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Spat fall and mature growth of large-shell brachiopods (Stricklandia lens lens) from the Solvik Formation (lower Silurian) at Sandvika in the Oslo Region of southern Norway

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A population of large-shell brachiopods belonging to *Stricklandia lens lens* from the lower Silurian Solvik Formation is exposed in a capstone layer covering approximately 300 m^2 on steeply dipping strata along the shores of Engervannet at Sandvika in the Oslo Region of southern Norway. Based on sample counts, a density estimated at 250 to 350 articulated shells per square meter resulted from crowding during growth. Given that the former sea bed on which the brachiopods settled can be traced over a lateral distance of 60 m with an average width of 5 m, it is calculated that a monospecific population exceeding 90,000 brachiopods matured from a single, extensive spat fall. Related large-shell brachiopods from the lower Silurian of North America, including *Virgiana decussata, Pentamerus oblongus, P. palaformis,* and *Pentameroides subrectus* are commonly preserved in growth position, but observed pavements rarely exceed more than 0.25 m^2 in size. Articulated shells within those populations are almost always truncated midway above the beak and hinge area due to post-mortem erosion by submarine scour. In contrast, the horizon with *Stricklandia* shells from Sandvika is enormous in scope and features many whole individuals pushed into a more recumbent position in the same direction by a marine current. Re-orientation of the steeply inclined limestone layer to a horizontal position suggests that such a current flowed from the present-day southwest to the northeast as it swept over the Silurian sea bed.

Introduction

The Suborder Pentameridina Schuchert & Cooper, 1931 features more than a score of large-shell brachiopods from the Silurian of North America, the British Isles, Scandinavia, western Russia, and parts of China commonly expressed with an elongated shell shape. Silurian genera within this classification include *Virgiana, Borealis, Pentamerus, Sulcipentamerus, Pentameroides, Ehlersella, Conchidium, Kikidium, Rhipidium, Stricklandia,* and *Costistricklandia*, among others. In particular, species attributed to *Pentamerus* and *Stricklandia* from the lower Silurian Llandovery Series are the dominant members associated with multiple co-existing species assigned to marine communities under those names.

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In the scheme introduced by Ziegler et al. (1968a), the *Stricklandia* Community was interpreted as possessing a higher diversity of species than the *Pentamerus* Community. It was shown to occupy deeper, more offshore waters as originally mapped from the coastal paleogeography of Wales and the Welsh Borderland with England (Ziegler et al., 1968b).

Boucot (1975, p. 13) codified these relationships in terms of quiet-water and rough-water settings inhabited by benthic-dwelling associations BA1 to BA5, in which the *Stricklandia* Community was assigned to BA4 and the *Pentamerus* Community to BA3. The advantage of the benthic-assemblage system was that paleocommunities from the Silurian and Lower Devonian systems could be identified and compared under the same organizational scheme related to an onshore-offshore gradient (Boucot & Lawson, 1999). Among some 25 regions with Silurian and Devonian strata from around the world with benthic assemblages, Baarli et al. (1999) defined those from the Oslo region of southern Norway, including the *Pentamerus oblongus* and *Stricklandia lens* communities. The *P. oblongus* Community is described as a high-dominance, low-diversity community that includes halysitid and favositid corals (Baarli et al., 1999, p. 340). Variations on a deeper-water community are listed in a form composed exclusively of *Stricklandia lens* and a more diverse form called the *Stricklandia lens* – Rugose Coral Community associated with ten other brachiopods, a mixture of rugose corals with halysitid and favositid corals, as well as assorted trilobites, gastropods, and bryozoans (Baarli et al., 1999, p. 345). In both cases, community membership is based on analysis of bulk samples in which a census was tabulated for all recognizable fossils.

Biologists perform census work under field conditions that provide a rigorous basis for defining the biodiversity of any living benthic community. The community concept, as applied to the fossil record, is flawed due in part to the fossilization process that typically excludes soft-bodied invertebrates and most marine algae. However, natural populations of a particular species in a genuinely biological sense are recorded in the fossil record, especially where those individuals are preserved in life position. Examples by Ziegler et al. (1966) pertain to densely packed clusters of 64 articulated *P. oblongus* shells and 52 articulated *S. lens* from the lower Silurian of Alabama in the United States and the Girvan district of Scotland, respectively. In both cases, brachiopod clusters were excavated from the undersides of a sedimentary stratum representing a small patch of the original sea bottom little more than 0.25 m^2 in coverage.

This contribution describes an extraordinary example of fossil preservation that entails an immense natural population of a large-shell brachiopod species from the lower Silurian Solvik Formation exposed near Sandvika in the Oslo–Asker Region of southern Norway. The project aims to achieve the following goals: 1) establish the stratigraphic succession in which the population is retained; 2) confirm the stage of evolution in the *Stricklandia mullochensis /S. laevis* lineage represented by the population according to criteria established by Baarli (1986); 3) quantify the size of the population given the total area of the outcrop exposure; 4) appraise environmental conditions that both preceded the establishment of the population and followed after to ensure its ultimate preservation; and 5) offer comparisons with similar large-shell brachiopod populations from other studies in Norway and elsewhere in the Silurian world.

Geologic setting

Lower Silurian strata from a dozen districts of southern Norway occur between Hamar in the north and Skien in the south within a 180-km-long graben structure that formed during Permian time (Worsley, 1989). Metropolitan Oslo, which borders Sandvika in the neighboring municipality of Bærum (Fig. 1A), is part of one such district that also includes islands where contact with the underlying Ordovician

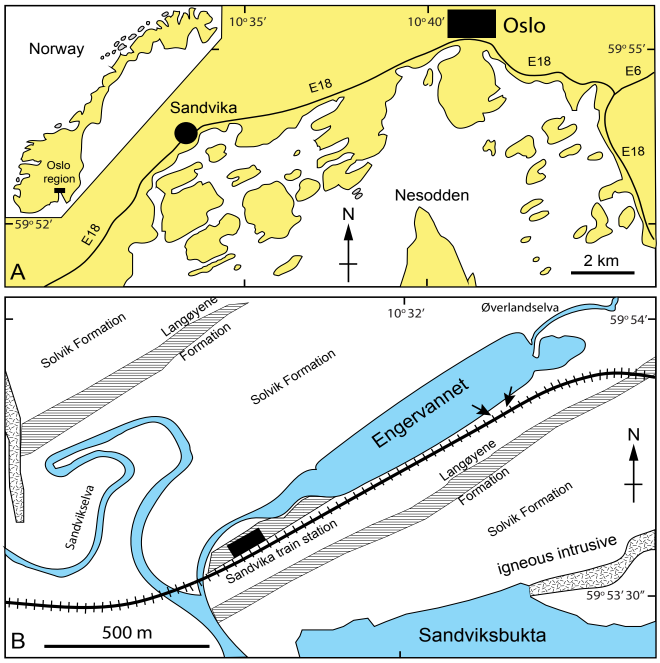

Figure 1. (A) Geographic map for the Oslo Region in southern Norway and (B) geological relationships in the vicinity of Sandvika surrounding Engervannet.

