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MORPHOLOGY, ONTOGENY AND AFFINITIES OF THE HIRNANTIAN TRIPLISIID
BRACHIOPOD *STREPTIS UNDIFERA* FROM BALTOSCANDIA by LINDA HINTS¹,
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Abstract: New silicified topotypic material of the Upper Ordovician *Streptis undifera* (Schmidt, 1858) from the stratotype of the Porkuni Regional Stage in Estonia provides important data on triplesiid morphology and ontogeny, which has substantial implications for our understanding of the affinity of this group of brachiopods. In particular, the new material shows that the early ontogeny of *Streptis* includes evidence for a cicatrix attachment and colleplax-like structure in the ventral valve. It is likely also that a lecithotrophic feeding habit evolved in triplesiidines sometime in the Ordovician, which sets them apart from all other known strophomenates. A neotype is selected among the specimens of *Streptis undifera* from the type locality in Porkuni. In Baltoscandia, *Streptis undifera* appears first in Norway in late Katian below the strata with the pentamerid brachiopod *Holorhynchus*. In Estonia, *Streptis undifera* is an index species of the early Hirnantian and occurs in association with stromatoporoid-coral reefs and related inter-reef deposits, which overly the strata with *Holorhynchus*. In Baltoscandia, the distribution areas of *Streptis* and *Holorhynchus* are more or less identical in spite of some differences in age.

Key words: Brachiopoda, Triplesiidae, morphology, ontogeny, Upper Ordovician, Estonia.

THE TRIPLESIID brachiopod *Streptis undifera* (Schmidt, 1858) has been used as an index species of the Baltic regional brachiopod biozone (Alichova 1965) corresponding to the lower part of the Porkuni Regional Stage. Hints (1998) defined the *Streptis* Association (*Streptis* fauna in sense of Harper and Hints 2001) in the succession of Ordovician brachiopod faunas in shallow water environments of northern Estonia. *Spirigerina?* (= *Streptis*) *undifera* was described shortly by Schmidt (1858) and listed in several localities of the ‘Borkholm’sche Schicht’ (=Porkuni Stage), including the stratotype section of the stage in the Porkuni quarry in north-eastern Estonia. It is also the type locality for *Streptis undifera* and for *Streptis incompta* described by Ulrich and Cooper (1936). However, the specimens illustrated by them are undistinguishable from *Streptis undifera* and *S. incompta* is presently considered as a junior objective synonym of *S.undifera* (Wright 1965).

The relatively thin valves of most known species of *Streptis* Davidson, 1881 often exhibit only exterior features due to the fact that the shells are most frequently articulated. Thus, the detailed morphology of the valve interiors is poorly known, and although Ulrich and Cooper (1936) described some dorsal interiors, especially the structures of cardinalia, the details of the ventral valve have been virtually unknown (Wright 1965).

Wright (1960, 1965, 1993) provided the most detailed studies of the morphology and taxonomy of the Triplesiidae, including *Streptis*. However, the interior morphology of all available Baltoscandian material of *Streptis* remained poorly understood. The occurrence of the monticulus, the pedicle tube and the keeled cardinal process with a hood are among distinctive features of *Streptis undifera* as discussed by Wright (1993). The species is also characterized by its small size, multicostellate radial ornament and by having a few frills. The new material provides the first information on the detailed interior morphology and ontogeny of *Streptis undifera*, showing that the early development of the triplesiids includes both a foramen, which belongs to the initial attachment structure as well as a cicatrix attachment that developed in the early postmetamorphic shell. This attachment structure can be considered as

modification of the colleplax (*sensu* Wright 1981) – a unique feature which is also known from the enigmatic chileate brachiopods (Rhynchonelliformea, Chileata; Williams *et al.* 1996; see also Popov and Holmer 2000; Holmer *et al.* 2009), including the exceptionally preserved lower Cambrian *Longtancunella* from Chengjiang, China (Zhang *et al.* 2011a). A colleplax has also been recorded from the enigmatic early Cambrian (Botoman) paterinate-like organophosphatic *Salanygolina obliqua* Ushatinskaya, 1987, from Mongolia (Holmer *et al.* 2009, 2011). The foramen and colleplax-like structure of *Streptis undifera* extends internally as a well developed pedicle tube.

