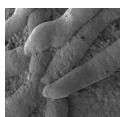


Reducing taxonomic noise in problematic fossils: revision of the *incertae sedis* genus *Allonema* based on shape analysis

EMILIA JAROCHOWSKA, FLORIAN HIERL, OLEV VINN & AXEL MUNNECKE



Organisms of unknown biological affinity are widespread in Paleozoic ecosystems and play key ecological roles. Recognition of these roles relies on consistent identification and sound taxonomy, yet many microproblematica lack complex morphological features that could be the basis for qualitative taxonomic diagnoses. *Allonema* is an *incertae sedis* calcareous sclerobiont widespread in Paleozoic carbonates. At least seven species of *Allonema* have been proposed, but their diagnoses based on size ranges overlap. In this work, dimensions of 590 individuals from the Silurian of Estonia and Sweden have been measured. Regression analysis of the dimensions revealed two groups, overlapping in size ranges, but differing significantly in proportions. These groups could be matched with previously described *A. botellus* and *A. moniliforme*, but both showed a wider range of sizes than previously reported. Another previously described species, *A. minimum*, fell within the range of dimensions of *A. moniliforme* and is proposed to be its junior synonym. Differences in proportions revealed in the study do not seem to be dependent on sedimentary environment or local growth conditions such as competition for space, and thus may represent consistent interspecific variability. Although the affinity of *Allonema* remains unknown, this quantitative approach to its taxonomy reduces unnecessary species in the genus. The success of this approach may encourage its application to other microproblematica populating the fossil record. • Key words: *Wetheredella*, sclerobionts, pseudobryozoans, microproblematica, encrusters, Baltica, Devonian.

JAROCHOWSKA, E., HIERL, F., VINN, O. & MUNNECKE, A. 2016. Reducing taxonomic noise in problematic fossils: revision of the *incertae sedis* genus *Allonema* based on shape analysis. *Bulletin of Geosciences* 91(1), 97–110 (6 figures, 4 tables, appendix). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received September 22, 2015; accepted in revised form December 22, 2015; published online February 12, 2016; issued March 17, 2016.

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Organisms of uncertain biological affinity, such as acritarchs, calcitarchs, chitinozoans, or calcareous tubeworms, constitute essential parts of ecosystems in deep time (e.g. Colbath & Grenfell 1995; Munnecke *et al.* 1999, 2000; Paris & Nölvak 1999; Malinky *et al.* 2004; Page *et al.* 2008; Vinn & Zatoń 2012). Paleozoic carbonate environments teem with calcareous microproblematica functioning as primary producers, reef builders, and key components of carbonate factories (e.g. Riding 1991, Riding & Soja 1993, Elicki 1999, Flügel 2004, Nose *et al.* 2006, Brett *et al.* 2012). Recognition of their affinities and ecological roles requires reliable identifications and precise communication of their occurrence and morphology. This is limited by the lack of complex features and susceptibility to taphonomic processes such as dissolution, micritization, and secondary mineralization (Pratt 1984, Berkýová & Munnecke 2010, Jakubowicz *et al.* 2014).

Many problematica, such as *Girvanella* Nicholson & Etheridge, 1880, *Rothpletzella* Wood, 1948, and *Renalcis* Vologdin, 1932, are extremely widespread in Paleozoic carbonates and commonly accepted as cyanobacteria, but are only described from thin sections (Wood 1948, Pratt 1984, Flügel 2004). In rare cases the growth habit and morphology can be reconstructed using three-dimensional models (Frisch *et al.* 2013), but isolated body fossils are almost never matched with their counterparts in thin sections. A rare exception is the Paleozoic microproblematicum *Allonema* (Ulrich & Bassler 1904), a calcareous sclerobiont known from rocks of Ordovician through Permian age (Condra & Elias 1944, Kiepora 1965, Simonsen & Cuffey 1980, Jarochowska & Munnecke 2014). *Allonema* is an organism composed of branching strings of vesicles with punctate calcareous walls, encrusting carbonate substrates (Ulrich & Bassler 1904; Figs 1–4). Long considered

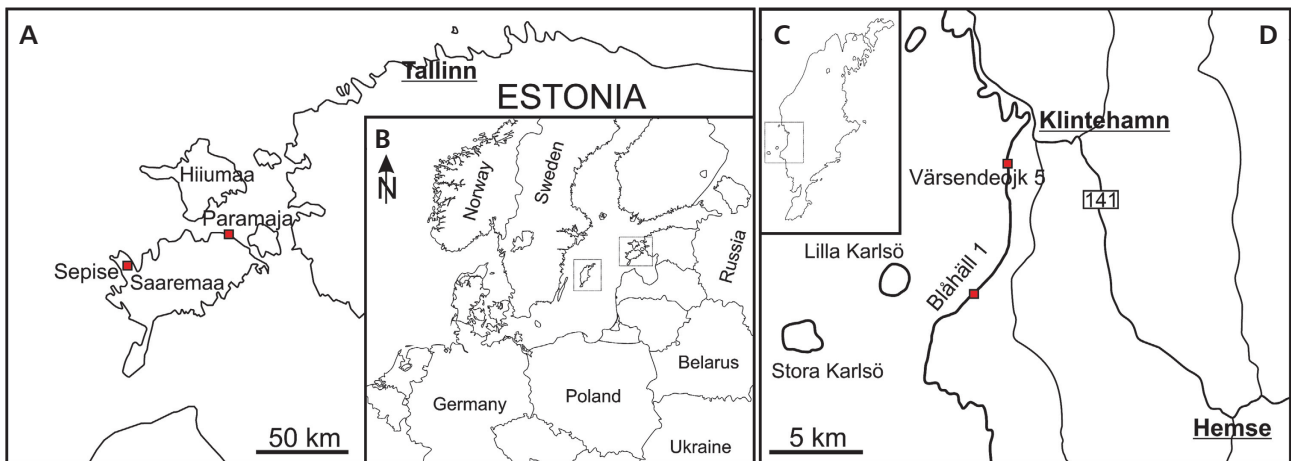


Figure 1. Localities from which new *Allonema* material for this study was derived. • A – close-up of the NW coast of Estonia, showing the Sepise and Paramaja sections. • B – political map of Europe with Gotland and western Estonia marked with dashed rectangles. • C – outline of Gotland; dashed rectangle marks the area shown in D. • D – close-up of Gotland coast near Klintehamn, with Blåhäll 1 and Värseendöjk 5 marked.

a ctenostome bryozoan (e.g. Ulrich & Bassler 1904, Kiepura 1965), an opinion rejected by Dzik (1975) and Wilson & Taylor (2001), *Allonema* remains in the *incertae sedis* group of “pseudobryozoans” (Wilson & Taylor 2001, 2014; Olempska & Rakowicz 2014). Jarochowska & Munnecke (2014) demonstrated that sections through *Allonema* are identical with the problematicum *Wetheredella* (Wood 1948), another Paleozoic sclerobiont known only from thin sections. Interpretations regarding the ecology and distribution of the two taxa differ widely – *Wetheredella* had been proposed to be an autotrophic organism based on its common occurrence in shallow-water environments, oncoids, and reefs, i.e. facies typically analyzed using thin sections, whereas *Allonema* had been mostly reported from off-platform marls and shales, from which extraction of body fossils is possible (Spjeldnaes 1984, Głuchowski 2005, Jarochowska *et al.* 2013). This discrepancy illustrates the importance of precise and exhaustive taxonomic diagnoses even in problematic fossils. Understanding their ecology may be affected by preservation biases, as well as biases introduced by researchers erecting new taxa based on insufficient samples that do not represent the morphological and ultrastructural variability.

The affinity of *Allonema* and other pseudobryozoans remains unknown, but many aspects of their ultrastructure and growth habit support the opinion that at least some organisms in this group might be foraminifers (Wood 1948, Elias 1950, Dzik 1975, Taylor & Wilson 2003, Olempska & Rakowicz 2014). *Allonema* shares its growth habit with other problematic organisms for which foraminiferal affinity has been proposed, such as *Aphralysia* (Bełka 1981, Vachard *et al.* 2001) Its association with filamentous cyanobacteria forming oncoids and microbially-dominated reefs resembles the oncoid-forming associations of Jurassic encrusting foraminifers and putative microbes (Grad-

ziński *et al.* 2004). So far, however, conclusive evidence for the affinity of *Allonema* is lacking, and its taxonomy remains a conundrum.

