Manuscript for

Geologiska Föreningens i Stockholm Förhandlingar (GFF)

Notes

The palaeobiogeographical spread of the acritarch *Veryhachium* in the Early and Middle Ordovician and its impact on biostratigraphical applications

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Abstract: The genus *Veryhachium* Deunff, 1954, is one of the most frequently documented acritarch genera, being recorded from the Early Ordovician to the Neogene. Detailed investigations show that *Veryhachium* species first appeared near the South Pole in the earliest part of the Tremadocian (Early Ordovician). The genus was present at high palaeolatitudes (generally > 60° S) on the Gondwanan margin during the Tremadocian, before spreading to lower palaeolatitudes on the Gondwanan margin and other palaeocontinents (Avalonia, Baltica) during the Floian. It became cosmopolitan in the Mid and Late Ordovician. Although useful for distinguishing Ordovician from Cambrian strata, the diachronous FADs of *Veryhachium* morphotypes means that they should be used with caution for long-distance correlation.

Keywords: Ordovician; acritarchs; *Veryhachium*; palaeobiogeography; stratigraphy.

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Introduction

Microfossils are recognized as outstanding tools for high-resolution biostratigraphy (e.g., Gregory et al. 2006). Among the marine palynological microfossils, several groups have been used, including the cysts of dinoflagellates in the Mesozoic and Cenozoic and the acritarchs and chitinozoans in the Palaeozoic (e.g., Jansonius and McGregor 1996). The last is now considered to be one of the major groups for Ordovician and Silurian biostratigraphy, together with the graptolites and conodonts (e.g. Verniers et al. 1995; Webby et al. 2004).

Acritarchs also contribute to international biostratigraphical correlations, although some morphotypes make better stratigraphical index fossils than others. Recent studies, for example, have demonstrated the usefulness of Ordovician acritarchs for correlation of sedimentary sequences at the base of the Floian Stage (Molyneux et al. 2007) and at the Lower-Middle Ordovician series boundary (Li et al. 2010).

Veryhachium is one of the most frequently recorded acritarch genera. Servais et al. (2007) showed that the genus first appeared in the early Tremadocian and thus served to distinguish Ordovician from Cambrian rocks. Closer investigation, however, also shows that different species (or morphotypes) of *Veryhachium* have diachronous and successive first appearances, starting with first occurrences near the South Pole in the Early Ordovician, leading to a subsequent broader distribution towards the north during the Middle and Late Ordovician.

This paper illustrates the palaeobiogeographical spread of *Veryhachium* and discusses its impact for biostratigraphical analyses.

First appearance data of *Veryhachium* morphotypes

Veryhachium was originally described by Deunff (1954) from the Ordovician of Britanny, western France. Over 250 species and subspecies have been recorded from the Ordovician to the Oligocene (Fensome et al. 1990), and the genus is generally widespread throughout its stratigraphical range. It can be found in marine facies from onshore to relatively deep marine settings, and can be abundant depending on stratigraphical position and palaeogeographical location. *Veryhachium* and related forms (veryhachid acritarchs) comprise 50% or more of specimens, for example, in Late Ordovician assemblages from Algeria (Paris et al. 2000) and Saudi Arabia (Miller and Al Ruwaili 2007). Given its long stratigraphical range and simple morphology, *Veryhachium* might be polyphyletic.

Species usually have polygonal vesicles with a few, simple, undivided, distally tapering and proximally open processes or spines that lie in a single plane. Morphotypes include triangular, rectangular or polygonal vesicles with three, four, or five and more processes respectively. Servais et al. (2007) proposed a simple classification scheme in which all triangular specimens are attributed to the *Veryhachium trispinosum* group and all rectangular specimens to the *Veryhachium lairdii* group. In order to classify the numerous morphotypes of the *Micrhystridium/Veryhachium* complex in the Permian, Lei et al. (2013) extended this approach and proposed a further informal group to include all *Veryhachium* morphotypes with ellipsoidal central body outlines, the *Veryhachium cylindricum* group.

