorus* new genus

Type species.—*Pentamerus gothlandicus* Lebedev, 1892, upper Slite beds, upper Wenlock, *Cyrtograptus lundgreni* Biozone, Gotland, Sweden (Bassett, 1977; Calner et al., 2004).

Species included.—Type species only. The species has been reported from Wenlock strata of Gotland (Slite beds; Bassett and Cocks, 1974), England (Much Wenlock Limestone; Bassett, 1977), and Podolia (Kitaigorod horizon; Nikiforova, 1978).

Diagnosis.—Shell very large, elongate, nearly equibiconvex with moderate convexity; ventral valve strongly trilobate, longer than dorsal valve, with prominent umbo and beak arched over dorsal umbo; trilobation of dorsal valve inconspicuous. Spondylium and ventral median septum same as for *Pentamerus*. Inner hinge plates low, subparallel to each other; outer hinge plates inclined ventromedially, discrete at posterior and anterior parts, commonly fused into single plate in middle part to form brachiophorium. Crura attached to medial sides of junctions between inner and outer hinge plates.

Etymology.—Named after the island Stora and Lilla Karlsö, Gotland, where the type species is most abundant and best preserved.

Remarks.—In external shell morphology, the new genus is most similar to *Pentamerus* in its subpentagonal shell outline and subequibiconvexity (Fig. 1.1–1.5), with the ventral valve slightly deeper than the dorsal valve, especially in the posterior half, and the strongly convex ventral umbo and a beak arched over the dorsal umbo. Internally, *Karlsorus* n. gen. resembles *Pentameridfera* Khodalevich, 1939 (see Sapelnikov, 1972) in having a tent-like brachiophorium formed by the inner and outer hinge plates (Fig. 1.7, 1.10, 1.11). *Pentamerifera*, from Ludlow strata of the eastern slope of the Ural Mountains, differs in having an extremely long spondylium and hinge plates that extend for more than three-fourths of the total shell length, whereas in *Karlsorus* n. gen. those internal structures do not exceed one half of the shell length (Figs. 1.1, 1.2, 2.8). A few other predominantly Ludlow pentameroids, such as *Brooksina* Kirk, 1922 from Alaska, Nevada, and the Ural Mountains, may also have developed a brachiophorium-like structure inconsistently (Boucot and Johnson, 1979, p. 107). Several dorsal valves of *Brooksina* from the C Fauna (Ludlow) of the Roberts Mountains Formation, central Nevada, illustrated by Johnson et al. (1976, pl. 19, figs. 3, 8, 15), possess a brachiophium similar to that of *Karlsorus* n. gen., in that only the middle part of the outer hinge plates are fused together. However, *Brooksina* has a distinctly ribbed shell and tends to have a reversed lateral shell profile compared to the new genus and *Pentamerifera* and has the dorsal valve larger and more convex than the ventral valve, and has the spondylium and hinge plates extending near the shell anterior margin (see Sapelnikov, 1972, 1985).

Karlsorus gothlandicus (Lebedev, 1892) (new combination)
Figures 1–3; Table 1

1892 *Pentamerus gothlandicus* Lebedev, p. 22, pl. 2, figs. 11a, 11b, 12.
non 1938 *Pentamerus* (*Pentameroides*) cf. *gotlandicus*; [sic] St. Joseph, pl. 5, figs. 7, 8, pl. 6, figs. 13, 15, text-figs. 1, 8. St. Joseph's material is from the Oslo region, assignable to *Pentameroides subrectus* (Hall and Clarke, 1893)
1974 *Pentamerus gothlandicus*; Bassett and Cocks, p. 23. No illustrations; localities and stratigraphic occurrences discussed.
1977 *Pentamerus gothlandicus*; Bassett, p. 170, pl. 47, figs. 1–3, text-fig. 19. Lectotype selected.
1978 *Pentamerus gothlandicus*; Nikiforova, p. 170, pl. 1, figs. 1–5.