At least seven species of *Allonema* have been proposed, mostly based on very small number of specimens and overlapping in their proposed morphological variability (summarized in Table 1). Further progress in understanding the ecology and affinity of this genus requires a taxonomic revision based on sufficient samples. In this paper, dimensions of 590 individual vesicles preserved three-dimensionally from five populations from Sweden, Estonia, and Poland are employed to evaluate previously proposed diagnoses and emend them based on quantitative shape parameters.

Material

Material used in this study is listed in Table 2. Specimens described for the first time from Gotland (EJ- and FH-) are stored at the Institute of Paleontology, University of Erlangen-Nuremberg. New specimens from Estonia at the Institute of Geology, Tallinn University of Technology (GIT) and Natural History Museum, University of Tartu (TUG). *Allonema* specimens from different localities were in this study treated as separate populations, to account for both taxonomic and environmental effects on morphology. Populations are further identified by locality names as follows. Observations on previously described specimens are included in respective populations below.

Nyhamn. – One valve of a leperditiid arthropod, with *Allonema* sp. encrustations on the internal side (Fig. 3A, B). The specimen was collected in fossiliferous limestone-marl alternations of the Lower Visby Formation at Nyhamn 1 (Gotland, Sweden; Laufeld 1974), interpreted

Table 1. Compilation of *Allonema* species characteristics from previous literature.

Species	Comments on taxonomy	Vesicle dimensions	Distinctive characters	Reported from localities
<i>A. botelloides</i> (Ulrich & Bassler, 1904)	Type species	Width 0.25 mm, length <i>ca</i> 0.5 mm (Ulrich & Bassler 1904)	Distinguished from <i>A. botellus</i> by its robust aspect and shorter vesicles	Gotland (Silurian) – type locality
<i>A. botellus</i> (Vine, 1884)	Originally described as <i>Rhopalonaria botellus</i>	Width 0.1–0.15 mm, length <i>ca</i> 0.5 mm (Ulrich & Bassler 1904)	Some vesicles are club-shaped and usually exhibit a zooecial attachment pore (Ulrich & Bassler 1904) – not observed in present study	Gotland (Silurian); “Buildwas beds of Wenlock shales” (Ulrich & Bassler 1904) – type localities
<i>A. moniliforme</i> (Whiteaves, 1891)	Originally described as <i>Stomatopora moniliformis</i>	Width 0.1 to 0.2 mm, length 0.3 to 0.5 mm (Kieppura 1965)	Similar to <i>A. botelloides</i> , but with slightly greater average width and bead-like vesicles (Ulrich & Bassler 1904)	Hay River, Canada – type locality (Devonian); Skały, Holy Cross Mountains (Middle Devonian)
<i>A. m. aggregatum</i> (Ulrich & Bassler, 1904)		Width 0.2 to 0.48 mm, length 0.4 to 1.0 mm (Kieppura 1965)		Hamilton Fm., Michigan – type locality; Skały, Holy Cross Mountains (Middle Devonian)
<i>A. m. parvum</i> Kieppura, 1965)		Width 0.03–0.07 mm, length 0.11–0.17 (Kieppura 1965)		Skały, Holy Cross Mountains (Middle Devonian) – type locality
<i>A. fusiforme</i> (Nicholson & Etheridge, 1877)	Originally described as <i>Ascodictyon fusiforme</i>	Similar as in <i>A. subfusiforme</i> (Ulrich & Bassler 1904)	Vesicles are frequently isolated, fusiform, often joined by long “necks”	Hamilton Fm., Michigan; Widder Fm., Ontario (Middle Devonian), Falls of the Ohio (Devonian)
<i>A. subfusiforme</i> (Ulrich & Bassler, 1904)		Vesicles very variable in size, from 0.22 wide and 0.4 mm long, to 0.6 mm wide and 1.0 mm long. On average 0.4 mm wide and 0.7 mm long (Ulrich & Bassler 1904)	Larger and more regular than <i>A. waldronense</i>	Gotland (Silurian) – type locality
<i>A. waldronense</i> (Ulrich & Bassler, 1904)		Width 0.3 mm, length <i>ca</i> 0.5 mm (Ulrich & Bassler 1904)	Vesicles show great diversity of forms. Similar to <i>A. fusiforme</i> and <i>A. subfusiforme</i> but with smaller vesicles	Waldron Shale, Indiana (Wenlock) – type locality
<i>Allonema?</i> <i>minimum</i> (Ulrich & Bassler, 1904)	Probably not <i>Allonema</i> at all	Width 0.1 mm, length 0.1 to 0.28 mm (Ulrich & Bassler 1904)	Vesicles often pear-shaped, with a single pore. No <i>punctae</i>	Upper Coal Measures, Illinois (Pennsylvanian) – type locality
<i>A. silurica</i> (Wood, 1948)	Originally described as <i>Wetheredella silurica</i> , moved to the genus <i>Allonema</i> by Jarochovska & Munnecke (2014)			Much Wenlock Limestone Fm., May Hill, Gloucestershire, UK (Wenlock) – type locality; reported from Gotland

as deposited in a distal shelf setting (Munnecke *et al.* 2003). Age: Telychian, Llandovery, lower Silurian; *Pterospiriferus amorphognathoides* conodont Zone (Jeppsson *et al.* 2006). Coordinates: λ N 57° 45′ 51.88″, ϕ E 18° 24′ 55.26″.

Jaani. – Brachiopods and rugose corals from the Paramaja cliff at Jaani (Saaremaa, Estonia; Figs 2B, C, 3C, D). The cliff is known as a rich fossil locality and the stratotype of the Paramaja Member of the Jaani Formation (*Conochitina tuba* Zone, Sheinwoodian, Nestor 1984). Exposed marlstones are rich in brachiopods, trilobites, rugose corals, and cornulitids (Vinn & Wilson 2013). Pyritization of skeletal fragments and burrows is common. Lithological composition of rocks and associated fauna suggest a quiet-water environment at the boundary of the open shelf

and transitional facies zone (Hints *et al.* 2008). Coordinates: λ N 58° 36′ 56″, ϕ E 22° 53′ 51″.

Sepise. – At Sepise (Saaremaa, Estonia) nodular limestones of Jaagarahu Formation are exposed. Raukas & Teedumäe (1997) characterized the Jaagarahu Fm. in northwestern Saaremaa as very variable, prevalingly sparitic coral-stromatoporoid limestones including reefs and bioherms, and fine-grained skeletal and pelletal grainstones, and inferred shallow-water environment of deposition. The age of the Jaagarahu Fm. is upper Sheinwoodian to lowermost Homeric (Wenlock; Männik 2014). Limestones at Sepise are rich in tabulate corals and other shelly fossils. The outcrop is recently becoming overgrown by vegetation. Coordinates: λ N 58° 27′ 18.4608″, ϕ E 22° 00′ 28.7496″.

Table 2. *Allonema* specimens used in this study.

