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ORDOVICIAN–SILURIAN CHILEIDA—FIRST POST-CAMBRIAN RECORDS OF AN ENIGMATIC GROUP OF BRACHIOPODA

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ABSTRACT—Brachiopods of the order Chileida have been recorded previously only from rocks of early to mid-Cambrian age (Botomian–Amgaian). They are typified by having a calcareous strophic shell with a delthyrium and colleplax, and these characters are shown to be present in species of the two new genera *Tolen* and *Trifissura*, from the Late Ordovician of Kazakhstan and the Silurian of Sweden and Britain, respectively. In specimens of *Trifissura*, the triangular colleplax is phosphatized secondarily by bacterial activity. It is suggested that the phosphatized colleplax represents an organic pad and that served as the original attachment structure of *Trifissura* by encrustation. *Tolen* and *Trifissura* represent the first post-Cambrian record of chileides from the Ordovician and Silurian; the new family Trifissuridae forms the first phylogenetic link between Cambrian chileides and Carboniferous–Permian isogrammides.

INTRODUCTION

THE ORDER Chileida Popov and Tikhonov, 1990, was previously known only from the early Cambrian (Botomian) to middle Cambrian (Amgaian), whilst brachiopods belonging to the order Dictyonellida Cooper, 1956, are known from the Late Ordovician to the Late Permian (Popov et al., 1996; Popov and Holmer, 2000). The chileides includes some of the stratigraphically oldest known brachiopods with a calcareous and strophic shell. The most remarkable morphological feature of the chileides is that they are provided with large ventral umbonal perforation anterior to the umbo. This subtriangular perforation is enlarged by resorption and sometimes covered posteriorly by a colleplax (Wright, 1981), and Williams et al. (1996) included all known brachiopods with this morphology in the rhynchonelliform class Chileata Williams, Carlson, Brunton, Holmer, and Popov, 1996.

Here we describe the first three known Ordovician–Silurian species of chileide brachiopods with an umbonal perforation and colleplax, referred to the new family Trifissuridae, and comprising the two new genera *Trifissura* and *Tolen*. The two new species, *Trifissura rigida* and *Tolen multicostatus*, are described. The ventral valve of *Trifissura* is provided with a thick phosphatic plug covering the umbonal perforation, and it is interpreted as the secondarily phosphatized remains of an originally organic attachment structure.

The exact phylogeny position of the Chileida and related groups is still poorly understood (Popov et al., 1996), and the position of the trifissurides needs to be further investigated. However, *Trifissura* and *Tolen* clearly provide an important first phylogenetic link between the Cambrian chileides and the Carboniferous–Permian Isogrammidae.

MATERIAL AND FOSSIL LOCALITIES

The described three brachiopod species assigned to the Trifissuridae were collected from localities in Kazakhstan, Sweden, and England. The age range is from the Upper Ordovician Katian Stage to the Llandovery (?) and Wenlock Series of the middle Silurian. As yet there is no record from the intervening Hirnantian Stage.

Kazakhstan.—The new genus and species *Tolen multicostatus* is the oldest known record of the Trifissuridae, from the Upper Ordovician (Katian) of Kazakhstan. It occurs sparsely in the upper part of the Akdombak Formation, Chokpar Regional Stage (late Katian) within the Ordovician–Silurian boundary section exposed west of the Tolen River in the Chingiz Range (locality 1783/1964 of O. P. Kovalevsky). The locality and stratigraphy is further described in Popov and Cocks (in press) and the occurrence of *To. multicostatus* is within the lower part of 'Unit T9'.

The associated fauna includes the trilobite *Pliomerina* sp., tabulate corals, and brachiopods characteristic of the *Holorhynchus giganteus* beds. Within the Ashgill Series, the *Holorhynchus* fauna is now known from boreholes in the East Baltic to immediately pre-date the widespread late Ashgill Hirnantian fauna (Rong et al., 2004).

Sweden.—The new genus and species *Trifissura rigida* occurs only on the Baltic island of Gotland, where all known specimens come from loose pebbles (old collections deposited in Naturhistoriska Riksmuseet, Stockholm) of grayish-blue nodules in the general coastal area north of Visby. The lithology of the nodules indicates that they most likely come from the upper Llandovery (?)–lower Wenlock Lower Visby Formation, and fairly certainly at or very close to the beach at Norderstrand (see Hedström, 1910, p. 1464; Jaanusson, 1986, p. 6), from where excellent outcrops of the Lower Visby Formation have been known historically. As noted by Jaanusson (1986, p. 6) the Norderstrand outcrops have been inaccessible for many years.

England.—*Trifissura transversa* (Salter in Davidson, 1866) is the youngest known member of the Trifissuridae, and all available material come from the mid-Silurian, Wenlock (Homerian), Coalbrookdale Formation of the West Midlands (Cocks, 1978, p. 21), preserved in old museum collections (see list below). Most specimens are from now inaccessible old outcrops in the general neighborhood of Wrens Nest National Nature Reserve, Dudley and Walsall (see, e.g., Davidson, 1853; Ray et al., 2011) or just from unspecified localities at "Dudley" as well as from temporary localities probably in connection with work on the Malvern and Ledbury tunnels, the Malvern Hills.

Abbreviations and locations of the museums holding type and studied material are as follows: BGS, British Geological Survey, Keyworth, Nottinghamshire; NHM, Natural History Museum, London; OUM, Oxford University Museum; RM, Naturhistoriska Riksmuseet, Stockholm; SM, Sedgwick Museum, Cambridge.

SHELL MORPHOLOGY

The brachiopods of the new family Trifissuridae are characterized by having strongly transverse, compressed, biconvex strophic shells. Notwithstanding the presence of a straight hinge line there is no evidence of any articulatory device. All studied specimens are preserved as compressed internal and external or composite molds in limestones or in argillaceous mudrocks. In characters of preservation, the specimens of *Trifissura rigida* from Gotland occur in similar preservation to gastropods from the same nodules at the same locality, with neomorphosed shells or as molds, whereas orthides and atrypides from the same samples retain an unaltered calcitic shell. In the British material, *Tr. transversa* is also preserved as internal and external molds whereas the calcitic shells of trilobites and rhynchonelliform brachiopods from the same samples are not affected by dissolution or neomorphism. These observations strongly support the interpretation that the shell in trifissurides was originally aragonitic, as in trimerellide brachiopods (Jaanusson, 1966; Balthasar et al., 2011). Valves of trifissurides were thin marginally, but somewhat thickened under the visceral areas of both valves, where phosphatic pads are commonly preserved in the umbonal area and under the muscle scars.