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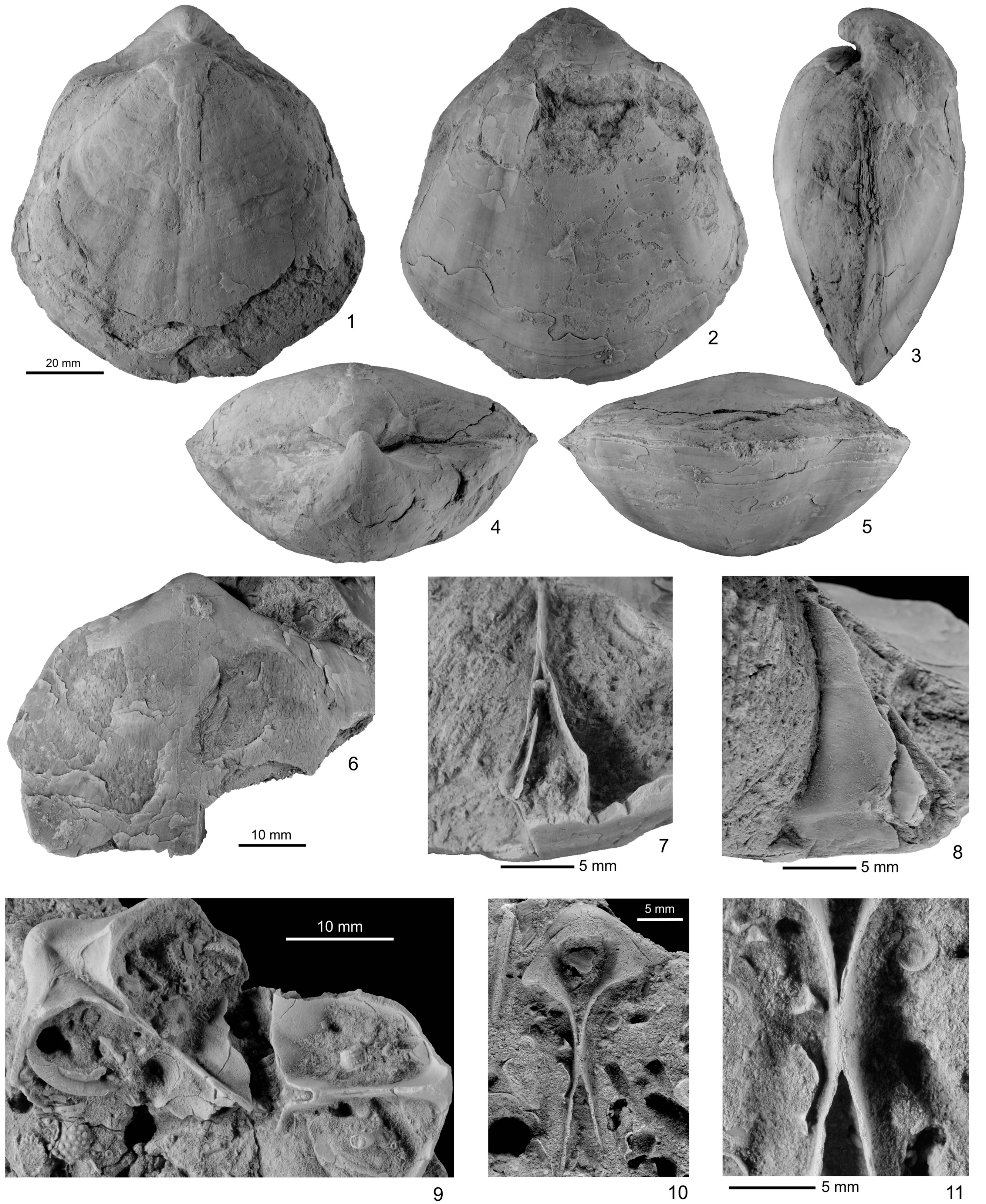