Collection ID	Substrate organism	Locality	Lithostratigraphy	Age	Associated sclerobionts
FH-2014-01	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-02	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	<i>Condranema parvula</i>
FH-2014-03	Brachiopod	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-04	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-05	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-06	Bryozoan	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-07	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-08	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-09	<i>Eoplectodonta</i> sp.	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-10	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-11	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-12	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	<i>Condranema parvula</i>
FH-2014-13	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-14	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-15	Unidentified	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-16	Bryozoan growing on an unidentified shell fragment	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	
FH-2014-17	Unidentified brachiopod	Värsendeojk 5, Gotland	Svarvare Mb., Fröjel Fm.	<i>O. b. longa</i> Zone, Homeric	<i>Condranema parvula</i>
EJ-2013-001	Trilobite	Blåhäll 1, Gotland	Mulde Brick-clay Mb., Halla Fm.	<i>O. b. longa</i> Zone, Homeric	<i>Condranema parvula</i>
EJ-2013-002	Trilobite	Blåhäll 1, Gotland	Mulde Brick-clay Mb., Halla Fm.	<i>O. b. longa</i> Zone, Homeric	<i>Condranema parvula</i> , bryozoans
EJ-2013-003	Bryozoan	Blåhäll 1, Gotland	Mulde Brick-clay Mb., Halla Fm.	<i>O. b. longa</i> Zone, Homeric	<i>Condranema parvula</i>
EJ-2014-001	Leperditiid arthropod	Nyhamn 1, Gotland	Lower Visby Fm.	<i>Pt. amorphognathoides</i> Zone, Telychian	Bryozoans
GIT 687-128	Unidentified	Sepise, Saaremaa	Jaagarahu Fm.	Upper Sheinwoodian to lowermost Homeric	<i>Palaeoconchus</i> sp., <i>Corynotrypa</i> sp.
GIT 687-132	Crinoid	Sepise, Saaremaa	Jaagarahu Fm.	Upper Sheinwoodian to lowermost Homeric	<i>Palaeoconchus</i> sp.
GIT 700-143	<i>Estonirhynchia estonica</i>	Jaani, Saaremaa	Jaani Fm.	<i>C. tuba</i> Zone, Sheinwoodian	
GIT 700-159	<i>Estonirhynchia estonica</i>	Jaani, Saaremaa	Jaani Fm.	<i>C. tuba</i> Zone, Sheinwoodian	Bryozoans
GIT 700-222	<i>Estonirhynchia estonica</i>	Jaani, Saaremaa	Jaani Fm.	<i>C. tuba</i> Zone, Sheinwoodian	<i>Ascodictyon venustum</i> , bryozoans, <i>Palaeoconchus</i> aff. <i>tenuis</i>
GIT 700-285	<i>Estonirhynchia estonica</i>	Jaani, Saaremaa	Jaani Fm.	<i>C. tuba</i> Zone, Sheinwoodian	<i>Craniops implicatus</i> , <i>Palaeoconchus</i> aff. <i>tenuis</i>
TUG 1704-1	Rugose coral	Jaani, Saaremaa	Jaani Fm.	<i>C. tuba</i> Zone, Sheinwoodian	<i>Condranema parvula</i> , <i>Palaeoconchus</i> sp.
TUG 1704-2	Rugose coral	Jaani, Saaremaa	Jaani Fm.	<i>C. tuba</i> Zone, Sheinwoodian	
TUG 1704-3	Rugose coral	Jaani, Saaremaa	Jaani Fm.	<i>C. tuba</i> Zone, Sheinwoodian	
TUG 1704-4	Rugose coral	Jaani, Saaremaa	Jaani Fm.	<i>C. tuba</i> Zone, Sheinwoodian	<i>Condranema parvula</i> , bryozoans, <i>Palaeoconchus</i> sp., <i>Craniops</i> sp.
TUG 1704-5	Rugose coral	Jaani, Saaremaa	Jaani Fm.	<i>C. tuba</i> Zone, Sheinwoodian	Bryozoans, <i>Craniops</i> sp., <i>Palaeoconchus</i> sp., <i>Condranema parvula</i>
TUG 1704-6	<i>Estonirhynchia estonica</i>	Jaani, Saaremaa	Jaani Fm.	<i>C. tuba</i> Zone, Sheinwoodian	Bryozoans

Mulde. – Trilobite and brachiopod fragments from marls of the Mulde Brick-clay Member of the Halla Formation at Blåhäll 1 (Gotland, Sweden; Figs 1, 2A). The locality was previously described by Laufeld (1974) and Calner & Jeppsson (2003). It represents a platform slope setting with rich and diverse encruster fauna (Spjeldnaes 1984, Jarochovska & Munnecke 2014). Age: Homerian, Wenlock, middle Silurian; *Ozarkodina bohémica longa* conodont Zone (Jeppsson *et al.* 2006). Coordinates: λ N 57° 18' 44.65", ϕ E 18° 09' 19.79".

Svarvare. – Brachiopods, bryozoans, and unidentified clasts from the Svarvare Mudstone Member of the Fröjel Formation at Vårsendeojk 5 (Gotland, Sweden; Figs 1, 3E, F, 4). The Svarvare Mb. was characterized by Calner (1999) and Calner & Jeppsson (2003) as dark, organic-rich, condensed argillaceous mud- and wackestones grading upwards into siliciclastic mudstones deposited in a platform slope setting. Hierl (2014) characterized the fauna of the Svarvare Mb. as dominated by brachiopods, including *Dicoelosia* sp., indicating low water energy. Associated fauna consists of trilobites and corals, with a smaller proportion of crinoids, bryozoans, ostracods, and tentaculitids. Age: Homerian, Wenlock, middle Silurian; *Ozarkodina bohémica longa* conodont Zone (Jeppsson *et al.* 2006). Coordinates: sampling transect along the shore, from λ N 57° 21' 40.8", ϕ E 18° 10' 25.1" to λ N 57° 21' 40.8", ϕ E 18° 10' 26.0".

Skały. – Measurements of *Allonema moniliforme aggregatum* used in the analysis were provided by Kiepura (1965). Original specimens could not be found in the collections of the Institute of Paleobiology, Polish Academy of Science (A. Halamski, personal communication 2015). They were described from several trenches in the Skały section located in the Holy Cross Mountains, central Poland. Kiepura (1965) reported that *Allonema* specimens were mostly found encrusting brachiopods from marly shales and marls of the Skały Formation, formed in a platform slope environment. Age: originally reported as Givetian (Kiepura 1965), according to newer studies the Skały Fm. spans the Eifelian–Givetian boundary (Szulczewski 1995). Coordinates: λ N 50° 53' 37.26", ϕ E 21° 9' 42.57".

Methods

Specimens from the Mulde and Svarvare populations were extracted from marly matrix using the surfactant Rewoquat according to the method described by Jarochovska *et al.* (2013). Other specimens were collected as body fossils weathered out from rock matrix. All were washed in an ultrasonic bath and photographed in reflected light. A subset was sputter-coated with gold and examined under SEM

(TESCAN Vega\XMU). Lengths and widths of complete, undamaged *Allonema* vesicles were measured from calibrated photographs in Adobe Photoshop. Lengths of curved vesicles were approximated by fitting several straight segments to the vesicle shape. Attempts to record vesicles belonging to the same specimen failed, as in most specimens the preservation did not allow distinguishing between overlapping chains. Measurements are provided in Appendix 1. Specimens from Nyhamn were too few to be included in regression analysis.

The relationship between vesicle dimensions in *Allonema* populations was examined using major axis regression (Legendre & Legendre 1998) in R version 3.2.2 (R Core Team 2015). Equality of regression slopes fitted to each population was tested using the Sidak adjustment (Westfall & Young 1993) implemented in the “smatr” package (Warton *et al.* 2012). Confidence intervals for each population separately were plotted using lmodel2. For specimens from Svarvare and Sepise, analyses were performed using two versions of the measurement dataset: complete and restricted. The complete version included outliers characterized by size and proportions different from the main dataset, marked in Appendix 1 as “rounded” (see also Fig. 5). In the restricted version these specimens were excluded when characterizing the dimensions within populations.

Results

Examined substrates showed different degrees of infestation, from single chains formed by less than ten vesicles (Nyhamn, Sepise, Figs 2A, B, 3A, B, F, 4) to dense, complex, overlapping networks (particularly from Jaani, Fig. 3C–E). Encrustation took place at least partially post-mortem, as the chains grew across the commissure in brachiopods and were observed on the internal side of a disarticulated arthropod valve (Fig. 3A, B). No preferred direction of growth was observed; in substrates with low density of *Allonema* the directions were approximately radial (Fig. 2B), *i.e.* branches starting in one site spread apart. Associated encrusters were mostly bryozoans, including *Corynotrypa* sp., microconchids *Palaeoconchus* sp., brachiopods belonging to the genus *Craniops*, and calcareous problematica *Condranema parvula* (Condra & Elias, 1944) and *Ascodictyon venustum* (Kiepura, 1965). No interactions were observed between *Allonema* and other encrusters. Also no connections were observed between the only specimen of *Ascodictyon venustum* and *Allonema*, an aspect reported by Wilson & Taylor (2014) from Givetian specimens collected from the Silica Shale in Michigan.