Veryhachium has its first occurrence in the Early Ordovician. Upper Cambrian forms previously attributed to the genus as *Veryhachium dumontii* are now interpreted as diacromorph acritarchs (Servais et al. 2007) and are placed in the genus *Ninadiacrodium* Raevskaya & Servais, 2009. In addition, Servais et al. (2007) considered a number of other Cambrian forms that had been assigned previously to *Veryhachium*, and concluded that none of them should be included the genus according to the emended diagnosis of Turner (1984). Among them is *Veryhachium minutum* Downie, 1958, which was transferred to the genus *Dorsennidium* Wicander, 1974, by Sarjeant and Stancliffe (1994). *Dorsennidium minutum* was reported as often having six processes (Downie 1958), although the diagnosis states four or six. However, specimens of *D. minutum* with four processes, all lying in the same plane as a rectangular vesicle and one arising from each corner, would resemble specimens of the *Veryhachium lairdii* group, albeit with much smaller vesicle dimensions. These were stated to range from 3µm to 15µm in the original diagnosis (Downie 1958). The absence of *Veryhachium* from the Cambrian is of biostratigraphical significance because this means that its occurrence in palynological assemblages indicates an Ordovician or younger age. The *Veryhachium lairdii* group appears before the *Veryhachium trispinosum* group in the fossil record.

White et al. (2012) recorded the *Veryhachium lairdii* group from beds containing the graptolite *Rhabdinopora flabelliformis flabelliformis* in Nova Scotia. According to data published by Zalasiewicz et al. (2009, fig. 3b), *R. flabelliformis flabelliformis* occurs in the *R. flabelliformis* Graptolite Biozone and the overlying *Adelograptus tenellus* Graptolite Biozone in England and Wales, which indicates correlation with the early Tremadocian Stage Slice Tr1 of Bergström et al. (2009; see Cooper and Sadler 2012, figs 20.1, 20.10, for correlation of graptolite zones and stage slices). However, the specimens figured by White et al. (2012, figs 8N, 8O, 10Q, 10R) all have vesicle diameters of about 10µm. In this respect they resemble rectangular specimens of *Dorsennidium minutum* rather than *V. lairdii*, although they conform in all other respects to the *Veryhachium lairdii* group.

Early Tremadocian specimens attributed to the *Veryhachium lairdii* group have also been reported from a core sample at a depth of 1590 m in the Tt1 borehole of southern Tunisia (Vecoli 2004; Vecoli & Le Hérissé 2004). Graptolites of the *Rhabdinopora flabelliformis* group are present at the same depth (Vecoli 2004), suggesting an assignment to Stage Slices Tr1 or Tr2 of Bergström et al. (2009) and to time-slices 1a or 1b of Webby et al. (2004). Elsewhere in North Africa, Combaz (1968) and Jardiné et al. (1974) recorded the *Veryhachium lairdii* group from the Grès d'El Gassi and Argiles d'El Gassi respectively in Algeria. Specimens figured by Combaz (1968), like those figured by White et al. (2012) from Nova Scotia, are small, around 10µm or less in vesicle diameter. Galeazzi et al. (2010) reported Combaz's specimens to be from the the early–mid Tremadocian Argiles d'El Gassi rather than the late Cambrian Grès d'El Gassi.

A further occurrence of *Veryhachium lairdii*?, in cuttings samples from the Mabrouk Member in the Kauther-1H1 well of Oman, is from a pre-*messaoudensis-trifidum* acritarch assemblage (Molyneux et al. 2006). The precise age of this occurrence has not been established, but it is probably older than Stage Slice Tr2 given that the oldest occurrences of the distinctive and widespread late Tremadocian *Cymatiogalea messaoudensis-Stelliferidium trifidum* acritarch assemblage (Molyneux et al. 2007) are thought to correlate with Tr2 (see below).

In Avalonian Europe, specimens of the *V. lairdii* group occur in core samples between depths of 3615.80m and 3835.30m in the Rügen 5 borehole on the island of Rügen, Germany (Servais & Molyneux 1997). At these depths, they form part of the *messaoudensis-trifidum* acritarch assemblage. This acritarch assemblage is present in the upper Tremadocian *Araneograptus murrayi* graptolite Biozone of NW England (= Stage Slices Tr2–Tr3; see Cooper and Sadler 2012, figs 20.1, 20.10) and ranges across the Tremadocian–Floian boundary there. Chitinozoans from the same depths in Rügen 5 are reported to indicate the *Lagenochitina destombesii* Biozone (Samuelsson et al. 2000; Servais et al. 2001), which is correlated with Stage Slices Tr1-Tr2. Hence the acritarch and chitinozoan data suggest that the *V. lairdii* group in Rügen 5 occurs in Tr2.

