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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 $> 60^{\circ}$ S) on the Gondwanan margin during the Tremadocian before spreading to lower palaeolatitudes on the Gondwanan margin and other palaeocontinents (Avalonia and Baltica) during the Floian. It became cosmopolitan in the Middle and Late Ordovician. Although useful for distinguishing Ordovician from Cambrian strata, the diachronous first appearance data of *Veryhachium* morphotypes mean that they should be used with caution for long-distance correlation.

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

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 & McGregor 1996). The last group is now considered to be one of the major biostratigraphical 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. Recent studies, for example, have demonstrated the usefulness of Ordovician acritarchs in the 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 article illustrates the palaeobiogeographical spread of *Veryhachium* and discusses its impact on 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 sometimes abundant and usually widespread throughout its stratigraphical

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range. 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. The absence of Veryhachium from the Cambrian is of biostratigraphical significance, because this means that its occurrence in palynological assemblages clearly indicates an Ordovician or younger age.

The first morphotypes of Veryhachium are triangular or rectangular, with one process arising from each of the corners and lying in the same plane as the vesicle. The oldest (Early Ordovician) rectangular specimens, attributed to the V. lairdii group, have 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). In Avalonian Europe, specimens of the V. lairdii group occur in core samples between depths of 3615.80 and 3835.30 m 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 (i.e. Stage Slices Tr2-Tr3) and ranges across the Tremadocian-Floian boundary there. International correlation suggests that the V. lairdii group in Rügen occurs in Tr2 (see also Molyneux et al. 2007).

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 the Stage Slice Tr2 or the lower part of Tr3. In addition to the Lake District record, the V. 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; Servais et al. 2007). In Ireland, Spain and Belgium, the assemblages containing the V. lairdii group are all correlated with the upper part of sub-assemblage 3 and the overlying subassemblage 4 of the messaoudensis-trifidum assemblage of the English Lake District and are probably therefore with 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. A further occurrence of *V. lairdii*?, in cuttings' samples from the Mabrouk Member in the Kauther-1H1 well of Oman, is from a pre-*messaoudensis*—*trifidum* Tremadocian acritarch assemblage (Molyneux et al. 2006) and is possibly older than Stage Slice Tr2, given that the oldest occurrences of the distinctive and widespread late Tremadocian *messaoudensis*—*trifidum* acritarch assemblage (Molyneux et al. 2007) are thought to correlate with Tr2.

More recently, White et al. (2012) recorded the *V. lairdii* group from beds containing the graptolite *R. flabelliformis* flabelliformis in Nova Scotia, indicating a possible early Tremadocian occurrence of the genus *Veryhachium*. However, the specimens figured by White et al. (2012, Figs 8N, 8O, 10Q, 10R) all have vesicle diameters of about 10 µm. In this respect, they resemble rectangular specimens of *Dorsennidium minutum* rather than *V. lairdii*, although they conform in all other respects to the *V. lairdii* group.

The V. lairdii group appears to have been restricted largely to the high-palaeolatitude margin of Gondwana, including Avalonia, during the Tremadocian. At lower palaeolatitudes on the Gondwanan margin, for example in South China and Argentina, the first occurrence of the V. 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 Tetragraptus approximatus graptolite Biozone (Yan et al. 2011), equivalent to the lower part of Stage Slice F11. There is, for example, no record of the V. 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 Baltograptus deflexus graptolite Biozone, equivalent to mid-Floain 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 *V. 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 2006a, 2006b). 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 first appearance data (FADs) 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 *Tetragraptus 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, but it nevertheless remains possible that the true FAD of *Veryhachium* is below the Lakity Beds.

Triangular specimens of *Veryhachium*, attributed to the "*V. trispinosum* group", generally appear later in the fossil record than the rectangular morphotypes of the *V. lairdii* group (Servais et al. 2007). The *V. 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 with

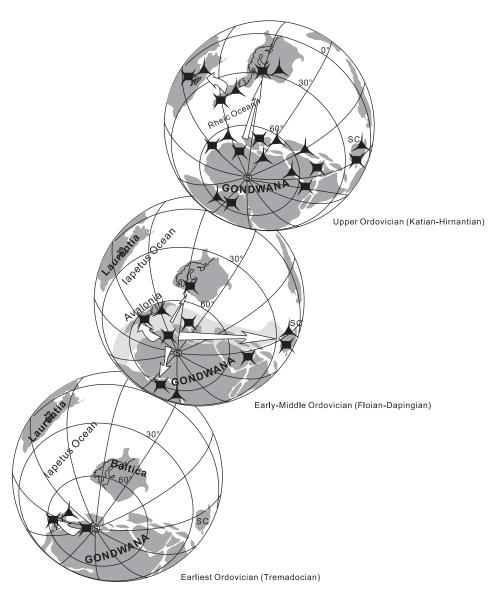


Fig. 1. Palaeobiogeographical distribution of the V. trispinosum group (triangles) and the V. lairdii group (rectangles), plotted on palaeogeographical reconstructions of the Early to Late Ordovician (reconstructions based on and modified after the BugPlates software www. geodynamics.no). S, South Pole; SC, South China.

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. lardii* group, has its first appearance at the base of the Floian, in the *T. 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 probably first appears at the base of Stage Slice Fl3 (de la Puente & Rubinstein 2013). The *trispinosum* group was also recorded in the Floian *Eremochitina brevis* chitinozoan Biozone (corresponding to time-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 *Tetragraptus 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 *V. 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 *V. 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 *V. 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

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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 V. lairdii and V. trispinosum groups were present only at high southern palaeolatitudes (Fig. 1), with first occurrences in North Africa (Gondwanan margin) and Avalonia (northern Germany and NW England). During the Floian, both 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 consider this apparently slow increase in biogeographical range through later Ordovician times.

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