Distribution of vesicle dimensions in examined *Allonema* populations is shown in Fig. 5 and summarized

in Table 3. Size ranges reported in the literature (Table 2) are overlain on Fig. 5 as grey dashed rectangles. Based on the relationship between width and height, two groups of populations could be distinguished. The Mulde and Jaani populations were characterized by elongated (up to 1420 μm), narrow (up to 462 μm) vesicles. The Skafy population and chains of exceptionally large vesicles from Svarvare and Sepise were similarly long (up to 1000 μm), but thicker and more rounded. The main difference between these two groups is not in the range of absolute dimensions, but in the proportions of vesicles (Fig. 6). Slopes of regression models fitted to vesicle dimensions did not differ significantly at $\alpha = 0.005$ within both groups, and differed between them (Table 4).

The Svarvare population did not differ significantly from that from Skafy in terms of vesicle proportions, but reached only about half of the size range of the other two, with its maximum length of 549 μm and maximum width of 265 μm . A short *Allonema* chain in this group was excluded from the regression analysis and marked separately in Fig. 5 as “Svarvare (rounded)”. The specimens are shown in Fig. 4A, B, where they co-occur on one substrate with typical *Allonema* from Svarvare. The tentative exclusion was based on the much larger dimensions and regular, circular shape of the vesicles, which marked them as clearly distinct from the rest of this population. They showed pores characteristic for *Allonema*, and very narrow (ca 70 μm) constrictions between vesicles. Two chains with outstandingly large vesicles were also observed on specimens from Sepise (Fig. 4C, D). They differ from those from Svarvare in much wider, fused constrictions between vesicles. After excluding these outliers, the slope of regression on main dimensions did not differ significantly from that of the Jaani and Mulde populations (Table 4). However, the size range was much narrower (Table 3).

Discussion

Species identification

Original descriptions of *Allonema* species by Ulrich & Bassler (1904) were based on one or a small number of chains, precluding an assessment of intra- and interspecific variability. Sources of intraspecific variation might include the type of substrate, environmental conditions, and competition for space with other epibionts. In the lack of complex features, *Allonema* taxonomy has been based on vesicle sizes and shapes (e.g. club-shaped, fusiform, Table 1), an aspect approximated in this study by analyzing vesicle proportions. Here we assume that vesicles observed in the same populations, i.e. collections derived from one type of lithology in one locality, and showing a continuum of di-

mensions, represent individual species. All of them correspond poorly to the size ranges reported for previously proposed *Allonema* taxa (Table 1), supporting the possibility that the large number of proposed species may have resulted from undersampling of intraspecific variability.

Very few vesicles in examined specimens fell within the size range reported for *A. botelloides* (Table 1, Fig. 5, Ulrich & Bassler 1904) – although this species was described as common on corals from Gotland, it was not found in the present study.

A. moniliforme encompasses a confounding list of subspecies. The original description by Whiteaves (1891) was based on four specimens with average length of 0.5 mm and width of 0.2 mm. Ulrich & Bassler (1904) observed that they were similar to *A. botelloides*, but broader and with bead-like vesicles. This was contradicted by Kiepurá (1965) based on material from the Middle Devonian of the Holy Cross Mountains, which she designated as *A. moniliforme moniliforme*, implicitly synonymous of *A. moniliforme* of Whiteaves (1891). In this population, the width range was smaller than in *A. botelloides* (0.1–0.2 mm), therefore the distinction between the two species remains unclear. Ulrich & Bassler (1904) introduced the subspecies *A. moniliforme aggregatum* from the Middle Devonian of the New York state without specifying in what did it differ from *A. moniliforme*. According to Kiepurá (1965), it is characterized by vesicles that are both larger and wider, branch frequently, and show a high variability. Her measurements were included in the present study as a reference population and found to overlap nearly perfectly with size ranges of *A. fusiforme* and *A. subfusiforme*, and to encompass entirely the range of dimensions reported for *A. botelloides*. What is more, *A. waldronense* shared the size range with all these species, being distinguished by a more winding growth habit and high variability of vesicles (Ulrich & Bassler 1904).

Differences between these taxa are based on vesicle shapes, *A. fusiforme* being fusiform, *A. subfusiforme* – bottle-shaped with narrow necks (not evidenced, however, by the original illustration), *A. botelloides* – oblong and sausage-shaped, and *A. moniliforme aggregatum* showing a wide variety of shapes, including fusiform, club-like, pear-like, elliptical, and rounded. None of the examined populations fell closely within the range of dimensions of any of the above species. Treating the Skafy population as a reference for the range of dimensions in *A. moniliforme aggregatum*, only outlier specimens from two specimens from Sepise (GIT 687-132-4 and GIT 687-128-5) and one specimen from Svarvare (FH-2014-02) were found to correspond to it. Populations from these localities showed a bimodal distribution, consisting of a few large vesicles forming separate chains and falling within the size ranges of *A. moniliforme aggregatum* (Fig. 4C, D), and the majority of chains of small vesicles differing significantly in

terms of their proportions (Fig. 5, Table 4). Regression parameters for dimensions in the Sepise population with outliers excluded did not differ significantly from those for the Jaani and Mulde populations, but the size range was closer to the Svarvare population. Regression parameters may have in this case been affected by the small sample size ($N = 41$), therefore we refrain here from assigning this population to any previously defined species until more material is available.

Size ranges of *A. moniliforme parvum* reported by Kiepuru (1965) were inconsistent: she indicated that 12 to 18 vesicles were found over a 2 mm length, indicating vesicle lengths in the range of 0.11 to 0.17 mm, consistent with measurements on specimen illustration therein; in her Table 6 reported vesicle length was 0.1 mm and width 0.4, and measurements from the illustrated specimens indicate width range of 0.03 to 0.07 mm. Dimensions based on the illustration are used here for comparison (Table 1) and indicate that *A. moniliforme parvum* was not found among examined specimens. The same holds for *Allonema? minimum*, tentatively classified in the genus by Ulrich & Bassler (1904) based on material from the Pennsylvanian of Illinois. The authors did not observe pores on the surface, but this feature is commonly obliterated in e.g. some vesicles in otherwise punctate chains, or in entire specimens in the case of abraded or strongly cemented material. The presence or absence of pores on the surface cannot be therefore used as a decisive criterion for taxonomic classification, but it can be verified by examining the ultrastructure (Wood 1948, Jarochovska & Munnecke 2014, Olempska & Rakowicz 2014). The single large terminal pore illustrated by Ulrich & Bassler (1904; pl. 67, figs 10, 11) and the dimensions resemble *Corynotrypa* sp., a bryozoan observed in the present study in association with *Allonema* sp.

The group of populations from Mulde and Jaani did not fit to any of the size ranges discussed above. It is, however, clearly distinguished by its elongate appearance. This trait corresponds with the distinctive feature of *A. botellus* described from the Silurian of Gotland and England (Vine 1884, 1887; Ulrich & Bassler 1904). We postulate that the continuum of sizes in these two populations ($N = 358$ in total) encompasses the range reported for *A. botellus*, and is here demonstrated to be significantly different, and possible to distinguish based on shape parameters, from other populations and species discussed. Mulde and Jaani specimens described in this study can be therefore treated as a more complete representation of intraspecific variability within *A. botellus*.

The Svarvare population did not differ significantly in terms of vesicle proportions from *A. moniliforme aggregatum* from Skały, but fell entirely below its size range and close to the range reported for *A. moniliforme moniliforme*. It also overlapped with the smaller part of

Table 3. Summary of vesicle dimensions in examined *Allonema* populations.