Specimens of the *V. lairdii* group have also been recorded from sub-assemblage 1 of the *messaoudensis-trifidum* acritarch assemblage in the English Lake District. They are from the lowest samples collected from the *A. murrayi* Biozone (Molyneux et al. 2007, fig. 3), and are therefore probably also from Stage Slice Tr2 or the lower part of Tr3, following the correlations in Cooper and Sadler (2012). There is no record of the *Veryhachium lairdii* group from older Tremadocian rocks in England and Wales, although '*Veryhachium minutum*' has been recorded, for example throughout the Shineton Shale Formation (Rasul and Downie 1974; Rasul 1979), which is older than the *A. murrayi* Biozone (Fortey & Rushton 2000, fig. 14) and so probably correlates with Stage Slice Tr1.

In addition to the Lake District record, the *Veryhachium lairdii* group has been recorded from *messaoudensis-trifidum* acritarch assemblages of south Wales, southern Ireland, Spain, Belgium, and the Czech Republic (for complete references see Molyneux et al. 2007 and Servais et al. 2007). In

Ireland, Spain and Belgium, the assemblages containing the *Veryhachium lairdii* group are all correlated with the upper part of sub-assemblage 3 and the overlying sub-assemblage 4 of the *messaoudensis-trifidum* assemblage of the English Lake District, and are probably therefore the upper part of Stage Slice Tr3. The occurrences in south Wales and the Czech Republic are correlated less precisely, but they are clearly late Tremadocian (*murrayi* or *copiosus* biozones) or possibly earliest Floian in age.

The *Veryhachium lairdii* group appears to have been restricted largely to the high-palaeolatitude margin of Gondwana, including Avalonia, during the Tremadocian. The questionable specimens from Oman might indicate the northward limit of the group's biogeographical range in the Tremadocian, between 30°S and 60°S on the Gondwanan margin (Torsvik and Cocks 2013).

At lower palaeolatitudes on the Gondwanan margin, for example in South China and Argentina, the first occurrence of the *Veryhachium lairdii* group is apparently in the lowermost Floian or higher (Servais et al. 2007). In South China, the first occurrence of rectangular *Veryhachium* specimens is in the *T. approximatus* graptolite Biozone (Yan et al. 2011), equivalent to the lower part of Stage Slice Fl1. There is, for example, no record of the *Veryhachium lairdii* group in late Tremadocian acritarch assemblages from South China (Wang et al. 2013). In Argentina, de la Puente & Rubinstein (2013) recorded the group's first occurrence in the *B. deflexus* Biozone, equivalent to the mid Floian Stage Slice Fl2, in sections from the Central Andean Basin.

Investigations of successions in Gondwanan intracratonic basins of

Australia, also situated at low palaeolatitudes, show that specimens of the *Veryhachium lairdii* group (recorded as *Veryhachium valiente*) are present in the oldest beds sampled in the Canning Basin, from the lower part of the Willara Formation (Quintavalle & Playford 2006*a*, *b*). These beds are correlated with the middle and upper Floian Stage (Stage Slices Fl2, Fl3), but a lack of data from underlying formations rules out any conclusion regarding the regional FAD of the group.

The oldest rectangular *Veryhachium* specimens from Baltica are also from the lower Floian. They occur in the Lakity Beds of the Leetse Formation, in the Lava River section of the St Petersburg region (Molyneux et al. 2007). Rectangular specimens of *Veryhachium* occur there in the *T. phyllograptoides* graptolite Biozone (lower part of Stage Slice Fl1), but were not recorded from the lowest sample collected from the *phyllograptoides* Biozone in the Lava River section. This might indicate that the FAD of the *Veryhachium lairdii* group is in the lower Floian in Baltica as it is in low-palaeolatitude Gondwana, although it is possible that the true FAD of *Veryhachium* is below the Lakity Beds.