Figure 1. *Karlsorus gothlandicus* (Lebedev, 1892) n. comb., Slite beds, upper Wenlock, Gotland. (**1–5**), LMG 5939, dorsal, ventral, lateral, posterior, and anterior views of nearly complete shell, labeled as from "Visby Norderstrand," which is most likely erroneous because this locality, once located outside Visby but now lost (see Jaanusson, 1986), was in the Visby Marl (Llandovery), which is much lower than the known stratigraphic range of *Karlsorus gothlandicus* n. comb. on Gotland. This well-preserved shell is most likely derived from Lilla Karlsö. (**6–8**) LMG 5940, dorsal valve embedded in lime-mud matrix, from the Valle 1 and 2 sections (see Laufeld, 1974, p. 140), showing brachiophorium in anterior (**7**) and lateral (**8**) views. (**9–11**) Br 143013, one small slab from Tjerldersholm 1 coastal bluff, with disarticulated ventral valves (**9**) and a dorsal valve showing the fused outer hinge plates in their middle portion (**10, 11**).

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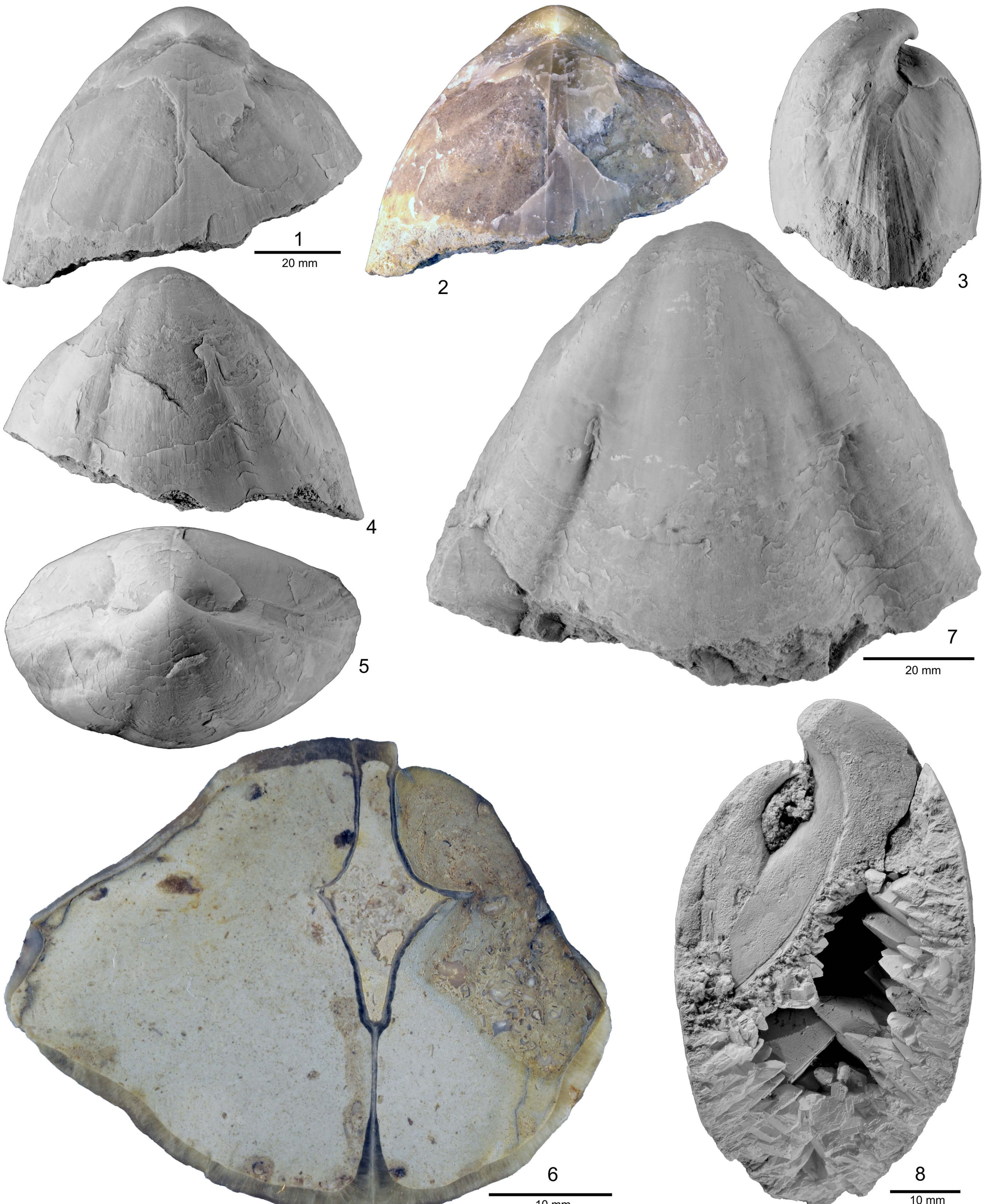