Some specimens of *Tr. transversa* preserve a thin phosphatic veneer bearing distinct pitted ornament, with circular depressions around 300 μm across (Fig. 1.2). SEM study reveals that the veneer consists of dense, irregular phosphatic filaments about 2–4 μm wide (Fig. 1.3, 1.4). These filaments are comparable to cyanobacterial sheaths (e.g., Goncharova et al., 1993). It is most probable that this phosphatic veneer is a cast of the originally organic periostracum, phosphatized secondarily by bacterial activity.

The ventral valve of trifissurides is characterized by mixoperipheral growth, with a wide, flat, almost orthocline interarea bearing a narrow triangular delthyrium covered by the convex pseudodeltidium (Fig. 2). The poor imprints of the shell surface in the molds make it difficult to determine the nature of the shell growth in the dorsal valve. Along the straight dorsal posterior margin there is a wide, flattened area, covered by closely spaced growth lines in *Tr. transversa* (Fig. 3.2, 3.4). This area can be seen as a simple thickening of the posterior margin that was composed exclusively of secondary shell. If this scenario is valid, the shell growth of the dorsal valve of trifissurides was hemiperipheral as in chileides. However, it could also be formed as a result of normal accretionary growth, including secretion of a primary shell by the posterior dorsal mantle lobes, but this is difficult to determine.

Radial ornament is characteristic only of the Ordovician trifissuride *Tolen*. It comprises low, fine bifurcating ribs, which are curved posteriorly in the posterolateral areas of the shell to cross the hinge line. The inner surface of the shell shows the presence of follicular embayments along the shell margins, suggesting the former presence of marginal setae.

Interiors of both valves are usually weakly impressed, but the visceral area is usually easily recognizable (Figs. 2.3, 2.4, 3.5, 3.6, 4). In the ventral valve it is usually bordered posterolaterally by a distinct rim, which is most pronounced in *Tr. rigida*. This rim may have supported outside lateral muscles similar to those of craniides, and which were attached anteriorly to the body wall and used for the hydraulic opening of the shell. Paired muscle scars along the lateral sides of the visceral area represent the posterior adductors (Figs. 2.3, 2.4, 4.3). They are usually accentuated by symmetrically placed phosphatic pads that are interpreted as having developed on the organic membranes within the shell underlying the muscles. Large ventral anterolateral scars, which are usually weakly impressed to almost unrecognizable, may represent combined attachment scars of the anterior adductors and internal oblique muscles (Figs. 2.4, 4.3). In the dorsal valve, internal oblique muscles were attached to the thickened callus developed in the posteromedian part of the visceral area, whereas posterior adductor scars are usually accentuated by the rim bounding them posterolaterally (Figs. 3, 5.6). Anterior adductor scars in *Trifissura* are usually weakly impressed, but in *Tolen* they are situated on a callus of secondary shell, and bounded laterally by a low rim. The anteromedian region of the dorsal visceral area in *Tolen* also has a small elevated muscle platform, which probably supported the brachial protractors.

Mantle canals in trifissurides are best preserved in *Tr. rigida*. They are pinnate in both valves, whereas coarsely tuberculate areas in the posterolateral areas of the valves suggest the position of *vascula genitalia*. In *Tr. transversa* mantle canals are observed only in the ventral valve, where they represent paired, anteriorly directed *vascula media* and *vascula lateralia* (Fig. 4.1, 4.4).

ATTACHMENT STRUCTURES

The ventral valve of trifissurides bears a triangular opening anterior to the umbo, which is enlarged anteriorly due to resorption of surrounding shell and is covered umbonally by a plate. This plate is interpreted here as a colleplax, and representing part of an attachment structure that is homologous to that of chileides and dictyonellides. An unusual feature of the colleplax in the Trifissuridae is the constant presence of a thick phosphatic plug covering the opening. The plug consists of numerous lamellae varying in thickness from 100 to 500 μm, directed slightly obliquely and overlapping each other in an anterior direction (Fig. 1.5, 1.8, 1.9, 1.12). In cross section, the external surface of these lamellae is uneven, suggesting that they were originally organic and growing over a hard ground, probably representing bioclasts (Fig. 1.5, 1.6). The original fine structure in these lamellae is generally not preserved, but is replaced by aggregates of irregular, tubular, phosphatic filaments about 2–4 μm wide (Fig. 1.9, 1.11) similar to those described above as probable casts of the periostracum. Some shells of *Trifissura rigida* show a different preservational pattern. In these specimens, the phosphatic pad covering the colleplax consists of dense, almost parallel solid fibers only about 1–2 μm wide running subparallel to the shell surface (Fig. 1.7, 1.10). Each fiber is built of a bunch of fibrils 100 nm across. These characters suggest a fine phosphatization of an original organic tissue, which may have been similar in composition to that of the periostracum, but functioning as a sticky organic pad (Wright, 1981) by which the trifissurides were attached to the substrate.

However, it is also conceivable that the phosphatic pad in *Trifissura* is the remains of the basal proximal portion of an elongated attachment structure, where the distal parts have not been preserved. The exceptionally preserved elongated attachment structure of the chileide *Longtancunella* from the early Chengjiang Lagerstätte is composed of numerous stacked pads emerging from a perforation and colleplax structure (Zhang et al., 2011).