Population	N	Length [μm]			Width [μm]		
		Min.	Mean	Max.	Min.	Mean	Max.
Jaani	275	70	577	1420	9	159	462
Mulde	83	240	660	1280	55	113	185
Sepise (restricted)	41	130	322	580	105	167	242
Sepise (rounded)	6	383	586	822	322	433	543
Skały	32	320	611	1000	100	323	600
Svarvare (restricted)	146	36	277	549	12	123	265
Svarvare (rounded)	3	406	463	500	386	408	419

the Sepise population. In both groups the slope of regression line was near 0.5 (0.4 for Svarvare and 0.6 for Sepise, Fig. 6), i.e. the length to width ratio was near 2:1. These populations can be reliably distinguished from *A. botellus* based on this shape parameter (Table 4). The continuum of dimensions encompasses *A. moniliforme moniliforme* and *A. minimum*, suggesting that their previously reported size ranges were small samples from this continuum. Therefore we postulate that *A. minimum* is a junior synonym of *A. moniliforme*, and the subspecies *A. moniliforme moniliforme* should be abandoned. Based on quantitative data available so far, *A. moniliforme* and *A. moniliforme aggregatum* have the same proportions (Fig. 6) but are clearly distinct in terms of size ranges. This permits to distinguish them as two species that can be identified based on their shape parameters. Therefore we propose to bring the subspecies *A. m. aggregatum* to the rank of species as *A. aggregatum* (Ulrich & Bassler 1904).

Controls on intraspecific variability

Except for the Skały population, all discussed specimens were early to middle Silurian and derived from a narrow area (Gotland and Saaremaa). All but the population from Sepise grew in calm, muddy environments below the fair-weather wave base. This homogeneity of sampled sites permits to speculate that differences between the populations were not phenotypic plasticity in reaction to water energy, turbidity or light conditions. Other factors that might affect vesicle shapes, particularly biotic interactions such as competition cannot be ruled out. Although *A. botellus* showed denser infestation, the species occurred also as solitary, rare chains (Figs 2B, 3A, B), where it could be clearly identified as the highly elongate form. This suggests that competition for space did not determine the shape of this species, unless *Allonema* competed with soft-bodied organisms, which could not be detected on fossil substrates.

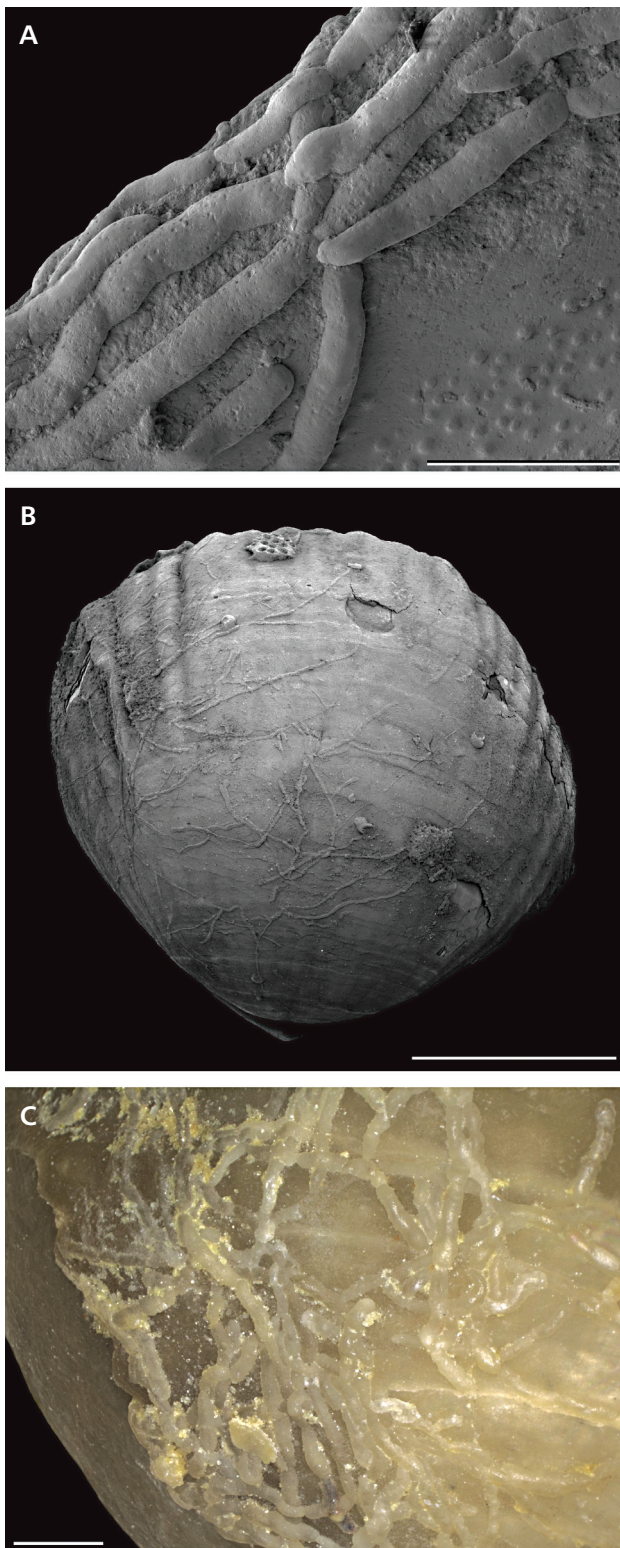


Figure 2. *Allonema botellus* from the Silurian of Sweden and Estonia.
 • A – EJ-2013-001. Trilobite fragment from the Mulde Brick-clay Mb. at Blåhäll 1 (Gotland), encrusted with *Condranema parvula*, scale bar 500 µm.
 • B, C – brachiopod *Estonirhynchia estonica* from the Jaani Fm. at Jaani (Saaremaa); B – GIT-700-222, scale bar 5 mm; C – GIT 700-143, scale bar 1 mm.

Systematic paleontology

Kingdom, phylum, class, order and family *incertae sedis*

Genus *Allonema* Ulrich & Bassler, 1904

1884 *Rhopalonaria* Vine (partim).

1887 *Rhopalonaria* Vine (partim).

Type species. – *Allonema botellus* (Vine, 1884).

Allonema botellus (Vine, 1884)

Figures 2, 3A–D

1884 *Rhopalonaria* Vine (partim), p. 87.

1887 *Rhopalonaria* Vine (partim), p. 179.

1904 *Allonema botellus* (Vine, 1884). – Ulrich & Bassler, pp. 281–282, pl. 67.1.

1948 *Wetheredella silurica* sp. nov.; Wood, pp. 21–22, pls 3b, 5b.

2014 *Allonema silurica* (Wood, 1948). – Jarochowska & Munnecke, pp. 653–656, figs 1a–f, 2a–c, 5a, c.

Material. – Fourteen substrates (brachiopods, trilobites, rugose corals, a bryozoan, and a leperditiid arthropod) from the Mulde Brick-clay Mb. of the Halla Fm. at Blåhäll 1 (Gotland) and the Jaani Fm. at the Paramaja cliff (Saaremaa) encrusted with *A. botellus*. Description is based on measurements of 358 vesicles.

Diagnosis (emended). – *A. botellus* is distinguished from other *Allonema* species by the elongate aspect of its vesicles, *i.e.* their length to width ratio ranging between *ca* 10:1 to 45:1 (Fig. 6).

Description. – Sparsely branching chains consisting of elongate vesicles ranging in the width from 9 to 399 µm (average 149 µm) and from 70 µm to 1420 µm in length (average 597 µm). Pores are visible on the surface of well-preserved specimens, but obliterated in most specimens by diagenesis or abrasion.

Occurrence. – Reported from the Silurian of England, Gotland, and Saaremaa. Known in its two-dimensional aspects as *Wetheredella silurica* (partim?), in which it is difficult to distinguish from other species of *Allonema*. Taking into account reported occurrences of *Wetheredella*, its stratigraphic range may extend at least into the Ordovician (summarized in Jarochowska & Munnecke 2014).

Allonema moniliforme (Whiteaves, 1891)

Figure 3E, F

1891 *Stomatopora moniliformis* Whiteaves, p. 12, fig. 10, pl. 28.