System is exposed (Bockelie et al., 2017). The sedimentology and benthic faunas of the basal Silurian Solvik Formation were investigated by Baarli (1985, 1987) with particular emphasis on the Oslo–Bærum–Asker areas. Subsequently, Baarli (2014, Fig. 2) determined that the Solvik Formation originates in the Upper Ordovician with as much as 8 to 10 meters overlying the Langøyene or laterally equivalent Langåra formations still below the Ordovician–Silurian boundary on islands in the Oslofjord as well as the coastal Asker area.

This study examines the area around Engervannet east of the Sandvika town center, where train tracks on the Oslo line cross a rise formed by the Solvik Formation adjacent to the lake (Fig. 1B). In particular, the Silurian interval of the Solvik Formation at the lakeshore is calculated to be 87 m above the top of the Ordovician Langøyene Formation based on map relationships available through the National Bedrock Database maintained by the Norwegian Geological Survey. The lithology and abundance of corals and stromatoporoids suggest that strata at that location belong to the Spirodden Member of the Solvik Formation, the second of three members that define the formation in Asker (Baarli 1985, 1987). The Langøyene/Solvik sequence is repeated in parallel bands trending southeast to northwest across the area due to the arrangement of fault blocks composed of steeply dipping layers (Fig. 1B).

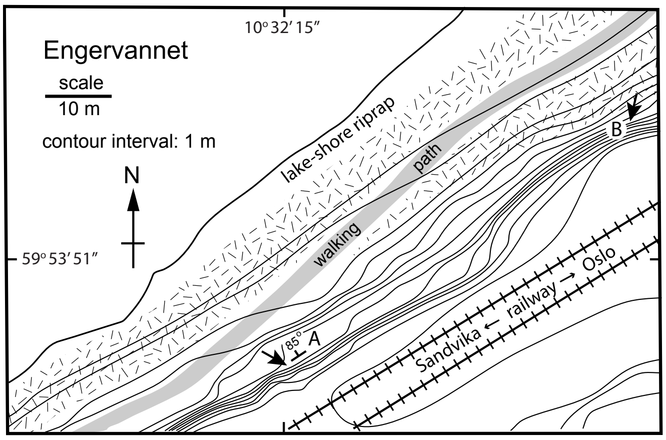

Figure 2. Topographic map representing the cliff exposure adjacent to the walking path along the southern shore of Engervannet (enlargement of the area between the two arrows in Fig. 1B). Details derived from the National Bedrock Database maintained by the Geological Survey of Norway. Field data collected from two localities labeled A and B.

Kiær (1908, p. 312) offered the earliest interpretation of this geological setting, illustrating repetition of fault segments in the Ordovician–Silurian succession surrounding Engervannet, although his otherwise detailed work provides no mention of fossils from strata around the lake's shoreline.

A more detailed map of the study site (Fig. 2) reveals the topography along the embankment between the railway line and the lake shore of Engervannet as delimited by a pair of arrows towards the east end of the lake seen in Fig. 1B. Access to the Engervannet area is by a walking path from the town center along the entire south shore of the lake. Eastward from the Sandvika train station, the rock outcrop is first encountered after a distance of 0.75 km at the end of a concrete retaining wall that reinforces the embankment protecting the train tracks (Longitude 10°32'15" and Latitude 59°53' 49"). The path varies between a meter or two above the lake surface, which is maintained barely above mean sea level before outflow to the Sandvikselva. Of particular interest is a bedding-plane with underlying rock layers from the Spirodden Member that dip steeply toward the lake at an angle of 85° on a strike of N30°E congruent with the trend of outcrop exposure expressed topographically by closely spaced lines at one-meter intervals. These trace out for a lateral distance of 60 m with an increase of six to seven meters between the walking path below and the train tracks above (Fig. 2, localities A & B).

Methods of study

Measurements for a stratigraphic profile within the Spirodden Member of the Solvik Formation were compiled at a spot on the outcrop close after the termination of the concrete retaining wall (coordinates provided above), where topographic lines are widely spaced across truncated rock layers (Fig. 2, west arrow). Data so assembled were plotted to summarize changes in lithology through a nearly 3 m-thick profile of strata perpendicular to dip. Fossil content also was recorded on a bed-by-bed basis. The stratigraphic sequence is capped by a single layer bearing large-shell brachiopods in life position.

Brachiopod samples from the bedding plane in the upper part of the sequence were collected for laboratory treatment by dilute hydrochloric acid to remove the calcareous shell. Casts of the brachial valve were made to reveal tell-tale features of internal shell structures that relate to evolution in the *Stricklandia mullochensis /S. laevis* lineage. These were first recognized by St. Joseph (1935) based on brachiopods from Wales. Subsequently, Baarli (1986) formulated a combination of measurements for biometric analyses based on sampled material from Wales, Norway, and Estonia. Easy Mold ™was used to make the casts after the dissolution of the calcareous shell. Measurements done under a binocular microscope include the length from the posterior point of the cardinalia to the anterior projection of the outer plates; the length from the posterior point of the cardinalia to the anterior point of the inner plates, where fused with the brachial processes; and the height measured from the anterior point of the inner plates, where fused with the brachial process vertically at the base of the valve floor (Baarli, 1986, p. 191).