SYSTEMATIC POSITION OF THE NEW FAMILY TRIFISSURIDAE

The family Trifissuridae includes only the two new genera *Trifissura* and *Tolen* with the two new species: *Tr. rigida* and

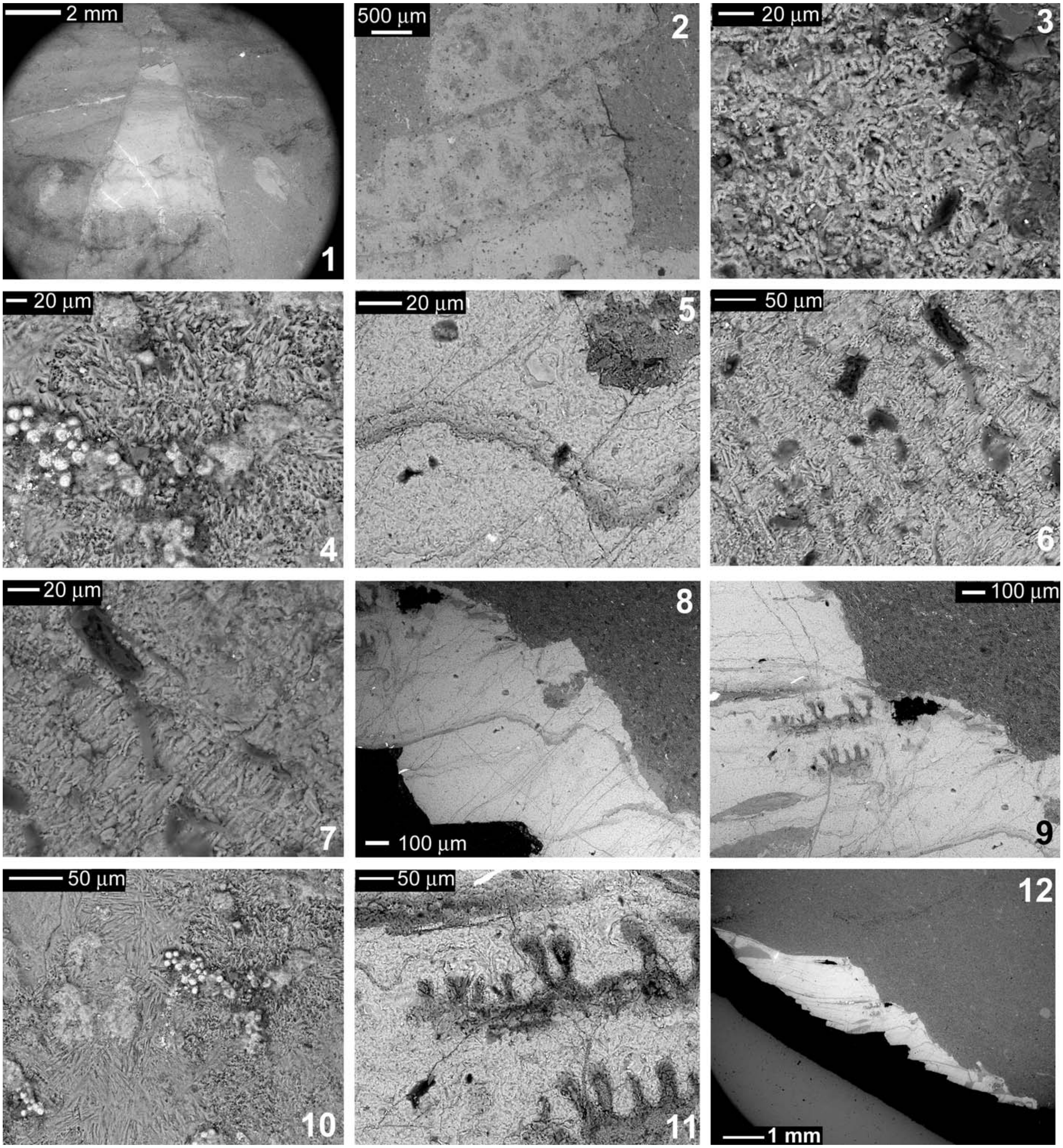

FIGURE *1*—*1*–*5*, *8*, *9*, *11*, *12*, *Trifissura transversa* (Salter *in* Davidson, 1866), Wenlock, Homerian, Coalbrookdale Formation: *1*–*4*, BM B.1104, ventral valve, Walsall: *1*, backscatter image of colleplax; *2*–*4*, phosphatized periostracum showing pitted micro-ornament and aggregation of cyanobacterial filaments; *5*, *8*, *9*, *11*, *12,* C20400, ventral valve, transverse section through the phosphatic pad covering the colleplax: *5*, *11*, microstructure showing aggregation of cyanobacterial filaments; *6*, *7*, *10*, *Tr. rigida* n. sp., Llandovery (?)–Wenlock, allochthonous boulder, "Visby", probably Norderstrand, RM Br 23486, back scatter image of colleplax showing dense, almost parallel fibers.

To. multicostatus as well as *Tr. transversa* (Salter *in* Davidson, 1866). All these taxa have very simple shell morphology, and they are inarticulated. Therefore, it is not surprising that the only previously described species *Tr. transversa* was assigned initially to the Trimerellida. However, trifissurides differ from all known trimerellides in the absence of thickened muscle platforms in both valves and in the possession of a dorsal median ridge. They also have a narrow delthyrium covered by a convex pseudodeltidium. Moreover, they lack the trimerellide type articulation, and most likely retained a hydraulic shell-