Triangular specimens of *Veryhachium*, attributed to the '*Veryhachium trispinosum* group', generally appear later in the fossil record than the rectangular morphotypes of the *V. lairdii* group (Servais et al. 2007). Jardiné et al. (1974) showed the FAD of the *Veryhachium trispinosum* group to be in the early Tremadocian Argiles d'El Gassi of Algeria, and this might be the oldest recorded occurrence, but no details were published.

The *Veryhachium trispinosum* group has its first occurrence in the English

Lake District in sub-assemblage 3 of the *messaoudensis-trifidum* acritarch assemblage (Molyneux et al. 2007), which probably correlates with Stage Slice Tr3. Its first occurrence in Belgium and the Czech Republic is in *messaoudensis-trifidum* assemblages that are correlated broadly with sub-assemblages 3–5 of the *messaoudensis-trifidum* assemblage in the English Lake District, probably corresponding to the Tremadocian Stage Slice Tr3 or possibly the lowermost part of the Floian Stage Slice Fl1.

In South China, the *V. trispinosum* group, like the *V. lairdii* group, has its first appearance at the base of the Floian, in the *Tetragraptus approximatus* Biozone of the Tonggao Formation in southern Guizhou and of the Dacao Formation in the Houping section in Chongqing (Yan et al. 2011). In South America, the *V. trispinosum* group first appears at the base of Stage Slice Fl3 (de la Puente & Rubinstein 2013). The *trispinosum* group was also recorded in the Floian *E. brevis* Biozone (corresponding to times-slice 2C of Webby et al. 2004) of the Suri Formation by Achab et al. (2006), in the peri-Gondwanan volcanic arc of the Famatina System in north-west Argentina, and earlier by Ottone et al. (1992) and Rubinstein et al. (1999) with a first occurrence in the *T. akzharensis* graptolite Biozone in the Central Andean Basin (Rubinstein et al. 2007). These records indicate that the *V. trispinosum* group was present in the Floian of South America.

The *Veryhachium trispinosum* group was thus present on the Gondwanan margin from at least the late Tremadocian at high palaeolatitudes, but there are no records from lower palaeolatitudes, for example in South China and Argentina, before the Floian. The *Veryhachium trispinosum* group first occurred on Baltica apparently much later, with the earliest record being in

Assemblage BIII of the Kunda Stage in the Rapla Borehole (Uutela & Tynni 1991), equivalent to the Darriwilian upper Stage Slice Dw1 and Stage Slice Dw2.

There are no records of *Veryhachium trispinosum* during the Tremadocian–Darriwilian interval (Lower and Middle Ordovician) from Laurentia and Siberia, but this might be due to a lack of data rather than a real absence. Nevertheless, its probable absence from Laurentia throughout this time interval is supported by a recent investigation of Middle Ordovician strata from Fossil Mountain, Utah, which have revealed diverse acritarch assemblages without any *Veryhachium* (Strother et al. 2009).

After the Middle Ordovician, *Veryhachium* morphotypes are very common at a global scale, with the genus and its different species being truly cosmopolitan.

The palaeogeographical spreading of *Veryhachium* morphotypes

Plotted on a palaeogeographical reconstruction (Fig. 1), the first appearances of *Veryhachium* suggest that the genus spread from high to low palaeolatitudes over an extended period through the Ordovician. During the Tremadocian (earliest Ordovician), the *Veryhachium lairdii* and *V. trispinosum* groups were only present at high southern palaeolatitudes (Fig. 1), with first occurrences in North Africa (Tunisia, Algeria?) and Avalonia (northern Germany and NW England). During the Floian, both groups have additional records around the margin of Gondwana, including South China and South America, and rectangular specimens are first recorded from the southern part of Baltica. By the Late Ordovician, the biogeographical range of the genus had expanded to include Laurentia and its distribution was apparently global.

Conclusion – implication for biostratigraphy

The relatively slow expansion of *Veryhachium* over some 20 million years, from a regional distribution at high palaeolatitudes in the early-middle Tremadocian to a cosmopolitan distribution in the Late Ordovician, introduces a note of caution for the use of the genus in biostratigraphical correlations. Although of great importance for regional stratigraphical correlations in the earliest Ordovician, intercontinental correlations using the genus need to take account of this apparently slow increase in biogeographical range through later Ordovician times.