Figure 2. *Karlsorus gothlandicus* (Lebedev, 1892) n. comb., Slite beds, upper Wenlock, Gotland. (**1–5**) Br 4516, dorsal, uncoated dorsal, lateral, ventral, and posterior views of incomplete shell from Lilla Karlsö, showing long, discrete inner hinge plates. (**6**), Br 110001, polished transverse section of a conjoined, anteriorly broken shell from Lilla Karlsö, showing internal structures similar to those of *Pentamerus* in posterior part of the shell, except for low inner hinge plates. (**7**) LMG 5943, large, anteriorly broken dorsal valve from the Blåhäll section, Fröjel, showing strong trilobation. (**8**) LMG 5944, medially split shell from Lilla Karlsö, showing longitudinal views of spondylium, hinge plates, and crura.

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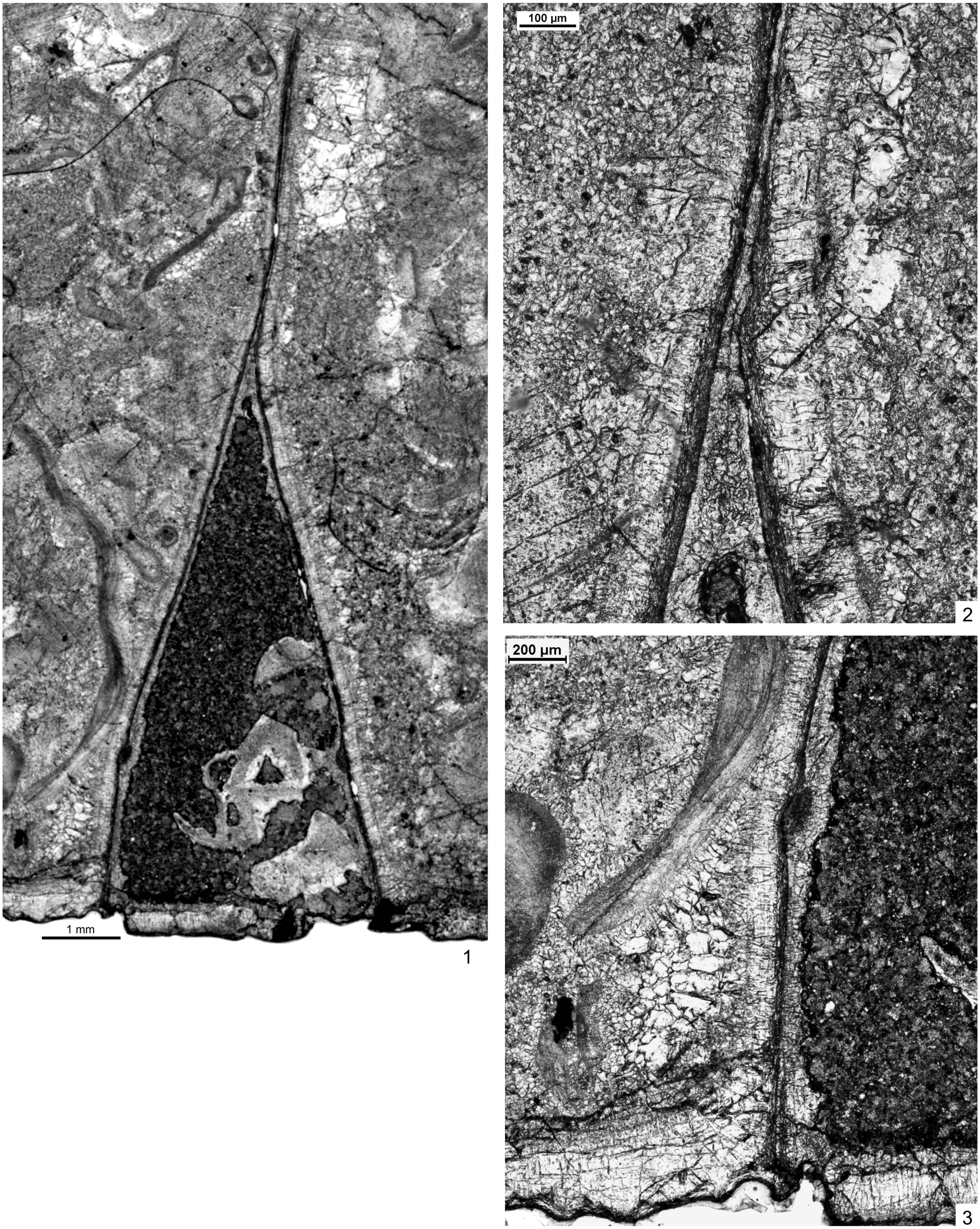