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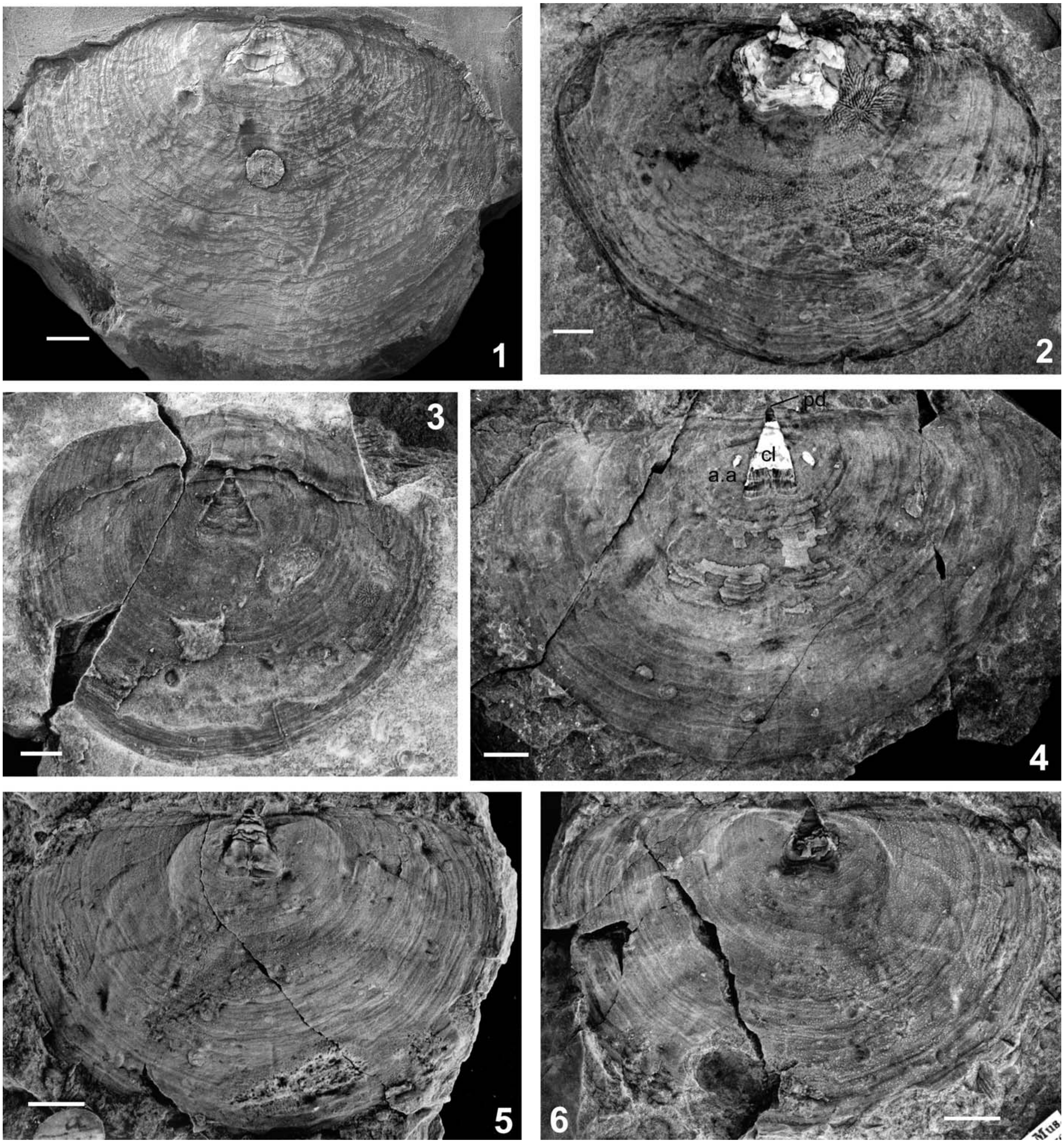

FIGURE 2—*Trifissura transversa* (Salter *in* Davidson, 1866), Wenlock, Homerian, Coalbrookdale Formation. *1*, NHM B.5941, lectotype, ventral valve exterior, "Parkes Hall" (probably close to Parkes Hall pool), Dudley; *2*, NHM B.820d, ventral internal mold, "Dudley" (unspecified); *3*, NHM B.9480, external mold of conjoined valves, "Dudley" (unspecified); *4*, BM B.1104, ventral valve, "Walsall" (unspecified); *5*, *6*, SM A13255a, b, ventral internal and external molds, "Dudley" (unspecified). Abbreviations: a.a.=anterior adductor scars; cl=colleplax; pd=pseudodeltidium. Scale bars=5 mm.

opening mechanism. The presence of a ventral umbonal perforation enlarged by resorption, in combination with a well-defined ventral interarea bearing a pseudodeltidium, a strophic shell lacking articulatory structures, and possible hemiperipheral growth of the dorsal valve, are known also in the early Cambrian family Chileidae and can be considered as diagnostic for the attribution of trifissurides to the order Chileida (Popov and Holmer, 2000; see also Holmer et al., 2009, 2011).

The shell structure of chileides is known only for the late early Cambrian *Kotujella* (family Matutellidae) from Siberia (Williams and Cusack, 2007), whereas all other taxa are known only from silicified material. According to Williams and Cusack (2007), the Cambrian chileides have a calcitic endopunctate

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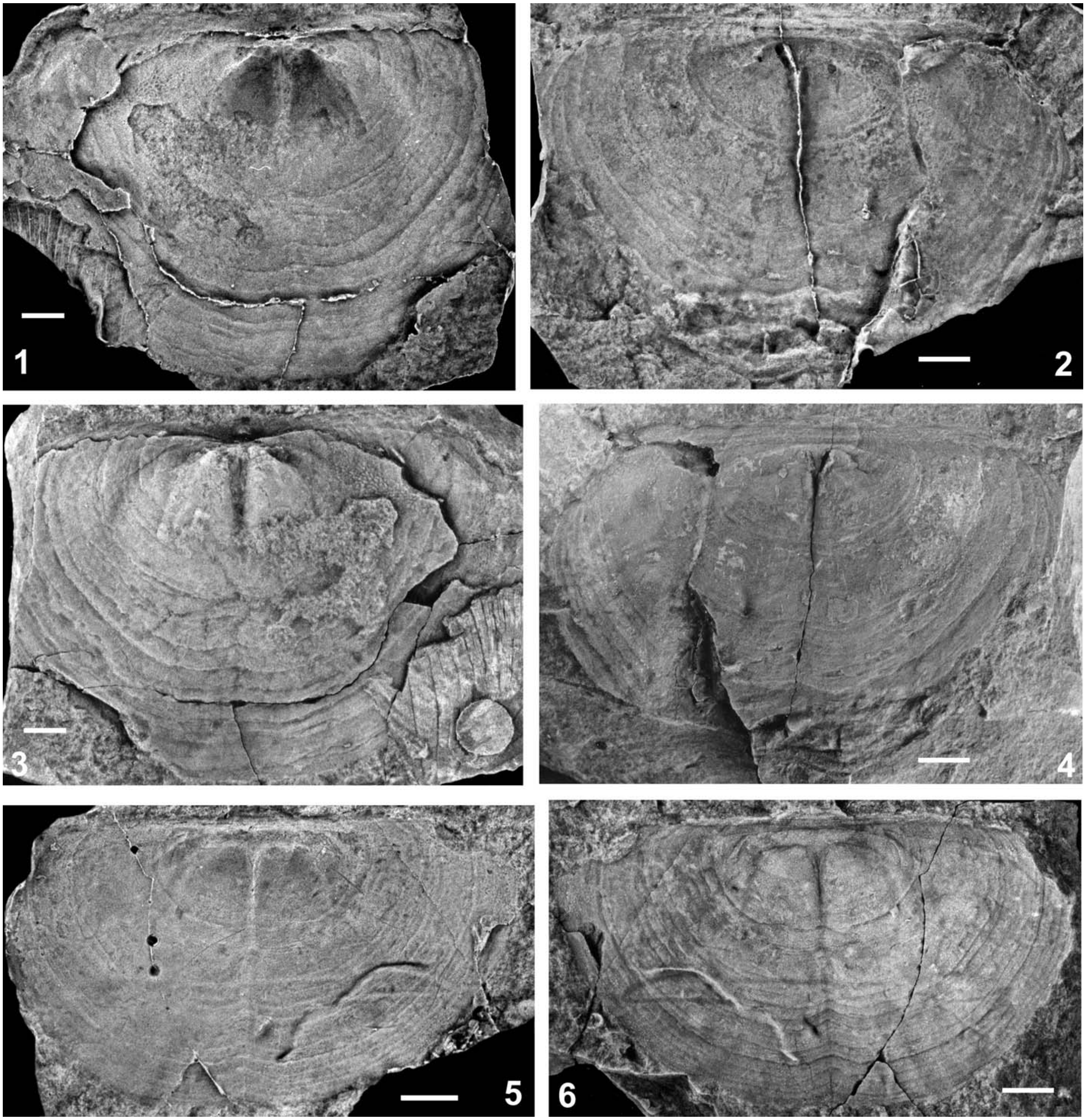