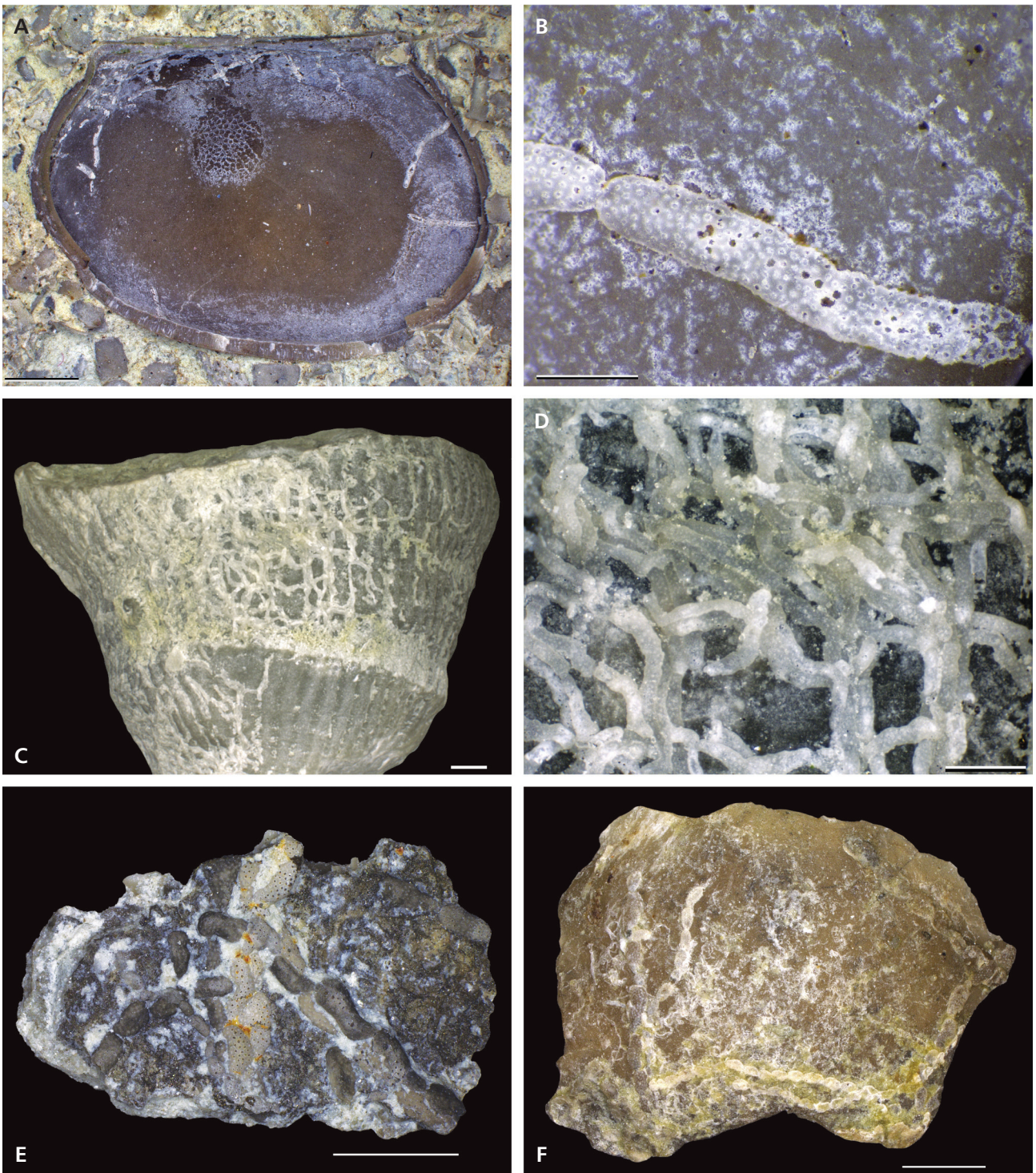


Figure 3. *Allonema* encrustations on components from the Silurian of Sweden (A, B, E, F) and Estonia (C, D). • A, B – EJ-2014-001. *Allonema botellus* on the inner side of a leperditiid arthropod valve from the Lower Visby Fm. at Nyhamn 1 (Gotland); A – scale bar 2 mm; B – scale bar 500 μ m. • C, D – TUG 1704-5. *A. botellus* on a rugose coral from the Jaani Fm. at Jaani (Saaremaa); C – scale bar 1 mm; D – scale bar 500 μ m. • E – FH-2014-11. *A. moniliforme* on an unidentified clast from the Svarvare Mb. at Värseendojk 5 (Gotland), scale bar 1 mm. • F – FH-2014-17. *A. moniliforme* and *Condranema parvula* on an unidentified brachiopod from the Svarvare Mb. at Värseendojk 5, scale bar 1 mm.

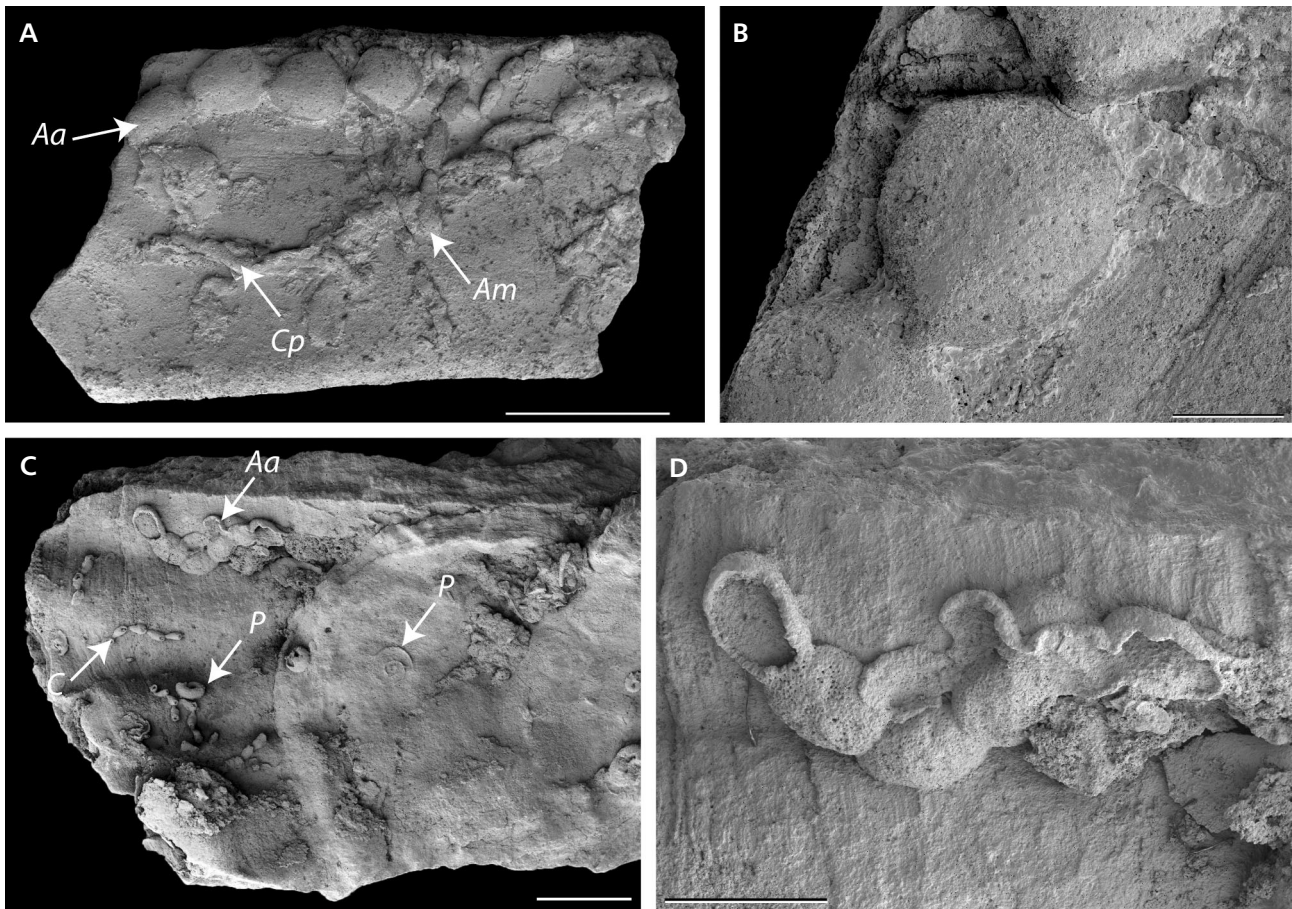


Figure 4. *Allonema aggregatum* from the Silurian of Sweden and Estonia. • A, B – FH-2014-02. Unidentified clast from the Svarvare Mb. at Värsendeojk 5 (Gotland), encrusted by *A. aggregatum* (Aa), *A. moniliforme* (Am), and *Condranema parvula* (Cp); A – scale bar 1 mm; B – scale bar 500 μ m. • C, D – GIT-687-128. Unidentified clast from the Jaagarahu Fm. at Sepise (Saaremaa), encrusted with *A. aggregatum* (Aa), *Allonema* sp., *Palaeoconchus* sp. (P), and *Corynotrypa* sp. (C); C – scale bar 2 mm; D – scale bar 1 mm.