Figure 3. (**1–3**) *Karlsorus gothlandicus* (Lebedev, 1892) n. comb., Slite beds, upper Wenlock, Lilla Karlsö, Gotland; LMG 5945. Transverse section (**1**) and local enlarged views (**2, 3**) of dorsal valve, showing the tent-shaped brachiophorium.

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Table 1. Measurements (mm) of shell dimensions for *Karlsorus gothlandicus* (Lebedev, 1892) n. comb., based on collections at the Swedish Museum of Natural History and the Gotland Museum, Sweden. Abbreviations: dv, dorsal valve; Ms/Ohp, length of median septum or outer hinge plates; sh, shell with conjoined valves; vv, ventral valve; *value estimated from damaged shell; — measurement could not be obtained from broken shell.

	Length	Width	Depth/Thickness	Ms/Ohp
Br 105773, sh	128.5	93.0*	66.5	56.5
Br 105774, dv	101.2	>70.0*	—	
Br 108382, dv	>94.0*	99.0	—	44.7
Br 108383, dv	123.2	93.8	—	56.0
Br 108385, dv	105.5	101.3	—	52.0
Br 108386, dv	106.8	87.4	—	49.6
Br 109995, vv	118.4	—	—	58.7
GM 5939, sh	99.3	92.1	50.6	42.5
GM 5943, vv	—	102.0	—	—

Types.—VSEGEI 102/324, selected by Bassett (1977; see also Nikiforova, 1978), exact locality and stratum unknown. On Gotland, the species is largely confined to the upper Slite beds, corresponding to the *Cyrtograptus lundgreni* Biozone of the upper Wenlock (Bassett and Cocks, 1974; Calner et al., 2004, fig. 2).

Occurrences.—On Gotland, *K. gothlandicus* is most abundant and best preserved in the Slite beds on Lilla Karlsö (see Hede, 1927), a tiny island about 5 km off the southwest coast near Djupvik. Other specimens examined are from coeval strata at Tjeldersholm 1 (57°37'56.4"N, 180°46'34.9"E; Laufeld, 1974), Blåhäll, Fröjel (57°18'53.6"N, 18°09'40.5"E; Laufeld, 1974), and Valle 1 and 2 (see Laufeld, 1974 for detailed locality information). There are many other localities in Gotland where the species has been reported, but such material was not examined in this study. More detailed information on *K. gothlandicus* localities can be found in Laufeld (1974) and Bassett and Cocks (1974).