Sample quadrates at two locations with well-preserved concentrations of brachiopods were outlined on the bedding surface of the capstone and photographed in place. These were subsequently viewed at an enlarged scale on a computer screen to determine population counts that were normalized to reflect the number of individuals in a square meter of the former seabed. In order to evaluate population dynamics, variations in shell size and possible orientation by bottom currents were appraised using the statistical package of software formulated by Hammer et al. (2001). Finally, the placement of articulated shells in the two sample populations also was analysed from field photos via the computer screen to detect any preferred orientation influenced by marine currents.

Results

Local stratigraphic profile

Fig. 3 depicts the stratigraphic profile compiled at the western end of the outcrop zone with nearly 3 m of Silurian strata confined to the Spirodden Member of the Solvik Formation. The sequence shows a transition from shale domination in the first meter through a shift from siltstone to very fine

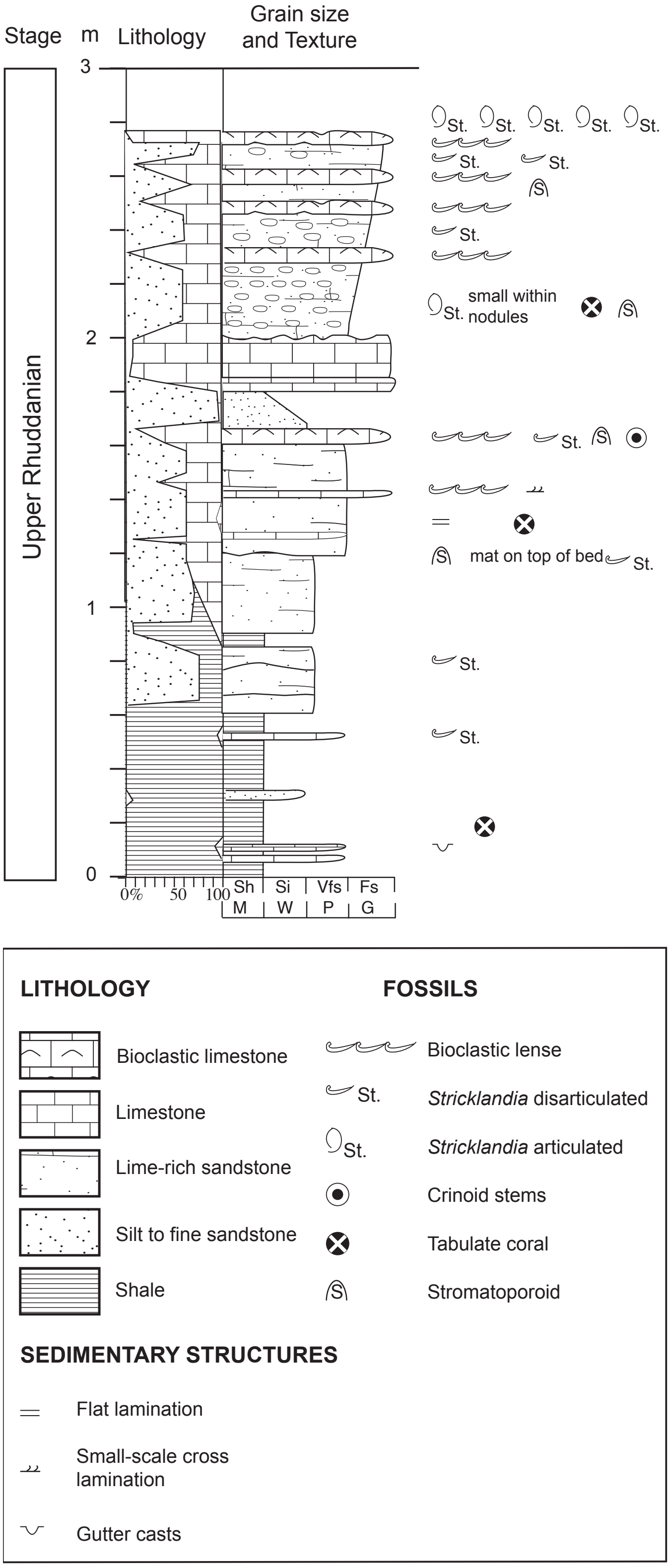

Figure 3. Stratigraphic column from Silurian cliffs that crop out along the southern shore of Engervannet capped by Stricklandia lens lens *preserved in growth position (see Figure 2 labeled with a strike of N30°E and dip of 85°). Sh = shale, Si = silt, Vfs = very fine sandstone, Fs = fine sandstone siliciclastic rock. M = mudstone, W = wackestone, P = packstone, and G =grainstone carbonates.*

sandstone upward through much of the second meter with the gradual introduction of more lime-rich material. The upper meter reveals the introduction of limestone interbeds formed by grainstone and shell debris. Disarticulated shells of *Stricklandia* occur through parts of the sequence but with few indications of whole shells until the final capstone. Tabulate coral colonies and stromatoporoids occur randomly through much of the succession, but never in clusters. Prominent gutter casts are found near the bottom part, and evidence of small-scale cross-lamination occurs in the middle of the sequence. Limestone nodules are limited to the upper part of the sequence, in some cases including the shells of *Stricklandia.* Overall, this short stratigraphic succession may be interpreted as a change in environment from a more quiet-water setting bearing fine clastic sediments to a markedly higher-energy setting with grainstone deposits enriched by shelly material. This section differs from the lithology at the type location of the Spirodden Member in nearby Asker (Baarli, 1985) by exhibiting a coarser clastic input and a higher frequency of bioclastic interbeds deposited in a more proximal or shallow-water setting. The appearance of a relatively pure limestone bed two meters up attests to periods when clastic input was reduced. The section ends with a 10 cm-thick, coarse, bioclastic bed that supports whole shells preserved in growth position.