The material studied is housed at the Institute of Geology at Tallinn University of Technology (institutional abbreviation GIT) and Museum of Geology, University of Tartu (TUG).

GEOLOGICAL SETTING

The section in the old quarry at Porkuni has been known for more than 150 years. It is situated in the Porkuni village (also known as Borkholm, by its old German name), about 20 km south-west of the town of Rakvere in north-eastern Estonia (Fig. 1). At Porkuni, the Ärina Formation (including four members of the Porkuni Regional Stage) rests on variably argillaceous dolomitic limestone of the Pirgu Regional Stage. The fine-crystalline dolostones of the Rõa Member (1.5 m thick) in the lowermost part of the Porkuni Stage are succeeded upwards by skeletal grainstones of the Vohilaid Member (1.0 m), bituminous wacke- and packstones of the Siuge Member (1.5 m), and by crystalline coral limestones of the Tõrevere Member (1.5+ m) (Hints *et al.* 2000; Hints 2012). The last three units are considered as a ‘reef complex’ (Kaljo *et al.* 2001) characterised by the *Streptis undifera* Association. The bituminous carbonates of the Siuge Member, which is the main source of a new material on *Streptis undifera*, are interpreted ‘as lagoonal deposits perhaps laid down in inter-reef depressions’ (Marshall *et al.* 1997).

The Hirnantian age of the Ärina Formation is based on the occurrence of chitinozoans characteristic of the *Spinachitina taugourdeau* Biozone including the index-species and chemostratigraphical correlation based on carbon isotope data (Marshall *et al.* 1997; Kaljo *et al.* 2001, 2004, 2008). The locality in Porkuni is still accessible unlike the Norwegian locality in Holmenskjaeret (Oslo-Asker region) from where *Streptis undifera* was described by Wright (1965) (D. Bruton, pers. comm. 2012).

NOTES ON TRIPLESIID ONTOGENY

The only previous account of early triplesiid ontogeny was provided by Freeman and Lundelius (2005). They briefly described and illustrated ‘raised protegula’ up to 400 Rm wide on the shell of *Streptis glomerata* Ulrich and Cooper, 1936 from the Silurian St Clair Formation of northern Arkansas. However, judging from the illustrations (Freeman and Lundelius 2005, fig. 4D, E) the single specimen is exfoliated and the so-called elongate protegulum is probably the cast of the internal pedicle tube, similar to those described in other triplesiids (e.g. Wright 1960, fig. 10; Popov *et al.* 2002, pl. 5, fig. 10).

The ventral umbonal area of *Streptis undifera* has neither pedicle sheath nor any structure that can be interpreted as the protegulum. In contrast, the area immediately anterior to the umbo is occupied by a subtriangular foramen, about 200 µm wide, opening into the internal ‘pedicle’ tube (Fig. 2A–C). Part of the shell around the foramen, up to 1.25 mm wide is strongly flattened and is o

ften surrounded by a high rim, which is almost orthogonal to the commissural plane (Fig. 2A). Outside the rim, the regular peripheral growth of the adult shell appears, marked by indistinct radial ornament and closely spaced dense growth lines (Fig. 2G). By contrast, the early growth in the dorsal valve lacks evidence of major growth disturbances. The dorsal umbo is occupied by a slightly inflated smooth area 230–250 µm wide, and outlined by a halo (ha on Fig. 2H, J, M, N), which is considered to represent the metamorphic shell. The dorsal