FIGURE 3—*Trifissura transversa* (Salter *in* Davidson, 1866); Silurian, Wenlock, Homerian, Coalbrookdale Formation. *1*, *3*, BGS 16513, latex cast of dorsal interior, dorsal internal mold, "May Hill", Gloucestershire; *2*, *4*, SM A13279, latex cast of dorsal valve interior, dorsal internal mold, Dudley; *5*, *6*, SM A13254, latex cast of dorsal valve interior, dorsal internal mold, Dudley. Scale bars=5 mm.

shell with a foliated secondary layer. However, characters of preservation of the shell in the Trifissuridae suggest significant differences in shell composition and structure by comparison with the Cambrian taxa, justifying their attribution to a separate new family.

Among chileates, the late Palaeozoic family Isogrammidae (order Dictyonellida) may also have had an aragonitic shell (Popov and Holmer, 2000). Isogrammides are characterized also by having a transverse strophic shell, and in having a colleplax, but they differ in having an open delthyrium, rudimentary articulation, and a cardinal process that suggests the presence of muscles acting as diductors. There is a possibility that isogrammides are more closely related phylogenetically to trifissurides casting doubt on the status of the order Dictyonellida, but this relationship requires further study.

SYSTEMATIC PALEONTOLOGY

Morphological terminology and taxonomic classification follow Popov and Holmer (2000).