Subspecies identification

Measurements from internal structures sampled from the brachial valves of *Stricklandia* are summarized in Table 1. These measurements from eight specimens were inserted to the equation (a + c) / b and vary in value between 1.43 and 1.66, with an average of 1.54. This result falls squarely in the middle of what is defined as the subspecies *S. lens lens* (Baarli, 1986). Fig. 4 illustrates the internal molds for three of the eight specimens used for measurements together with the casts recovered for their respective internal structures. Locally, the same subspecies also occurs in the Spirodden Member at the type locality in nearby Asker. Smaller concentrations of *S. lens lens* are registered there (Baarli, 1987). However, the sheer number and robust size of individuals (maximum 9.5-cm shell width in the plane of the commissure) at Sandvika far surpass anything known from the Asker area. Addition of the Sandvika discovery adds to the overall recognition of the *Stricklandia mullochensis /S.* laevis lineage and its stratigraphic range in the Oslo region (Baarli & Johnson, 1988). Outside Norway, the same subspecies of *S. lens lens* from the lineage also occurs in lower Silurian strata from Wales and Estonia (Baarli, 1987).

Table 1. Measurements (mm) from internal structures on the brachial valve of Stricklandia *inserted to the formula (a + c) / b for determination of subspecies following the method of Baarli (1986).*

Sample	PMO number	Outer plate (a)	Inner plate (b)	Height (c)	(a + c) / b
1	234.646	3.71	3.18	1.11	1.51
2	234.647	6.79	5.29	1.69	1.57
3	234.648	6.69	5.36	1.91	1.60
4	234.649a	4.24	3.36	1.34	1.66
5	234.649b	4.55	4.07	1.35	1.45
6	234.64	5.12	4.92	1.91	1.43
7	234.649d	4.01	3.36	1.52	1.65
8	234.649e	6.25	6.04	2.28	1.41
Average		4.46	3.98	1.19	1.54

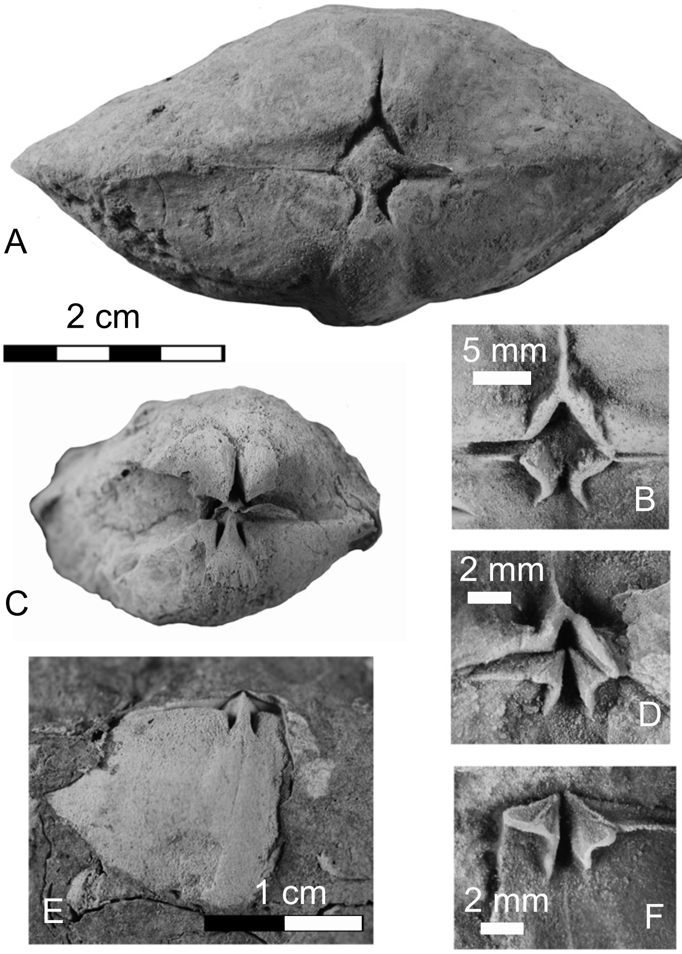

Figure 4. Brachiopods tested for evolutionary position in the Stricklandia mullochensis /S. laevis *lineage: (A) Internal mold of* Stricklandia lens lens *(PMO 234.646), (B) cast from the brachial valve of the same specimen, (C) Internal mold of* S. lens lens *(PMO 234.648), (D) cast from brachial valve of the same specimen, (E) Internal mold of* S. lens lens *brachial valve (PMO234.647) and (F) cast from same.*

Population density and dynamics

The capstone layer bearing articulated shells of *S. lens lens* starts at the western end of the outcrop where the stratigraphic profile is established (Fig. 3). Here, the layer is limited in dimensions and no observations on population density were attempted. The same bedding plane extends eastward without interruption within easy reach of the walking path. The steeply dipping capstone layer rises to a height of 5 m roughly 12 m from the west end (Fig. 3, locality A). There, ample opportunity was available for a random census sample as outlined by a white rectangle superimposed on the outcrop photo (Fig. 5). Using a close-up photo of the same rectangle oriented to fit as many shells as possible within an x and y axis 60 cm by 50 cm, an overlay traces articulated shells shown in cross-section as beveled by erosion (Fig. 6). Some spots within the sample area are corroded, but 74 well-defined individuals occur within an area of 3,000 cm^2, which represents 30% of a square meter. A comparable population with the same density scaled to a square meter would amount to 247 individuals.

The same bedding plane extends another 50 m eastward without interruption, although access from the walking path is difficult due to the accumulation of talus below the cliff face. Crossing by foot to the top of the talus pile, it is possible to follow the bedding plane over that distance. However, dense vegetation makes it difficult to both photograph the surface and establish census counts. A superior opportunity for unimpeded access to the bedding surface occurs at the eastern end of the outcrop area (Fig 2, locality B), where it is exposed 6 m above the pathway at the top of the talus slope. Here, the bedding plane rises 7 m at a steep angle. A field photo recorded from this area demonstrates the large surface area of the exposed bedding plane with a white rectangle superimposed to show the

Figure 5. Cliff face of tilted Silurian limestone along the walking path on the southern shore of Engervannet 12 m distal from the western end of the outcrop as mapped in Figure 2, with the coauthor for scale. White rectangle demarks a sample area with a cluster of Stricklandia lens lens *preserved in growth position.*