protegulum in *Streptis undifera* is covered posteriorly by the chilidium (*ch* on Fig. 2J), which was secreted at a later growth stage. Closely spaced growth lines appear immediately outside the halo and they are almost indistinguishable from those in mature shell, but radial ornament is absent. Irregular radial plications only appear in the shells that exceed 1.2-1.3 mm in width, and outside a strong growth disturbance. There is no apparent lobation in the dorsal umbonal area. The size of the metamorphic protegulum in *Streptis undifera* is close to the maximum size of the brachiopod egg (Williams *et al.* 1997; Freeman and Lundelius 2005), whereas the absence of lobation may suggest that it was a rigid structure and probably at least partly mineralised. The shell outside the halo exhibits continuous peripheral growth, which is characteristic of the postmetamorphic shell, thus it was secreted by an adult mantle. The shell was evidently mineralised and calcareous since secondary silicification often occurs in calcified matrix. There is no metamorphic shell or protegulum in the ventral valve, but the observed size of the foramen is closely comparable to the size of the dorsal metamorphic shell. The flattened umbonal area between the rim and the foramen is considered to represent a cicatrix attachment. The absence of growth lines on the cicatrix may suggest that silicified shell belongs to the secondary shell layer, which was secreted under the thick organic pad. The shell, outside the rim, was secreted by the adult mantle. The differences in the initial shell formation of the dorsal and ventral valves in *Streptis undifera* suggest that the onset of shell secretion in the dorsal and ventral valves was diachronous. The metamorphic dorsal protegulum was probably secreted shortly after settlement, whereas secretion of the ventral valve was delayed until the end of metamorphosis. Soon after settlement, the larva was attached by the ventral side of the body and the cicatrix attachment developed shortly after the completions of metamorphosis. This suggests that the attachment structure of the triplesiids represent a modified ventral mantle epithelium and therefore it was not homologous to the pedicle of recent rhynchonelliforms (for further discussion see Popov *et al.* 2007; Holmer *et al.* 2011). The presence of a functional foramen and the ‘internal pedicle’ tube may suggest

that adult triplesiids retained attachment structure, which was probably composed of stacked tabular elements secreted by the specialized mantle epithelium similarly to that described from exceptionally preserved obolellides (Zhang *et al.* 2011b) and chileate *Longtancunella* (Zhang *et al.* 2011a). Thus the attachment structure of *Streptis* most probably represents a modification of a colleplax-like attachment and in wider aspect it can be considered as homologous to the ventral attachment structures that are secreted by the ventral mantle in craniiforms and other strophomenates (Bassett *et al.* 2008; Popov *et al.* 2007, 2010, 2012). However, in comparison to the derived billingsellide *Antigonambonites* (Popov *et al.* 2007) and strophomenides (Bassett *et al.* 2008), the metamorphic shell of *Streptis* is considerably smaller, it lacks lobation and there is no pedicle sheath.

The orthotetidines, which are the closest group to the triplesiidines, also lack pedicle tube and possess a rudimentary colleplax structure; however, they have a significantly larger dorsal metamorphic shell, which encloses the metamorphic protegulum and two pairs of lobes showing position of larval setal sacs (M. G. Bassett pers. comm. 2012). These differences suggest that the larval stage in *Streptis* was considerably shorter than in other strophomenates and it is in favour of a lecithotrophic larval feeding habit. In that respect, the ontogenetic sequence of *Streptis* shows striking similarity to those of Early Palaeozoic craniides and craniopsides (Popov *et al.* 2012). All these brachiopods had a dorsal metamorphic shell of similar sizes and lacking lobation, which suggest an early onset of mineralization. The foramen of *Streptis* is comparable and probably homologous to the initial attachment scar of craniides and craniopsides, whereas the cicatrix suggests a presence of the attachment structure secreted by the modified ventral mantle epithelium. It is likely that the lecithotrophy in craniiforms and triplesiidines evolved independently during the Ordovician.

SYSTEMATIC PALAEONTOLOGY

Order ORTHOTETIDA Waagen, 1884

Suborder TRIPLESIIDINA Moore, 1952

Superfamily TRIPLESIOIDEA Schuchert, 1913

Family TRIPLESIIDAE Schuchert, 1913

Genus STREPTIS Davidson, 1881

Type species. Terebratula grayii Davidson, 1848; from the Silurian Wenlock Limestone of Staffordshire, England.