Acknowledgements. We thank two anonymous referees and the guest-editor Guillermo Albanesi for revising the manuscript. This is a contribution to the French ANR project RALI, and to IGCP 591 'The Early to Middle Paleozoic Revolution.' Stewart Molyneux publishes by permission of the Executive Director, British Geological Survey.

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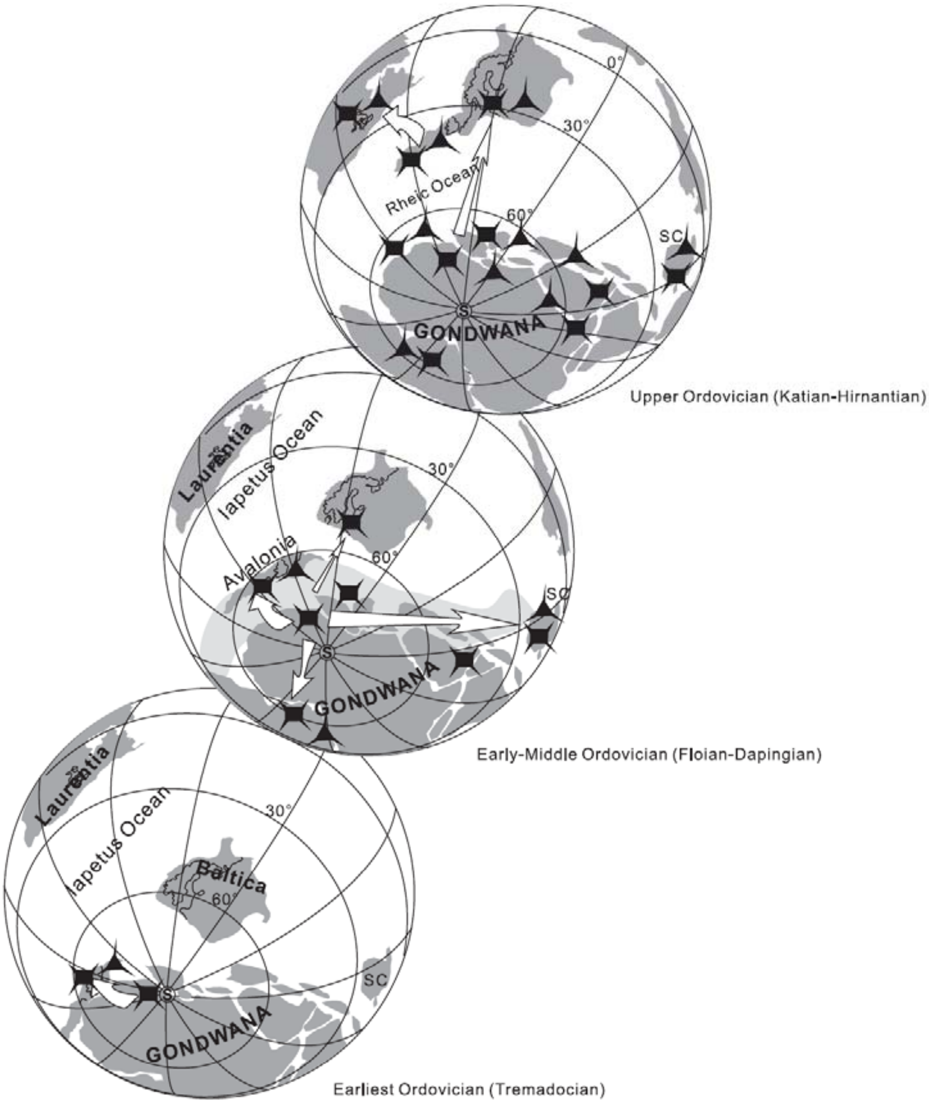
Figure Caption:

Fig. 1:

Palaeobiogeographical distribution of the *Veryhachium trispinosum* group (triangles) and the *Veryhachium lairdii* group (rectangles), plotted on palaeogeographical reconstructions of the Early to Late Ordovician (reconstructions based on and modified after the BugPlates software www.geodynamics.no). S: South Pole; SC: South China



Upper Ordovician (Katian-Hirnantian)

Early-Middle Ordovician (Floian-Dapingian)

Earliest Ordovician (Tremadocian)