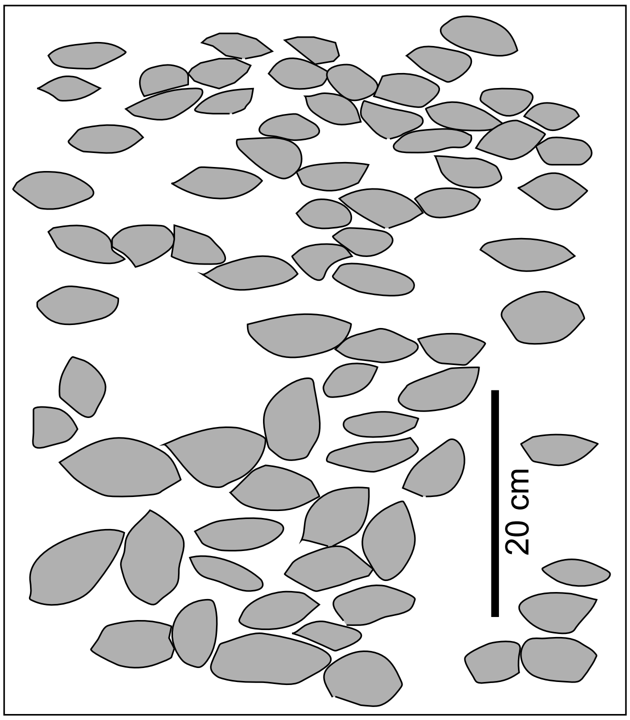

Figure 6. Outlines of articulated brachiopods in the cluster of Stricklandia lens lens *traced from the sample rectangle in Figure 5.*

boundaries of a census sample (Fig. 7). The surface sampled represents an area of 3,744 cm^2 within which a total of 132 articulated brachiopods are recognized (Fig. 8). As before with the previous census sample (Fig. 6), some spots are too corroded to allow a more accurate count. However, a comparable population with the same density scaled to a square meter would amount to 350 individuals at this locality. The single bedding plane visible in the field photos (Figs. 7 & 8) covers 15 m^2 with an estimated population of 5,250 brachiopods preserved in life position. Using a more conservative estimate of 300 brachiopods per square meter, the total number of brachiopods retained in the same condition over the entire exposure of 300 m^2 on the south shore of Engervannet would equal at least 90,000 individuals.

Abundant whole shells are preserved at locality B (Fig. 2), but their removal in order to conduct an accurate analysis of variations in shell size would result in significant degradation of the outcrop. Locality A near the western end of the outcrop was used to register measurements for the maximum width of the exposed commissure in a consistent way not possible at locality B. All brachiopods at locality A were beveled at an unknown distance above the beak and hinge area (Figs. 5 & 6), but those measurements are regarded as proportional to one another. A histogram based on a sample divided into six bins (Fig. 9) shows a normal curve with a skewness value indicative of growth dynamics in a natural population. That is, fringe values from the smallest and largest individuals are reasonable in the context of mean shell size. Evidence for a unified population from a single spat fall draws from examples of shell deformation during growth by the impingement of neighboring individuals (see upper part of Fig. 6).

Figure 7. Cliff face of tilted Silurian limestone 5 m above the hiking path on the southern shore of Engervannet near the distal east end of the outcrop as mapped in Figure 2, with the first author for scale. White rectangle demarks a sample area with an exceptionally well-preserved cluster of Stricklandia lens lens *preserved in growth position.*

Figure 8. Enlarged image of the sample area on the bedding plane outlined in Figure 7 with many whole shells of Stricklandia lens lens *preserved in growth position. The notebook at the side is 18 cm in length.*

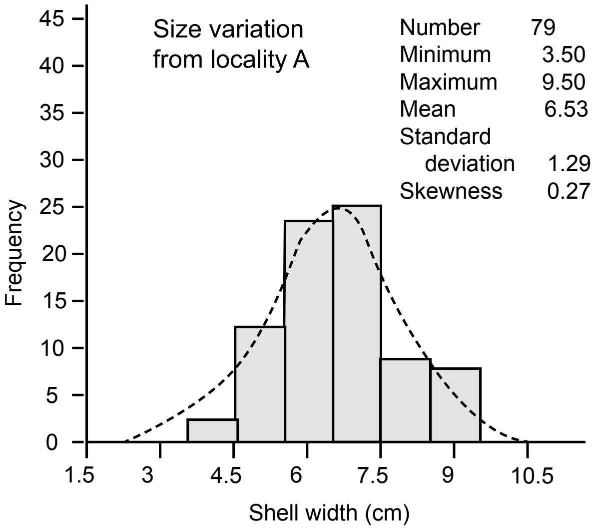

Figure 9. Histogram based on size variation in maximum observable shell width from a population of brachiopods at locality A (see Figs. 5 & 6).

Marine current dynamics

The orientation of individual brachiopods within large populations preserved at a single stratigraphic level above Engervannet suggests a relationship to bottom currents on the former Silurian sea bed. Whole shells reside on a cemented shell pavement that originated as a high-energy event. Most likely, a bottom current scoured the seafloor leaving a firm surface for settlement of an enormous spat fall of *Stricklandia*. Patterns of orientation attained in life are reflected by rose diagrams that indicate the likely direction of fair-weather current flow (Fig. 10). Based on orientations recorded from the census sample at locality A near the western end of the outcrop area (Figs. 5 & 6), it is found that maximum shell width measured in the commissural plane falls into a preferred alignment well defined in the rose diagram (Fig. 10A). In this case, the brachiopods are truncated by erosion midway above the beak and hinge area. Shell width is the best measurement because those lines are well defined and yield the most accurate entry as data points in a rose diagram. In their study of atrypide brachiopods, Manceñido & Gourvennec (2008) suggested that such a uniform pattern of orientation is related to the most efficient method of respiration for water circulation entering the shell cavity. The sub-horizontal pattern resulting from 100 measurements (Fig. 10A) implies a current flow that passed over the brachiopod population to impact each individual against its broad surface before being deflected to enter through the commissure of the individual from the sides. Theoretically, such a current could originate from one direction or reverse flow under some diurnal mechanism to switch back and forth from opposite directions.