- 1904 *Allonema moniliforme* (Whiteaves, 1891). – Ulrich & Bassler, p. 282, pl. 67.
 1904 *Allonema minimum?* sp. nov.; Ulrich & Bassler, pp. 284–285, pl. 67.
 1965 *Allonema moniliforme moniliforme* (Whiteaves, 1891). – Kiepara, pp. 26–28, fig. 4, pl. 4, fig. 1, pl. 6, figs 1, 6.

Material. – Nineteen components (unidentified carbonate grains, a bryozoan, a brachiopod, and a fragment of articulated crinoid stem) from the Svarvare Mb. of the Fröjel Fm. at Värsendeojk 5 (Gotland) encrusted with *A. moniliforme*. Description is based on measurements of 146 vesicles.

Diagnosis (emended). – *A. moniliforme* is distinguished from other species of *Allonema* by vesicle length to width ratio close to 2:1 (Fig. 6). It is similar to *A. aggregatum* in terms of proportions, but differs in the smaller size of vesicles (not exceeding ca 300 μ m in width and ca 600 μ m in length).

Description. – Sparsely branching colonies consisting of plump vesicles ranging in the width from 12 to 265 μ m (average 123 μ m) and from 36 μ m to 549 μ m in length (average 277 μ m). Pores are visible on the surface of well-preserved specimens, but obliterated in most specimens by diagenesis or abrasion.

Occurrence. – Reported from the Middle Devonian of the Northwest Territories (Canada) and Poland, here also from the Wenlock (middle Silurian) of Gotland. See comments on the stratigraphic range of *A. botellus* above.

***Allonema aggregatum* (Ulrich & Bassler, 1904)**
 Figure 4

- 1904 *Allonema moniliforme* var. *aggregatum* var. nov.; Ulrich & Bassler, pp. 282–283, pl. 67.
 1965 *Allonema moniliforme aggregatum* Ulrich & Bassler, 1904. – Kiepara, pp. 28–30, fig. 5, pl. 5, figs 1, 2.

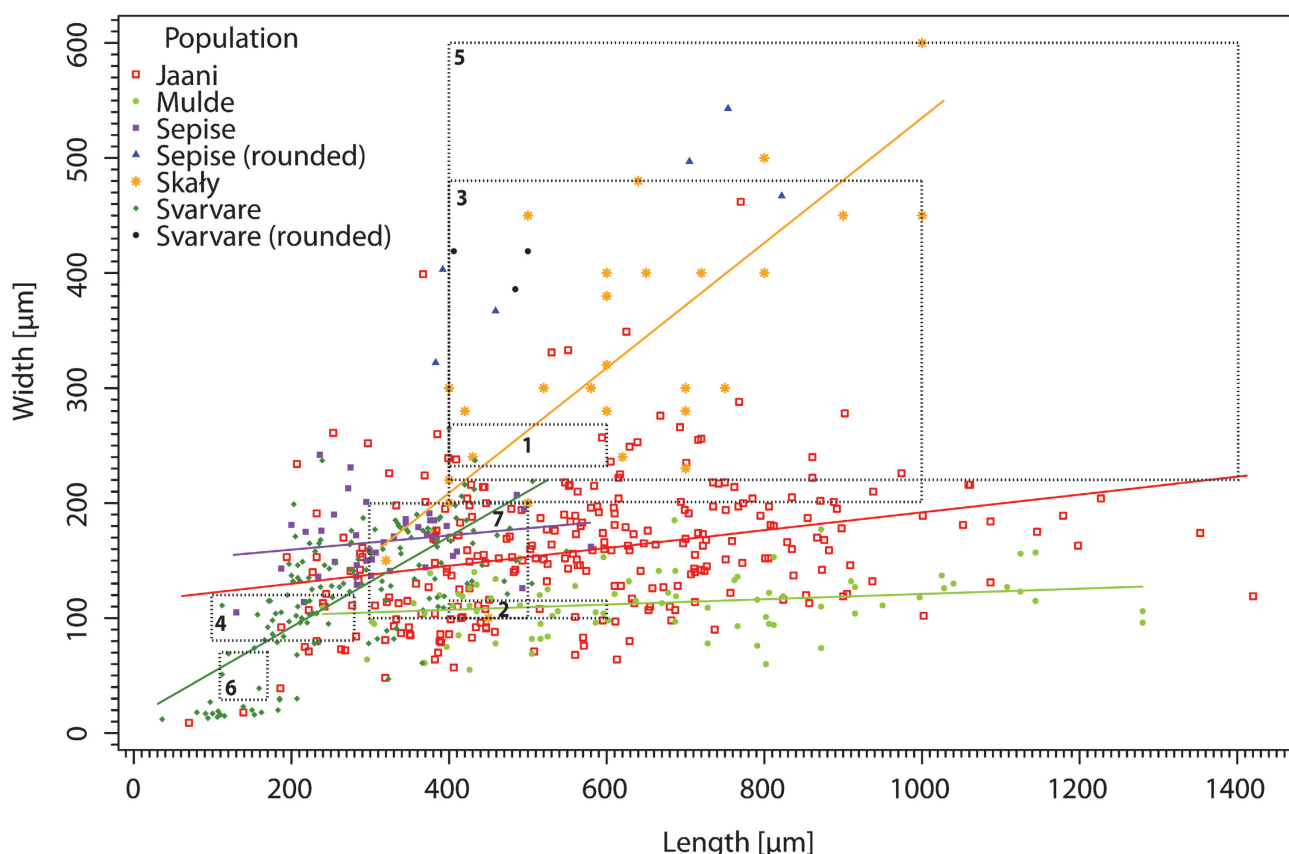


Figure 5. Scatter plot of dimensions of studied *Allonema* specimens, with major axis regression lines fitted for each population. Dashed boxes indicate size ranges for *Allonema* species reported in the literature (Table 1): 1 – *A. botelloides* (Ulrich & Bassler, 1904), 2 – *A. botellus* (Vine, 1884), 3 – *A. moniliforme aggregatum* (Kiepura, 1965), 4 – *A. minimum* (Ulrich & Bassler, 1904), 5 – *A. fusiforme* and *A. subfusiforme* (Ulrich & Bassler, 1904), 6 – *A. moniliforme parvum* (Kiepura, 1965), 7 – *A. moniliforme moniliforme*.

Material. – Two specimens from the Jaagarahu Fm. at Sepise (Saaremaa), encrusting an unidentified clast (GIT 687-132) and a crinoid stem (GIT 687-128), and one specimen encrusting an unidentified clast from the Svarvare Mb. of the Fröjel Fm. at Värseendeojk 5 in Gotland (FH-2014-02). Description is based on measurements of 9 vesicles marked in Fig. 5 as “Sepise (rounded)” and “Svarvare (rounded)”.

Diagnosis (emended). – *A. aggregatum* is distinguished from other species of *Allonema* by vesicle length to width ratio below 2:1 (Fig. 6) and the large size of vesicles – length larger than *ca* 350 µm and width larger than *ca* 300 µm (Fig. 5, Table 4).