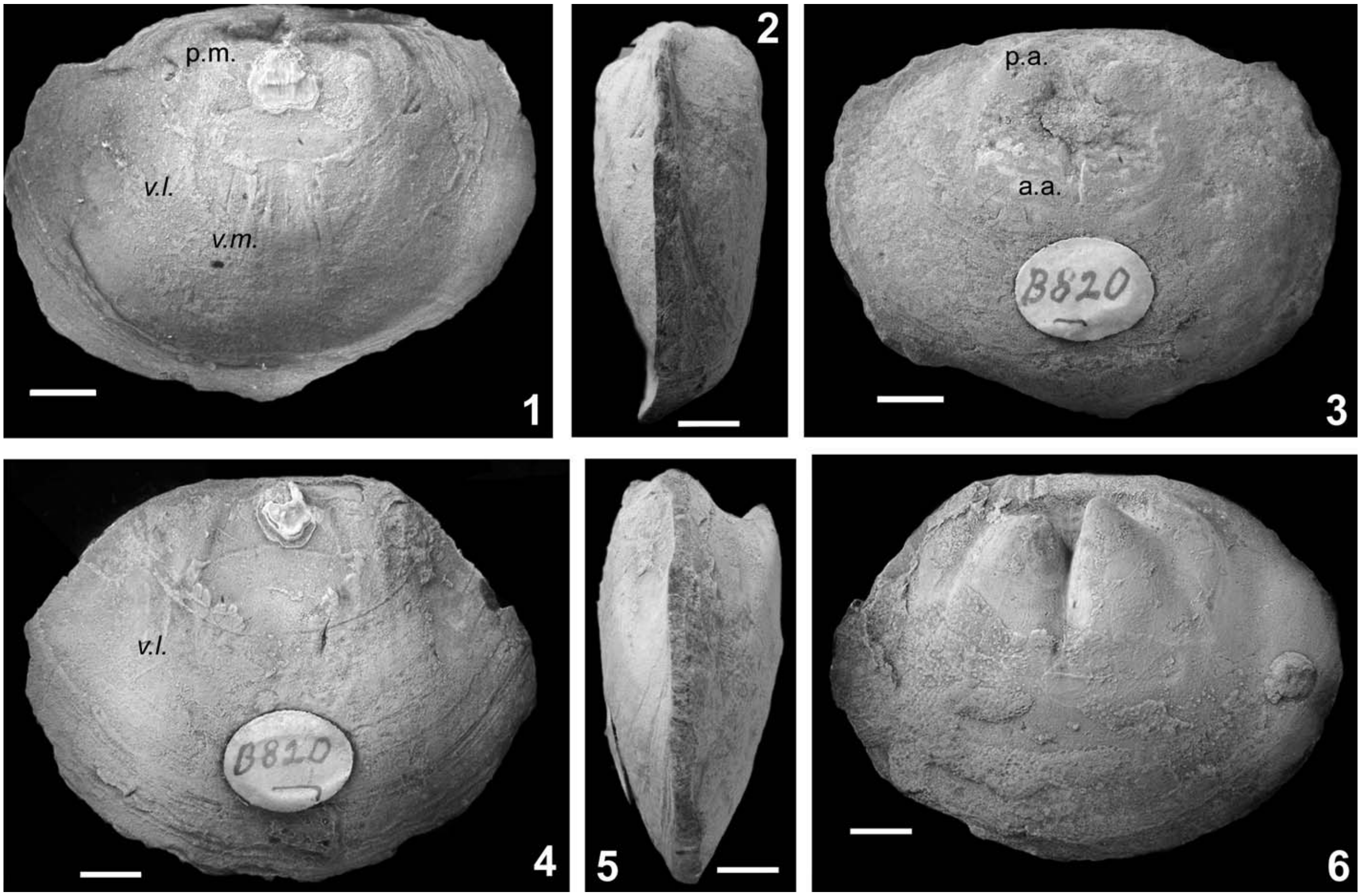

FIGURE 4—*Trifissura transversa* (Salter *in* Davidson, 1866), Wenlock, Homerian, Coalbrookdale Formation, "Dudley" (unspecified). *1–3*, B820a, internal mold of conjoined valves, ventral, lateral and dorsal views; *4–6*, B820b, internal mold of conjoined valves, ventral, lateral and dorsal views. Abbreviations: a.a.=anterior adductors; p.a.=posterior adductors; p.m.=composite attachment scars of posterior adductors and outside oblique muscles; *v.l.=vascula lateralia*; *v.m.=vascula media*. Scale bars=5 mm.

Class CHILEATA Williams, Carlson, Brunton, Holmer, and Popov, 1996
Order CHILEIDA Popov and Tikhonov, 1990
TRIFISSURIDAE new family

Diagnosis.—Shell biconvex, transversely oval, with wide, straight posterior margin; anterior commissure rectimarginate; ventral valve with mixoperipheral growth; ventral interarea low and wide, divided by narrowly triangular delthyrium and convex pseudodeltidium; ventral umbonal area perforated by subtriangular opening, becoming enlarged by shell resorption, and covered by colleplax; dorsal valve with mixoperipheral or hemiperipheral growth; dorsal interior with slightly raised, elongate, suboval visceral area bounded by rim; muscle system with two pairs of adductors and paired internal oblique muscles attached dorsally to the thickened, semioval plate in the median part of the posterior margin; mantle canal system pinnate in both valves; shell fabric possibly originally aragonitic.

Remarks.—The Trifissuridae n. fam. are closely comparable with the Isogrammidae in having a transverse, flattened shell exhibiting hemiperipheral growth of the dorsal valve and a colleplax in the umbonal region of the ventral valve. However, the new family can be distinguished by the absence of a cardinal process, and in having a weakly developed median ridge, with a delthyrium covered apically by a convex pseudodeltidium. In having the large opening anterior to the ventral umbo, and a narrow triangular delthyrium covered apically by a convex pseudodeltidium. Members of the Trifissuridae are also somewhat similar to the family Chileidae, but differ from the latter in having the colleplax completely covering the ventral umbonal opening.

Presently only the two new genera *Trifissura* and *Tolen* are included, but the phylogenetic position of the morphologically similar *Gasconsia* Northrop, 1939, is uncertain. *Gasconsia* lacks all evidence of a chileide ventral umbonal perforation and colleplax, but has a straight posterior margin and clearly lack the trimerellide type articulation and musculature (Hanken and Harper, 1985; Mergl, 1989; Popov et al., 1997).

TRIFISSURA new genus

Type species.—*Obolus davidsoni* var. *transversus* Salter in Davidson, 1866; Silurian, Wenlock, Homerian, Coalbrookdale Formation; West Midlands.

Other species.—*Trifissura rigida* n. sp.

Diagnosis.—Trifissuridae with dorsal muscle platforms weakly developed, bisected by a low median ridge separating shallow umbonal cavities.

Etymology.—From Latin, *fissura*, a crack or cleft, and triangular, referring to the triangular colleplax.

Occurrence.—Silurian, Llandovery (?)–Wenlock, of Sweden and Britain.

Remarks.—*Trifissura* differs from the problematic *Gasconsia* mainly in having an umbonal perforation and colleplax as well as in the lack of solid visceral platforms.

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TRIFISSURA TRANSVERSA (Salter *in* Davidson, 1866)
Figures 1.1–1.5, 1.8, 1.9, 1.11, 1.12, 2–4

1866 *Obolus davidsoni* var. *transversus* [SALTER MS] DAVIDSON; p. 59, pl. 5, figs. 1–6.
1874 *Dinobolus transversus* (Salter), DAVIDSON AND KING, p. 163, pl. 18, fig. 12.

Diagnosis.—*Trifissura* with moderately dorsibiconvex shell, with large colleplax, and dorsal median ridge extending for about two-fifth of valve length, separating shallow umbonal cavities; ventral mantle canals with paired *vascula media* and *vascula lateralia*.

Description.—Shell slightly dorsibiconvex, transversely suboval in outline, on average 70% as long as wide (observed range 55–98%, N=31) and about two-fifths as thick as long in one specimen. Hinge line straight, about three-fourths as wide as maximum shell width at mid-length. Anterior commissure rectimarginate. Ventral valve gently and evenly convex, on average 37 mm long (observed range 26–58 mm, N=20) and 53 mm wide (observed range 34–74 mm, N=20), with a low, planar almost orthocline interarea divided by narrow, triangular delthyrium, covered apically by convex pseudodeltidium (Fig. 2.2, 2.3). Umbonal area with slightly elongate, subtriangular colleplax, on average 142% as long as wide (observed range 102–176%, N=20) and occupying on average 16% of total width of valve (observed range 11–30%, N=20) and 23% of total length of valve (observed range 15–42%, N=20), sealed by phosphatic pad. Dorsal valve on average 38 mm long (observed range 27–55 mm, N=11) and 56 mm wide (observed range 38–76 mm, N=11), moderately convex, with lateral profile more strongly curved in posterior one-third valve length. Shell surface smooth with fine, regular filae (Figs. 2, 3); periostracum rarely preserved by secondary phosphatization, with pitted micro-ornament (Fig. 1.2).

Ventral interior with weakly impressed visceral area. Anterior adductor muscle scars situated on anterior termination of paired linear muscle tracks and often accentuated by secondary phosphatization and placed laterally to colleplax (Fig. 2.2). Posterolateral parts of ventral visceral area occupied by callus of secondary shell, representing attachment scars of the anterior adductors and oblique lateral muscles. Ventral mantle canals weakly impressed with thin straight closely spaced, subparallel *vascula media* in medial part of valve and broad, anteriorly directed *vascula lateralia* (Fig. 4.1, 4.4). Dorsal interior with weakly impressed posterior and anterior adductor scars (Fig. 4.3, 4.6); median ridge low and broad, extending for about two-fifths of total valve length and bisecting both visceral area and a pair of shallow umbonal cavities (Fig. 4.5, 4.6).