A different but complementary pattern appears from the orientation of brachiopods analysed from the census sample at the east end of the outcrop area (Fig. 2, locality B & Fig. 7). In this case, a substantial number of individuals are preserved in a semi-recumbent position that resulted in burial and fossilization of the entire brachiopod (Fig. 8). A subsample of that population (Fig. 11) depicts the orientation of whole brachiopods pushed into a semi-recumbent position such that the anterior portion of each shell overlaps onto the beak or posterior area of its nearest neighbor. The view above the capstone layer is what one would expect to see as an observer swimming over the Silurian seabed. In this case, measurements were taken along the observable axial length of 73 shells (Fig. 10B). Based on those measurements, the resulting rose diagram is perpendicular to that obtained from the sample at the western end of the outcrop area recording shell widths (compare Figs. 10A & 10B). As the brachiopods from both samples reside on the same extensive bedding plane, it is more likely that the same unidirectional current influenced populations across the entire surface of the seabed. If that were the case, the population at the western end of the outcrop area was better anchored to remain fully upright in position.

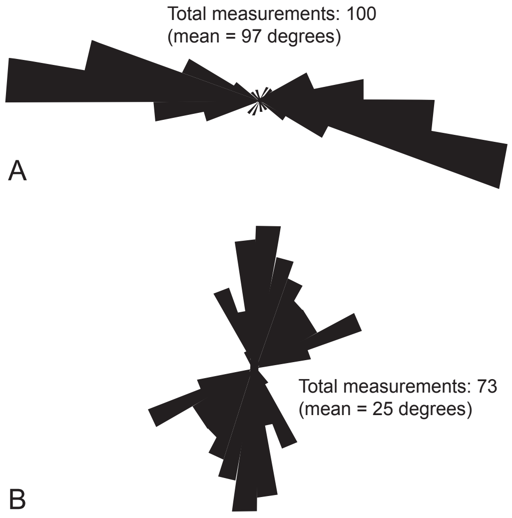

Figure 10. Rose diagrams showing preferred orientation of articulated shells of Stricklandia lens lens. *(A) Census sample from locality A near the western end of the outcrop area (Figs. 2, 5, & 6) where the orientation of maximum shell width is traced parallel to the hinge line. (B) Census sample from locality B at the eastern end of the outcrop area (Figs. 7 & 8) where the orientation of observable shell length is traced perpendicular to the hinge line. In both examples, up corresponds to up on the rock face and left or right to the same on the rock face.*

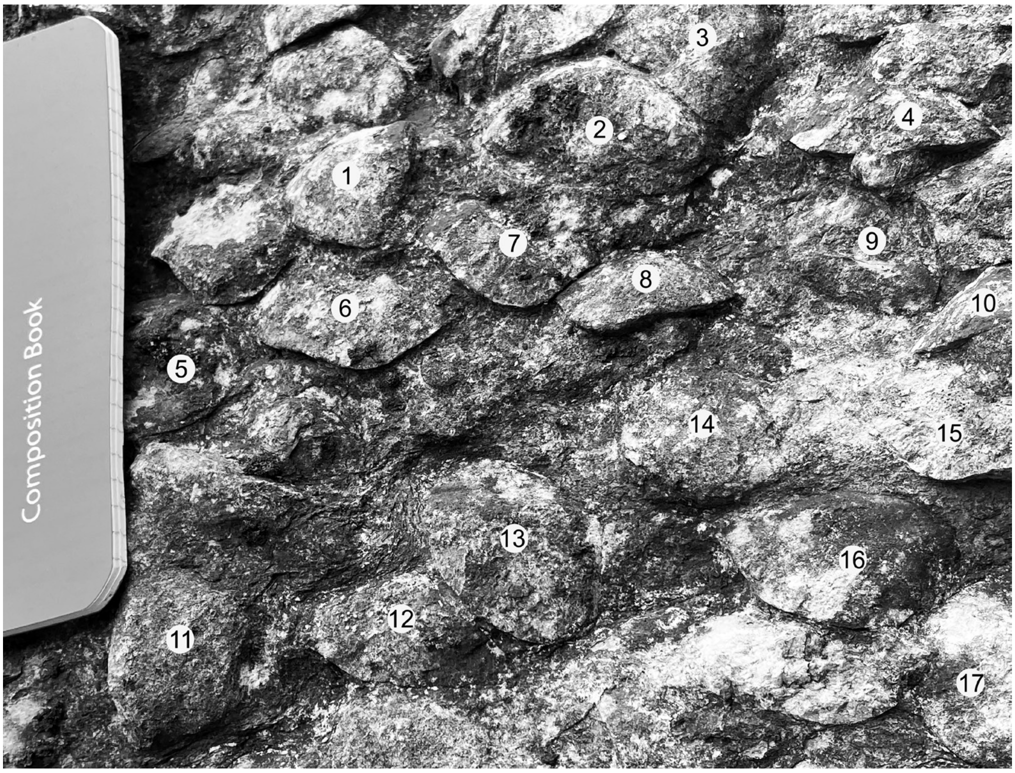

Figure 11. Part of the sample area from Figure 8, showing a cluster of 17 whole Stricklandia lens lens *in a semi-recumbent position in which shells partially overlap one another (notebook for scale is 18 cm in length).*

Comparisons with other Silurian brachiopod populations

The capstone layer from the lower Silurian Solvik Formation with an enormous population of *S. lens lens* at Engervannet benefits from comparisons with the same or related kinds of large-shell brachiopods in the Suborder Pentameridina (Schuchert & Cooper, 1931). The earliest published example that illustrates *S. lens lens* in growth position derives from lower Silurian strata in the Girven district of Scotland (Ziegler et al., 1966). A population of 52 brachiopods was excavated from the bottom of a rock layer with the beak and hinge areas of those shells preserved as a cluster. The same report (Ziegler et al., 1966) illustrates *P. oblongus* preserved in life position from the lower Silurian of Alabama in the USA. It was followed by a similar description of a *P. oblongus* population that features a sublayer of tiny individuals nestled beneath the beak and hinge areas of normal-size adults from the lower Silurian of Iowa in the USA (Johnson, 1977).