Streptis undifera (Schmidt, 1858)

Text-Figures 2–4

1858 *Spirigerina? undifera* n. sp. Schmidt, p. 212.

1923 *Atrypa undifera* Schmidt; Bekker, p. 55, pl. IVh.

1936 *Streptis incompta* n. sp. Ulrich and Cooper, p. 345, pl. 50, figs 13, 25–217, 29, 30, 33–35.

1960 *Streptis incompta* Ulrich and Cooper; Nikiforova, pl. 26, figs 11–13.

1965 *Streptis undifera* (Schmidt); Wright, p. 474.

1986 *Streptis undifera* (Schmidt); Hints, p. 21, pl. 1, figs 1–18, pl. 2, figs 1–10.

2000 *Streptis undifera* (Schmidt); Wright, p. 689, fig. 497, 3d.

Neotype (selected here). Dorsal valve GIT 626-49, Fig. 3A–E; Porkuni quarry, sample C95-658 (P. Männik), 0.50–0.75 m below the upper boundary of the Siuge Member, Ärina Formation Porkuni Stage, NE Estonia.

The Schmidt's species was first illustrated in a drawing by the Estonian geologist H. Bekker (1923, p. 55, pl. 4). Unfortunately the illustrated specimen was lost and despite an extensive search it cannot be located. Therefore a neotype is selected among the topotypes.

Other material. GIT 626-39–44; 626-50–55; 626-86–103; 156–176; GIT 230-1–26. Data on all specimens see Geological collections of Estonia: Online catalogue.

Description. Medium-sized *Streptis* with a dorsibiconvex shell, about 70 to 80 per cent as long as wide, and with hinge line occupying about 60 per cent of maximum shell width. Cardinal angles rounded; anterior commissure with asymmetrical plication. Ventral valve acuminate, subtriangular in outline, with a conical umbonal part extending over the hinge line; ventral interarea triangular, apsacline, planar, slightly curved immediately below the beak, about 25 per cent as high as wide. Pseudodeltidium with a monticulus forming a sharp crested median fold. Umbo with a vestigial colleplax-like structure and a slightly elongate, subtriangular foramen, opening into the internal pedicle tube. Ventral median sulcus weakly defined anterior to the cicatrix attachment, deepening anterior to mid valve. Dorsal valve transversely oval with maximum convexity in the posterior part and a vestigial interarea. Convex chilidium (hood) developed above the proximal end of the cardinal process. Dorsal median fold asymmetrical, originating near mid valve.

Concentric ornament of up to eight thin frills up to 2 mm long, commonly with 4–5 frills on each valve; distance between frills varying from 0.2 to 2.0 mm, but most commonly 1.4–1.5 mm apart. Shell surface with fine concentric filae, about 15 per 1 mm. Radial ornament of uneven, rounded ribs, with 5–20 ribs appear outside of the halo, ribs increasing anteriorly in number by intercalation and widening towards the edge of every frill.

Ventral valve with blade-shaped teeth, supported by thin dental plates with slightly divergent bases. Delthyrial cavity occupied mainly by a truncated conical pedicle tube with a circular interior aperture. Inner side of the pseudodeltidium merged with a thin arched plate supporting the pedicle tube. Ventral muscle field generally poorly defined, but a single specimen exhibits two weakly developed ridges, possibly representing myophragms.

Dorsal cardinal process keeled; prongs long, diverging at an angle of about 30–35 degrees. Distal dorsal ends of prongs deeply grooved. Socket ridges small, laterally directed, merging

with the cardinal process base. Adductor muscle field suboval, extending to mid valve, with narrow, wedge-like posterior scars and large suboval anterior scars.