Description. – Branching chains were not observed, but this may be due to the very small sample size. Vesicles are plump, nearly round or egg-shaped in their outline. In all studied specimens pores were visible on the surface and in broken vesicle walls (Fig. 4C). *A. aggregatum* co-occurs with smaller *Allonema* sp. (see below) on substrates from Sepise, and with *A. moniliforme* on specimens from Värseendeojk 5.

Table 4. P-values for pairwise comparisons of major axis regression slopes for dimensions in examined *Allonema* populations. Asterisks indicate significantly different pairs at $\alpha = 0.005$.

Population 1	Population 2	P-value
Jaani	Mulde	0.1042
Jaani	Sepise (restricted dataset)	1.0000
Jaani	Skały	0.0007*
Jaani	Svarvare (restricted dataset)	0.0000*
Mulde	Sepise (restricted dataset)	1.0000
Mulde	Skały	0.0002*
Mulde	Svarvare (restricted dataset)	0.0000*
Sepise (restricted dataset)	Skały	0.0013*
Sepise (restricted dataset)	Svarvare (restricted dataset)	0.0004*
Skały	Svarvare (restricted dataset)	0.9625
Jaani	Sepise	0.0000*
Jaani	Svarvare	0.0000*
Mulde	Sepise	0.0000*
Mulde	Svarvare	0.0000*
Sepise	Skały	0.9997
Sepise	Svarvare	0.8788
Skały	Svarvare	1.0000

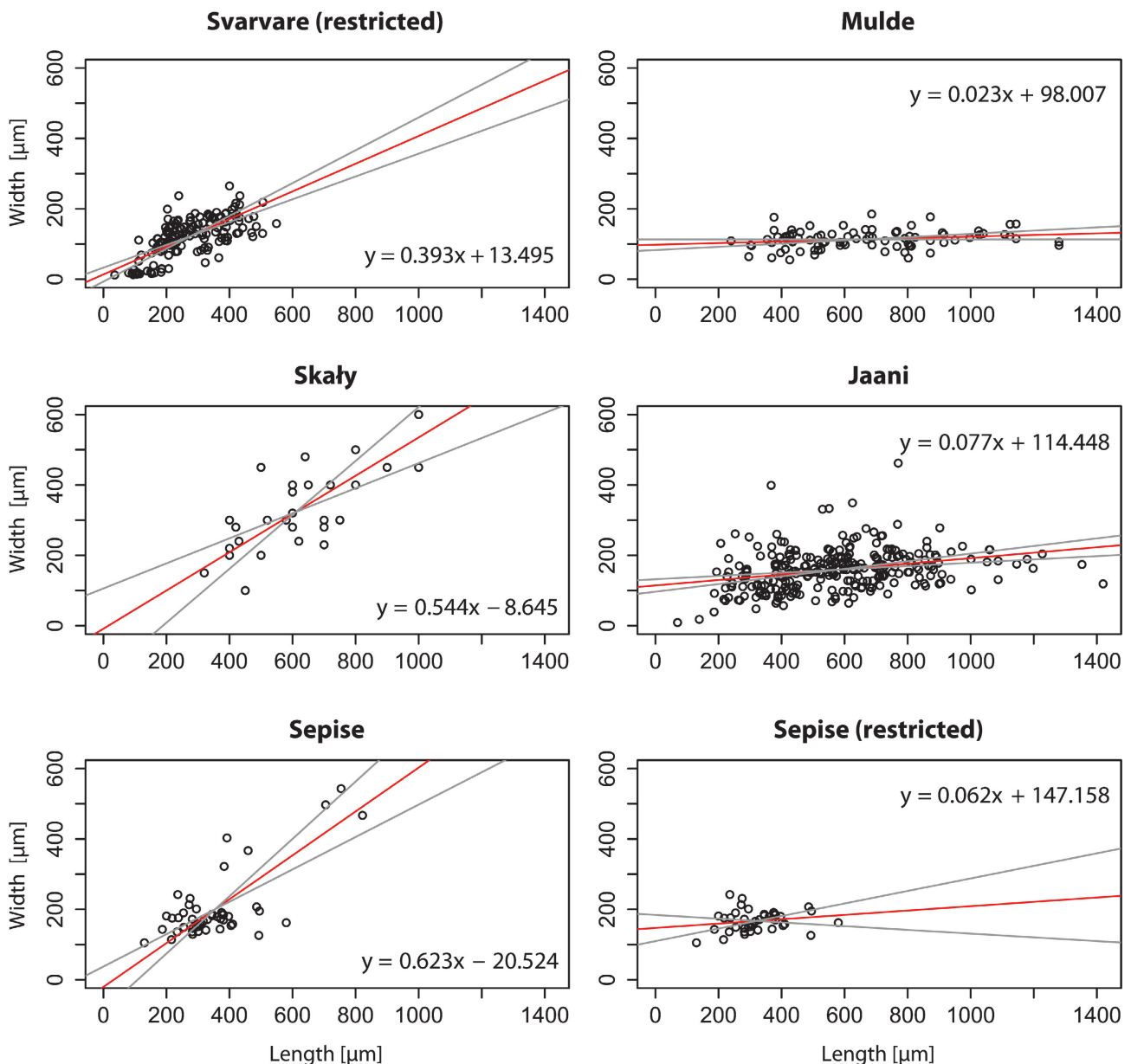


Figure 6. Major axis regression lines with 95% confidence intervals fitted to vesicle dimensions in studied *Allonema* populations.

Occurrence. – Reported from the Middle Devonian of Michigan and Poland, here also from the Wenlock (middle Silurian) of Saaremaa.

***Allonema* sp. indet.**

Material. – One unidentified clast and a crinoid stem from the Jaagarahu Fm. at Sepise (Saaremaa), encrusted with *Allonema* sp. and *A. aggregatum*. Description is based on measurements of 41 vesicles (six largest vesicles belonging to two specimens, visible in Fig. 5 as outliers within the Sepise population are here excluded).

Description. – Sparsely branching chains formed by short (max. 322 µm, on average 130 µm long) vesicles with the length to width ratio close to 16:1. In most vesicles pores are not visible. *Allonema* sp. co-occurs with larger and more rounded *A. aggregatum* (see above).

Conclusions

1. At least seven species of *Allonema* were based on insufficient samples that failed to capture intraspecific size variability. Their diagnoses were not sufficient to distinguish these species.

2. *Allonema botellus* and *A. moniliforme* show a wider range of sizes than previously reported, but can be distinguished based on their proportions, *A. botellus* being at least five times more elongated than *A. moniliforme*. *A. minimum* falls within the range of dimensions of *A. moniliforme* and is proposed to be its junior synonym.

3. *A. moniliforme aggregatum*, *A. botelloides*, *A. fusiforme* and *A. subfusiforme* entirely overlap in their range of dimensions, differing only in vesicle shapes. Further studies are required on material representing these species to determine whether they are valid species. *A. moniliforme aggregatum* is similar to *A. moniliforme* in terms of dimensions but differs by its larger size, and is tentatively proposed here to be raised to the rank of species based on its larger size range, which distinguishes it from *A. moniliforme*.

4. *Allonema* is an example of a long-known, widespread organism, for which the understanding of affinity, ecology, and functional morphology is lacking. The absence of qualitative features that would allow taxonomic evaluation of its morphological variability may be overcome by quantitative shape analysis. The successful use of this approach in the present study may encourage its application to other problematica.

Acknowledgements

EJ, FH and AM acknowledge funding from the Deutsche Forschungsgemeinschaft (project no. Mu 2352/3). Financial support to OV was provided by the Palaeontological Association Research Grant, Paleontological Society Sepkoski Grant, Estonian Research Council projects ETF9064 and IUT20-34. We are grateful to M. Wilson and F. Schlagintweit for constructive reviews and language corrections, to A. Hüter, M. Hopkins and J. Spicer for help in collecting material from Värsendeojk 5, U. Toom for handling deposited material, G. Buono for discussions on the growth habit of *Allonema*, P. Taylor for identification of *Corynotrypa* sp., and C. Schulbert for help with SEM. This paper is a contribution to the International Geoscience Programme (IGCP) Project 591 – The Early to Middle Paleozoic Revolution.

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