Lectotype.—Selected by Cocks (1978, p. 21), NHM B.5941, Silurian, Homerian, Coalbrookdale Formation; "Parkes Hall" (variably referred to, e.g., as "Park Hall" in Davidson and King 1874, p. 163; possibly from temporary exposures close to the present location of the Parkes Hall Pool), Dudley, West Midlands.

Other material.—Dudley (unspecified localities); conjoined valves: NHM B.280a, OUM C.20395, NHM BB97704; ventral valves: SM A.12281, SM A.13255, NHM B.280b, NHM B.280d, NHM B.3658, NHM B.9480; dorsal valves: SM A.12280, NHM B.1104, SM A13279; NHM B.280c), NHM B.280e–g, NHM B3658. "Parkes Hall", Dudley, West Midlands; NHM BB.34720, dorsal valve. Ledbury, Malvern (collected by R. B. Grindrod): ventral valves: OUM C.20386, OUM C.20387, OUM C.20389, C.20392, OUM C.20393, OUM C.20397, OUM C.20399), OUM C.20400, OUM C.20401, OUM C.20403, OUM C.20404, OUM C.20407, OUM C.20408, C.20412, C.20413, NHM B.3658, NHM B3923; dorsal valves: OUM C.17817, OUM C.20394, OUM C.20398, OUM C.20402, OUM C.20405, OUM C.20409, OUM C.20410. May Hill, Malvern; BGS 16513, dorsal valve. Knapp Lane, Malvern (collected by G. H. Piper, 1898); NHM B.16859, dorsal valve. Ledbury Tunnel, Malvern; NHM B.16860, ventral valve. Walsall (collected by J. Grey, 1898); NHM B1104, ventral valve.

Remarks.—Most of the studied specimens are deformed and compressed in various degrees, and frequently the preservation is a complex combination of composite external/internal molds. Therefore described characters of the internal shell morphology are mostly based on a few three-dimensionally preserved internal molds (Fig. 4). *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*.

TRIFISSURA RIGIDA new species
Figures 1.6, 1.7, 1.10, 5.4–5.10

Diagnosis.—*Trifissura* with flattened shell, smooth; colleplax small, not extending to mid-valve; mantle canals of both valves pinnate.

Description.—Shell flattened, smooth, only slightly biconvex, transversely suboval, on average 71% as long as wide (observed range 60–78%, N=6), with strophic posterior margin, shorter than maximum shell width. Anterior commissure rectimarginate. Ventral valve 22–30 mm long and 31–41 mm wide in three specimens, only slightly convex in transverse and lateral profile, with flattened rim around margin. Colleplax almost triangular, 129–155% as long as wide and occupying 14–47% of total width of valve and 21–68% of total length of valve in three specimens. Surface of colleplax uneven, ornamented by undulating growth lamellae and slightly elevated above surrounding shell. Dorsal valve with hemiperipheral growth, only slightly convex with flattened rim around margin.

Ventral visceral area, extending anteriorly about 55–60% of total valve length, bordered posterolaterally by an elevated rim. Dorsal interior with visceral area extending anteriorly about 60–65% of total valve length, and bordered posterolaterally by rim. Dorsal internal oblique muscle scars situated on high transverse ridge, undercut anteriorly present along posterior margin of dorsal visceral area. Dorsal median ridge very short, rapidly fading anteriorly, separating rudimentary umbonal cavities. Mantle canals pinnate with tuberculate impressions of *vascula genitalia* on posterolateral sides of both valves.

Etymology.—After Latin–*rigidus*, stiff, rigid, referring to the rigid shell.

Holotype.—RM Br23486, internal mold of conjoined valves, Silurian, Llandovery (?)–Wenlock, allochthonous boulder, "Visby" most likely Norderstrand.

Other material.—RM Br 23484, ventral valve; RM Br23485, dorsal internal mold; RM Br 23487, ventral internal mold; RM Br23216; RM Br23292, ventral internal mold; RM Br23279, dorsal internal mold.

Occurrence.—Silurian, Llandovery (?)–Wenlock, of Sweden and Britain.

Remarks.—This new species from Gotland differs from the type species, *Trifissura transversa*, in having distinct, pinnate mantle canals in both valves, as well as a short dorsal median ridge and rudimentary dorsal umbonal cavities.

TOLEN new genus

Type species.—*Tolen multicostatus* n. sp., from the Late Ordovician, Katian, upper Akdombak Formation (*Holorhynchus giganteus* Beds), Chingiz Range, Kazakhstan by monotypy.

Diagnosis.—Trifissuridae with triangular colleplax extending to mid-valve length, slightly raised slightly above outer surface; dorsal valve with radial ornament of low, bifurcating ribs; dorsal valve lacking median ridge and umbonal cavities, with paired anterior adductor and brachial protractor muscle scars thickened and bounded by high rim.

Etymology.—Referring to the Tolen River, near the type locality.

Occurrence.—Late Ordovician of Kazakhstan.