Remarks. The type species *Streptis grayii* (Davidson) as revised by Bassett (1972) can be easily distinguished from *Streptis undifera* in having numerous, densely spaced frills and a strongly twisted shell. According to Wright (1993) the type species differs from *S. undifera* in having a grooved cardinal process, instead of a keeled process in *S. undifera*.

Streptis monilifera (M'Coy) from the Upper Ordovician (Katian) of Ireland and *Streptis altosinuata* (Holtedahl) from the Llandovery of Norway are two closely related species that were considered by Wright (1960) as members of a single phyletic lineage including *Streptis undifera* as a transitional taxon. *Streptis undifera* and *Streptis altosinuata* are similar in size, both usually not exceeding 10 mm in width. However, *Streptis undifera* has a high ventral interarea and fewer number of frills (not exceeding eight), whereas *Streptis altosinuata* has up to 12 densely spaced frills (Wright 1960, pl. 1, fig.11).

There is little difference in concentric ornament between *Streptis undifera* and *Streptis monilifera*, but the latter species has a relatively low ventral interarea and a strongly developed ventral sulcus and dorsal median fold.

Occurrence. Upper Katian (5a) in Norway. Hirnantian Porkuni Regional Stage, Ärina Formation in Estonia.

STREPTIS IN BALTOSCANDIA

Streptis undifera is most common in the Porkuni (Hirnantian) reef complex of the marginal confacies belt (Nestor and Einasto 1997), which is distributed over 200 km from the northwestern (Island of Hiiumaa) to north-eastern Estonia (Fig. 1). In Hiiumaa (NW Estonia), the uppermost Adila Formation occasionally contains the pentameride brachiopod *Holorhynchus*, which is otherwise widely spread in south-eastern Latvia and Lithuania (Hints 1993, 1998). The earliest (late Katian) representatives of *Streptis undifera* in Norway (Wright

1965) occur in the Langara Formation of the Holmenskjaeret section (Wright 1965; Brenchley and Newall 1975; Owen *et al.* 1990) below the algal *Palaeoporella* limestone (D. Bruton, pers. comm. 2012) and the *Holorhynchus* Shale (Bockelie 1982) of pre-Hirnantian age (Rong and Harper 1989; Brenchley *et al.* 1997). It may be noted that apart from Baltoscandia, both genera *Streptis* and *Holorhynchus* are known also from Kazakhstan, where they occur in the Upper Ordovician Chokpar Regional Stage (Nikitin *et al.* 1980, 2006).

Streptis monilifera (M'Coy) is another Ordovician species, which inhabited off-shore environments and it has been reported from carbonate mud mounds in Ireland, including Chair of Kildare and Portrane limestones (Wright 1960, 1964) and in northern England, e.g. Keisley Limestone (Cherns and Wheeley 2007). These mounds, as well as the Boda mud mound in Sweden, where *Streptis cf. monilifera* occurs (Wright 1993), belong to the offshore environments (Nestor 1995, Cherns and Wheeley 2007; Suzuki *et al.* 2009) unlike onshore stromatoporoid-coral reefs in northern Estonia, which were inhabited by *Streptis undifera*. *Streptis* is among just a few brachiopods that survived the end-Ordovician extinction (Cocks and Rong 2007). The early Silurian (Rhuddanian) species *S. monilifera* and *S. altosinuata* were replaced by *S. grayii* (Davidson) at the beginning of the late Llandovery (Wright 1960; Temple 1970, 1987; Rubel 2011). This species has much wider spatial distribution as compared with the Ordovician representatives (Baltoscandia, UK, Bohemia, Podolia; Rubel 2011; Tsegel'nyuk 1976; Havlíček and Štorch 1990). The Wenlock species *Streptis glomerata* is restricted only to North America (Arkansas, Ulrich and Cooper 1936; Arctic Canada, Zhang 2001). *Streptis* may have evolved from some earlier triplesiid taxon that inhabited carbonate mud mound environments in Baltoscandia or Avalonia; however, it may also represent an immigrant to the region as a part of the *Holorhynchus* Association. It is also likely that the stromatoporoid-coral build-ups in North Estonia might represent a refugium, where these brachiopods survived the terminal Ordovician extinction and later spread to Laurentia sometime during the early Silurian.