The usual excavation of blocks with such a population of brachiopods preserved in growth position is from the bottom of a rock layer. In geographic regions where strata remain horizontal with no post-depositional tilting or folding, such examples are likely to be detected in cross-section against the vertical walls of quarries or road cuttings. Under certain circumstances, a better sense of an occupied bedding surface may be calculated based on the correlation of a distinct horizon. In the case of the Iowa *Pentamerus* bed with a gradation of smaller to larger individuals, the same layer may be traced in cross-section for 45 m along both sides of a highway separated by a 25 m-wide roadway amounting to a minimum estimated seabed of 1,125 m^2. Because the top part of the Iowa *Pentamerus* bed was truncated by marine scour, recognition of such a large planar surface during excavation from the top is unlikely. In retrospect, it can be estimated that the Iowa example signifies a massive population at least 90,000 mature-size individuals within the known spatial limits of the correlated horizon. This ghost example comes close to approximating the size of the *S. lens lens* population exposed at Engervannet. The notable difference is that the Norwegian example may be viewed mostly intact as if swimming above the original seabed.

A review by Johnson (1997, tables 7.1 and 7.2) summarizes additional examples of *P. oblongus* populations, as well as populations of *Virgiana decussata, Pentameroides subrectus, Sulcipentamerus dorsoplanus, and Kirkidium* sp. Much additional information on pentamerid brachiopod communities from shell beds in the Lower Silurian of Anticosti Island in Canada's St. Lawrence seaway is available (Copper, 1997, Jin & Copper, 2000), illustrating cross-sections of layers with material preserved in life position. Jin (2008, Fig. 7J) subsequently demonstrated the species *P. palaformis* with whole shells oriented uniformly in a semi-recumbent position much like *S. lens lens* from the Engervannet locality (Fig. 10). Another example shows *P. oblongus* in life position atop a shell pavement much like Engervannet (Jin, 2008, Fig. 6H). A similar example from the Lower Silurian of China (Rong et al., 2007, Fig. 3A) demonstrates a bedding plane as viewed from above for the species *Sulcipentamerus dorsoplanus*. Previously, this large-shell brachiopod was known to occur in life position, but only from strata viewed on edge in cross-section (Johnson et al., 1985, Fig. 4D).

No large-scale bedding planes with abundant *P. oblongus* preserved in life position are documented from Norway. However, Johnson (1989) reported small-scale examples of this species from the lower Silurian Rytteråker Formation in the context of post-mortem disruption and consequential bioclastic sedimentation. In particular, a cross-section through a limestone stratum shows the degradation of articulated shells to disarticulated shells all from the same horizon (Johnson, 1989, Fig. 5.1). Another example illustrates thin limestone layers with finely crushed *Pentamerus* shells interlayered with siltstone (Johnson, 1989, Fig. 5.8), and interpreted as the result of recurrent storm events that produced thin tempestite deposits. A similar study from lower Silurian strata in southern China is diagnostic of tempestite deposits generated from large shell brachiopods belonging to the species *Paraconchidium shiqianensis* and *Virgianella glabera* (Li & Rong, 2007). In those examples, individual shell layers vary in thickness between 10 cm and more than 4 m.

Storm tracks related to hurricane-strength disturbances are recognized based on inter-formation channels in the Upper Ordovician of southern Norway (Johnson & Baarli, 2018). In some cases, coarse clastic sediments from the lower Silurian fill such channels eroded in Upper Ordovician strata. Yet, no comparable inter-formation channels are recognized higher in the Silurian column in southern Norway. The geographic location of the Baltica paleocontinent changed little from the latest Ordovician to early Silurian times (Baarli et al. 2003). During that time, the southern Norway region was likely to have remained subject to storms of sub-hurricane intensity. Sea-bottom currents are interpreted to have impacted the event horizon preserved in strata from the Spirodden Member of the Solvik Formation at Engervannet (Fig. 9), but were not as disruptive as indicated by tempestites in the succeeding Rytteråker Formation (Johnson, 1989). When the steeply inclined Silurian strata at Engervannet are restored to a horizontal position, the indicators of current movement suggest a source from the present southwest sweeping to the northeast. That direction is inconsistent with the typical hurricane track expected across the Baltica paleocontinent during late Ordovician to early Silurian times (Johnson & Baarli, 2018).

Conclusions

Analysis of brachiopods sampled from the capstone of lower Silurian strata on the south shore of Engervannet indicates the occurrence of the subspecies *Stricklandia lens lens* from an evolutionary progression in the *Stricklandia mullochensis /S. laevis* lineage. The horizon and underlying rock sequence are attributed to a stratigraphic position within the Spirodden Member of the Solvik Formation in the Oslo–Asker District. A reasonable interpretation for the Engervannet example is that an extensive spat fall with *Stricklandia* propagules settled on a barren shell pavement covering a large area during a brief interval of calm, after which a monospecific population quickly grew to maturity over only a few years. The ratio of largest and smallest individuals to the rest of the population is regarded as normal in the context of growth dynamics. Similar examples of shell deformation by crowding during growth are commonly found elsewhere in *Pentamerus* populations. Currents that swept the seabed during the lifetime of the population caused some mature shells to be re-oriented in a more recumbent position shingled against their neighbors in the same cluster. Exposure of large bedding surfaces due to tilting and folding of Silurian strata in the Oslo region is a key to recognizing marine assemblages with large populations of brachiopods and other fossils such as rugose and tabulate corals. In regions left unaffected by tectonics, such as large parts of the midwestern USA, comparably large Silurian brachiopod populations are found as ghost populations from excavations normally recognized only in cross-section in quarry exposures or road cuttings.

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References

Baarli, B.G. 1985: The stratigraphy and sedimentology of the Early Llandovery Solvik Formation in the central Oslo Region, Norway. *Norwegian Journal of Geology 65,* 255–275.

Baarli, B.G. 1986: A biometric re-evaluation of the Silurian brachiopod *Stricklandia lens/S. laevis* lineage. *Palaeontology 9*, 187–205.

Baarli, B.G. 1987: Benthic faunal associations in the Lower Silurian Solvik Formation of the Oslo-Asker Districts, Norway. *Lethaia 20,* 75–90. https://doi.org/10.1111/j.1502-3931.1987.tb00763.x

Baarli, B.G. 2014: The early Rhuddanian survival interval in the Lower Silurian of the Oslo Region: A third pulse of the end-Ordovician extinction. *Palaeogeography, Palaeoclimatology Palaeoecology 395,* 29–41. https://doi.org/10.1016/j.palaeo.2013.12.018

Baarli, B.G. & Johnson, M.E. 1988: Biostratigraphy of key brachiopod lineages from the Llandovery Series (Lower Silurian) of the Oslo Region. *Norwegian Journal of Geology 68*, 259–274.