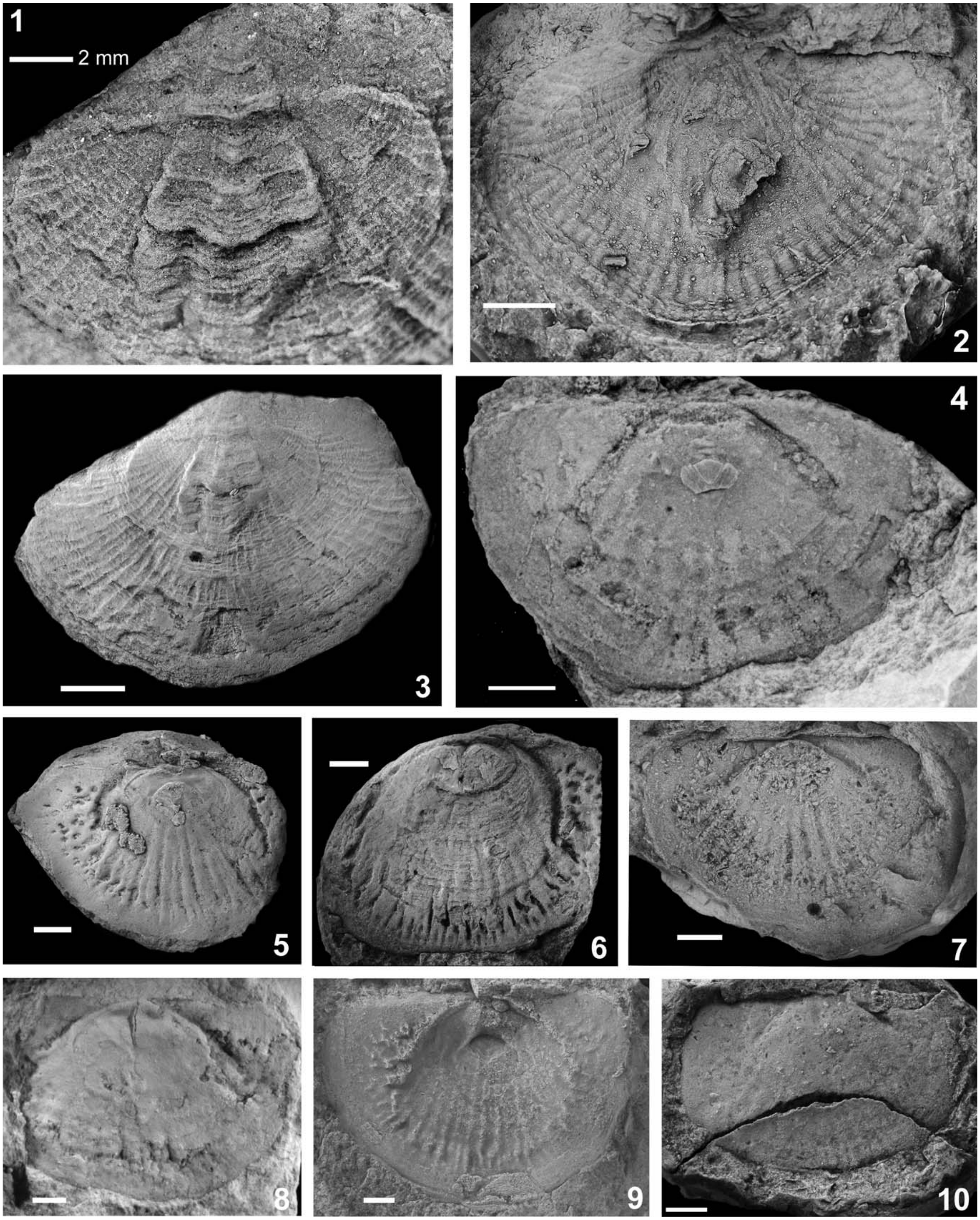

FIGURE 5—*1–3*, *Tolen multicostatus* n. sp., Upper Ordovician, Katian, Akdombak Formation, sample 1783, Tolen River, Bakanas River basin, Chingiz Range, Kazakhstan: *1*, *3*, NMW 2001.38G.801, enlarged umbonal area and latex cast of ventral interior; *2*, NMW 2001.38G.802, holotype, dorsal internal mold; *4–10*, *Trifissura rigida* n. sp., Llandovery (?)–Wenlock, allochthonous boulder, "Visby", probably Norderstrand: *4*, RM Br23292, ventral internal mold; *5*, *6*, RM Br 23486, holotype, internal mold of conjoined valves ventral and dorsal views; *7*, RM Br23485, dorsal internal mold; *8*, RM Br23279, dorsal internal mold; *9*, RM Br 23487, ventral internal mold; *10*, RM Br 23484, ventral internal mold. Scale bars=5 mm unless otherwise noted.

Remarks.—*Tolen* n. gen. differs from *Trifissura* n. gen. in having a well-developed costellate radial ornament and a large colleplax extending to mid-valve length, and in having raised anterior adductor and brachial protractor muscle scars bounded by a rim, as well as in the complete absence of a dorsal median ridge and umbonal cavities.

TOLEN MULTICOSTATUS new species
Figure 5.1–5.3

Diagnosis.—Shell transverse, strophic, subequally biconvex; ventral valve with triangular colleplax extending to mid-valve length, slightly raised slightly above outer surface; dorsal valve with hemiperipheral growth; radial ornament of low, bifurcating ribs curved posteriorly towards hinge line; dorsal interior with paired anterior adductor and brachial protractor muscle scars situated on thickened callus of secondary shell and bounded anteriorly and laterally by high rim.

Description.—Shell gently and subequally biconvex, transversely suboval, about 80% as long as wide, with strophic posterior margin occupying about 75% of maximum shell width. Anterior commissure rectimarginate. Ventral valve 23 mm long and 30 mm wide in one specimen, gently and evenly convex in transverse and lateral profile. Colleplax almost triangular, about twice as long as wide, originating at the marginal umbo and extending to mid-valve length. Surface uneven, ornamented by undulating growth lamellae, and slightly raised above surrounding shell surface. Dorsal valve 25 mm long and 32 mm wide in holotype, gently and evenly convex with hemiperipheral growth. Radial ornament costellate, with low rounded, bifurcating ribs about 3–4 per 3 mm along the anterior margin. Ribs separated by wide interspaces and curved posteriorly towards hinge line in posterolateral parts of the shell. Concentric ornament of evenly spaced filae, about 3 per 1 mm.

Ventral interior unknown. Dorsal interior with visceral area extending anteriorly to about 70% of total valve length and bordered anterolaterally by rim. Anterior adductor scars large, elongate suboval, situated at about mid-valve. Brachial protractors on thick callus of secondary shell, situated near anterior termination of visceral area, anterior to mid-valve. Posterior adductors weakly impressed, situated close to posterior margin and bordered laterally by low rim.

Etymology.—Referring to the multicostate radial ornament.

Holotype.—NMW 2001.38G.801, dorsal external mold; Upper Ordovician, Katian, Akdombak Formation, sample 1783, Tolen River, Bakanas river basin, Chingiz Range, Kazakhstan.

Other material.—NMW 2001.38G.801, ventral external mold.

Occurrence.—Late Ordovician of Kazakhstan.

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