Description.—Shell very large, with maximum observed length of 128 mm and width 102 mm (Table 1); subpentagonal in outline, with maximum width located at about two-thirds length from apex; nearly equibiconvex, or with ventral valve slightly deeper than dorsal valve in umbonal area. Anterior commissure rectimarginate to gently sulcate (Fig. 1.1–1.5). Hinge line varying from short to relatively long, about one-third to two-thirds of shell width. Ventral umbo strongly convex, narrow, with apical angles ~90°, relatively low for shell size, raised ~15 mm above hinge line in shells over 100 mm long; palintrope defined by fairly clear ridge; beak strongly incurved, arched over but not touching dorsal umbo; pseudodeltidium present, strongly concave, almost appressed to floor of spondylium in apical area (Fig. 1.9). Ventral valve trilobate, with medial lobe broadening rapidly from valve apex to anterior margin, approximately twice as wide as each lateral lobe, delimited by gentle to prominent furrow on each side to separate from lateral lobes (Figs. 1.2, 2.4, 2.7), forming slightly protruding tongue at anterior margin. Dorsal umbo moderately and evenly convex, not marked by sulcus or fold, with small beak buried in delthyrial area of ventral valve; antero-medial portion of valve gently and faintly depressed in some shells, or marked with faint development of trilobation. Shell essentially smooth, except for randomly developed, concentric growth lines, especially close to anterior margin.

Interior of ventral valve characterized by very small and week teeth; spondylium narrow, deep, extending for less than one-half of shell length; supported by relatively long and high median septum for about one-half of spondylium length (Fig. 2.6, 2.8); thick prismatic layers of median septum forming wedge-shaped junction with prismatic layer of valve floor.

Interior of dorsal valve with correspondingly minute hinge sockets; inner hinge plates extending for about two-fifths of valve length from valve apex, discrete along entire length (Figs. 1.1, 2.2, 2.6), very low, attaining about 1/4 height of outer hinge plates (Figs. 1.7, 1.8, 2.6, 2.8, 3.1); outer hinge plates about same length as inner hinge plates, discrete in posterior and anterior portions, fused in medial portion to form tent-like brachiophorium, with ventro-medial portion forming crest-like structure (Figs. 1.7, 1.8, 1.10, 1.11, 2.1, 2.2); crura slender, rod-like, fused to inner surface of junction between inner and outer hinge plates (Fig. 3.1, 3.3), becoming free only at distal ends. Muscle scars not observed in either ventral or dorsal valves.

Remarks.—The internal structures of *K. gothlandicus* are partially similar to those of *Pentamerus*, especially in the relative size and shape of the spondylium, and the configuration of the posterior part of the hinge plates. In addition to the brachiophorium, however, the inner hinge plates of the Gotland species are proportionally much lower than in *Pentamerus*, in which the inner hinge plates are about half as high as the outer hinge plate (see Jin and Copper, 2000). In the Gotland species, the inner hinge plates are only about one-quarter of the height of the outer hinge plates, with the outer-inner plate junction, marked by the crura, being close to the valve floor. The unusually large shell size of *K. gothlandicus*, typically exceeding 100 mm in length, is very rarely achieved by various *Pentamerus* species of Llandovery age (Jin and Copper, 2000).

From the limited number of exposed shell interiors and sectioned specimens available for study, it appears that the fusion of outer hinge plates in the new genus occurs only in the middle portion of the plates. In their anterior and posterior potions, the configuration of the hinge plates is very similar to that in *Pentamerus*, except for the notably low inner hinge plates (Figs. 1.10, 2.6). There has been some doubt that the medially coalesced hinge plates may have been the result of preservation artifact, which explains why the brachiophorium was not considered an important diagnostic character in the revised brachiopod volumes of the Treatise on Invertebrate Paleontology (Boucot et al., 2002). In this study, however, a thin section of a well-preserved dorsal valve clearly shows that the lamellar layers of the two outer hinge plates are fused into a single lamellar layer in the coalesced part (Fig. 3.1, 3.2), which strongly suggests that the fusion was not a random compression of the two plates together during post-mortem taphonomic or diagenetic processes.

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