Baarli, B.G. & Johnson, M.E. & Antoshkina, A.I. 2003: Silurian stratigraphy and paleogeography of Baltica, *In* Landing, E. & Johnson, M.E. (eds.): Silurian Lands and Shelf Margins Exclusive of North America. *New York State Museum Bulletin 492,* 3–34.

Baarli, B.G., Keilen, H.B. & Johnson, M.E. 1999: Silurian communities of the Oslo region, Norway, *In* Boucot, A.J. & Lawson, J.D. (eds.): *Paleocommunities – a case study from the Silurian and Lower Devonian.* Cambridge University Press, 327–349.

Bockelie, J.F., Baarli, B.G. & Johnson, M.E. 2017: Hirnantian (latest Ordovician) glaciations and their consequences for the Oslo Region, Norway, with a revised lilthostratigraphy for the Langøyena Formation in the inner Olofjorden area. *Norwegian Journal of Geology 97*, 119–143. https://doi.org/10.17850/njg97-2-01

Boucot, A.J. 1975: *Evolution and Extinction Rate Controls*, Elsevier Scientific Publishing Company, Amsterdam, 472 pp.

Boucot, A.J. & Lawson, J.D. 1999: *Paleocommunities – a case study from the Silurian and Lower Devonian.* Cambridge University Press, Cambridge 895 pp.

Copper, P. 1997: Articulate brachiopod shellbeds: Silurian examples from Anticosti, eastern Canada. *Geobios 30*, 133–148. https://doi.org/10.1016/S0016-6995(97)80019-8

Hammer, Ø., Harper, D. A.T. & Ryan, P.D. 2001: Past: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica, vol. 4, issue 1, art. 4: 9pp., 178kb. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Jin, J. 2008: Environmental control on temporal and spatial differentiation of Early Silurian pentameride brachiopod communities, Anticosti Island, eastern Canada. *Canadian Journal Earth Sciences 45,* 159–187. https://doi.org/10.1139/E07-045

Jin, J. & Copper, P. 2000: Late Ordovician and Early Silurian pentamerid brachiopods from Anticost Island, Québec, Canada, Palaeontopograhica Canadiana 18, 1–75.

Johnson, M.E. 1977: Succession and replacement in the development of Silurian brachiopod populations. *Lethaia 10*, 83–93. https://doi.org/10.1111/j.1502-3931.1977.tb00595.x

Johnson, M.E. 1989: Tempestites recorded as variable *Pentamerus* layers in the Lower Silurian of southern Norway. Journal of Paleontology 63, 195–205. https://doi.org/10.1017/S0022336000019211

Johnson, M.E. 1997: Silurian event horizons related to the evolution and ecology of pentamerid brachiopods *In* Brett, C.E. & Baird G.C. (eds.): *Paleontological Events – Stratigraphic Ecological, and Evolutionary Implications.* Columbia University Press, New York, 162–180.

Johnson, M.E. & Baarli, B.G. 2018: Storm tracks predict land-to-sea sediment transfer: Erosional patterns from the Upper Ordovician (Hirnantian) in the Oslo Region, Norway. *Journal of Geology 126,* 352–42. https://doi.org/10.1086/697038

Johnson, M.E., Rong, J.-Y. & Yang, X.-C. 1985: Intercontinental correlation by sea-level events in the Early Silurian of North America and China (Yangtze Platform). *Geological Society of America Bulletin 96*, 1384–1397. https://doi.org/10.1130/0016-7606(1985)96<1384:ICBSEI>2.0.CO;2

Kiær, J. 1908: Das Obersilur im Kristianiagebiete: Eine stratigraphische-faunishtische Untersuchung. *Skrifter Videnskapelige Selskap, Matematisk Naturvidenskaplig, Klasse 1906*, Kristiania, 596 pp.

Li, Y. & Rong, J. 2007: Shell concentrations of Early Silurian vigianid brachiopods in northern Guizhou: Temporal and spatial distribution and tempestite formation. *Chinese Science Bulletin 52,* 1680–1691. https://doi.org/10.1007/s11434-007-0224-y

Manceñido, M. & Gourvennec, R. 2008: A reappraisal of feeding current systems inferred for spire-bearing brachiopods. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 98, 345–356. https://doi.org/10.1017/S1755691007078462

Rong J., Jin, J. & Zhan, R. 2007: Early Silurian *Sulcipentamerus* and related pentamerid brachiopods from South China. *Palaenotology 50,* 245–266. https://doi.org/10.1111/j.1475-4983.2006.00604.x

Schuchert, C. & Cooper, G.A. 1931: Synopsis of the brachiopod genera of the suborders Orthoidea and Pentameroidea, with notes on the Telotremta. *American Journal of Science* (series 5) 22, 241–255. https://doi.org/10.2475/ajs.s5-22.129.241

St. Joseph, J.K.S. 1935: A critical examination of *Stricklandia* (= *Stricklandinia lirata* J. de C. Sowerby) 1839 forma typica. *Geological Magazine 72*, 401–424. https://doi.org/10.1017/S0016756800092748

Worsley, D. 1989: The Llandovery Series in the Oslo Region. *In* Holland, C.H. & Bassett, M.G. (eds.): A Global Standard for the Silurian System, *Geological Series No. 9*, National Museum of Wales, Cardiff, 108–116.

Ziegler, A.M., Boucot, A.J. & Sheldon, R.P. 1966: Silurian pentameroid brachiopods preserved in position of growth. *Journal of Paleontology 40*, 1032–1036.

Ziegler, A.M., Cocks, L.R.M. & Bambach, R.K. 1968a: The composition and structure of Lower Silurian marine communities. *Lethaia 1*, 1–27. https://doi.org/10.1111/j.1502-3931.1968.tb01724.x

Ziegler, A.M., Cocks, L.R.M. & McKerrow, W.S. 1968b: The Llandovery transgression of the Welsh Borderland. *Palaeontology 11*, 736–782.