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ZHANG, Z., HOLMER, L. E., OU, Q., HAN, J. and SHU, D. 2011a. The exceptionally preserved Early Cambrian stem rhynchonelliform brachiopod *Longtancunella* and its implications. *Lethaia*, **44**, 490–495.

----, L. E., POPOV, L. E. and SHU, D. 2011b. An obolellate brachiopod with softpart preservation from the early Cambrian Chengjiang Fauna of China. *Journal of Paleontology*, **85**, 462–465. **FIG. 1.** Location map showing distribution of Baltoscandian facies belts and the distribution of the Porkuni Stage, with inset map showing drill cores and outcrops with *Streptis undifera* along the northern part of the distribution area of the Ärina Formation (after Schmidt 1858; Rõõmusoks 1967; Hints 1986; and new data). Outcrops: 1, Vohilaid; 2, Heltermaa (erratic boulders); 3, vicinity of Varbola: Ruunavere, Kännu village (erratics); 4, Seli-Metsküla and Seli-Russalu; 5, Roa and Roa-Jakobi; 6, Hargla (Harküla) and Habaja; 7, Siuge; 8, Roosna; 9, Koigi; 10, Porkuni; 11, Ärina; 12, Veadla; 13, Aruküla; drill cores: 14, Vodja (No 192); 15, Puhmu; 16, Vistla-I; 17.

FIG. 2. *Streptis undifera* (Schmidt, 1858), sample 658 (Männik), 0.5–0.75 m below the upper boundary of the Siuge Member, Arina Formation, Porkuni Stage; A–D, F, GIT 626-39, ventral valve exterior, umbonal area, oblique lateral view of umbonal area, oblique posterior view of umbonal area showing internal pedicle tube (ipt) inside of foramen and internal foramen (if); E, GIT 626-177-1, ventral interarea; G, GIT 626-177-2, ventral valve exterior; H–I, N, GIT 626-96, dorsal valve umbonal area showing halo (ha) and anterior part of the metamorphic shell (ms), dorsal exterior; J, GIT 626-94, dorsal umbonal area showing chilidium and metamorphic shell; K–L, GIT 626-94, dorsal valve exterior, posterolateral view of umbonal area; M, O, GIT 626-95, oblique posterior and oblique lateral views of umbonal area; N, GIT 626-177d, oblique lateral view of dorsal umbonal area.

FIG. 3. *Streptis undifera* (Schmidt, 1858), sample 658 (Männik), 0.5-0.75 m below the upper boundary of the Siuge Member, Ärina Formation, Porkuni Stage. A–E, neotype, GIT 626-64, dorsal valve, interior, exterior, oblique interior (with weakly expressed adductor fields), lateral and anterior views on the cardinal process. F and G, GIT 626-51, oblique view on the interior and exterior view of incomplete dorsal valve. H, GIT 626-55, view on cardinalia with keeled cardinal process. I and J, GIT 626-156-1, exterior and interior views of dorsal valve. Scale bar is 1 mm.

FIG. 4. *Streptis undifera* (Schmidt, 1858); A, B and D–G sample M 658 (P.Männik), 0.5–0.75 m, and C and H, sample M 335, 0.3–0.4 m below the upper boundary of the Siuge Member, respectively; Ärina Formation, Porkuni Stage. A–C, GIT 626-40, ventral valve exterior and interior (with a bryozoan colony) , and oblique view on pedicle tube, teeth and arched plate above the pedicle tube. D–E, GIT 626-168, views on the interarea with monticules, and oblique view on pedicle tube, teeth and arched plate above the tube of the incomplete ventral valve. F, GIT 626-169, oblique view on pedicle tube and teeth of ventral valve. G and H, GIT 626-158, view on interior and interarea with monticules of the incomplete ventral valve. Scale bar is 1 mm.