First Appearance Data of selected acritarch taxa and correlation of Lower and Middle Ordovician Stages

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Abstract

First Appearance Data (FADs) of selected, easily recognizable acritarch morphotypes are assessed to determine their potential contribution to correlation of Lower and Middle Ordovician stages and substage divisions along the Gondwanan margin (Perigondwana) and between Perigondwana and other palaeocontinents. The FADs of nineteen genera, species and species groups are recorded throughout their biogeographical ranges. The taxa investigated fall into three groups. Some have FADs at about the same level throughout their biogeographical ranges and are useful for long-distance and intercontinental correlation. Among these are: *Coryphidium*, *Dactylofusa velifera*, *Peteinosphaeridium* and *Rhopaliophora* in the upper Tremadocian Stage; *Arbusculidium filamentosum*, *Aureotesta clathrata simplex* and *Coryphidium bohemicum* in the lower–middle Floian Stage; *Dicrodiacrodium* in the upper Floian Stage; *Frankea* in the Dapingian–lower Darriwilian stages; and *Orthosphaeridium* spp., with FADs in the Dapingian–lower Darriwilian stages of Perigondwanan regions and at about the same level in Baltica. Other taxa, however, have diachronous (or apparently diachronous) FADs, and this needs to be taken into account when using them for correlation. A second group of genera and species, comprising *Striatotheca*, the *Veryhachium lairdii* group and the *V. trispinosum* group, have a recurring pattern of FADs in the Tremadocian Stage on Avalonia and in South Gondwana and West Gondwana, but in the Floian Stage of South China and East Gondwana. The third group, consisting of *Arkonia*, *Ampullula*, *Barakella*, *Dasydorus*, *Liliosphaeridium* and *Sacculidium*, have FADs that are markedly diachronous throughout their biogeographical ranges, although the global FADs of *Arkonia*, *Ampullula*, *Liliosphaeridium* and *Sacculidium* are apparently in South China and/or East Gondwana. It is possible that diachronous FADs are only apparent and an artefact of sampling. Nevertheless, an alternative interpretation, suggested by recurring

patterns, is that some as yet undetermined factor controlled a slower biogeographical spread over time, resulting in diachroneity.

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The Ordovician System comprises three global series (Lower, Middle and Upper Ordovician) and seven global stages (Tremadocian, Floian, Dapingian, Darriwilian, Sandbian, Katian and Hirnantian). The global stages have been further divided into units of shorter duration by Webby *et al*. (2004), who introduced 19 time slices, and Bergström *et al.* (2009), who defined 20 stage slices. Time slices and stage slices are each shorter than a stage but longer than a faunal zone, and so correspond to a substage or a superzone (Fig. 1). The ages of stages and the stage slice boundaries were revised by Cooper & Sadler (2012). The bases of the global stages (Global Boundary Stratotype Section and Point, GSSP) are all defined on the first occurrence of either a conodont species (bases of the Tremadocian and Dapingian stages) or a graptolite species (bases of the Floian, Darriwilian, Sandbian, Katian and Hirnantian stages) (Bergström *et al.* 2009). The same is true for the stage slices, except for the uppermost Hirnantian Stage Slice H2, which extends from the end of the Hirnantian Isotopic Carbon Excursion (HICE) to the top of the Ordovician. Complementing the graptolite and conodont biozonations, chitinozoan biozonation schemes have been used in global correlation (e.g. Cooper & Sadler 2012) although no chitinozoan marker species is used to define any chronostratigraphical division.

Acritarchs have long been used for biostratigraphical dating and correlation of Ordovician successions, often in sediments devoid of other fossils, but biozonation schemes to complement those of the graptolites, conodonts and chitinozoans have not been developed (e.g. Servais & Paris 2000). Nevertheless, acritarchs have the potential to correlate global stages and stage slice boundaries in the Lower and Middle Ordovician. Molyneux *et al.* (2007), for example, discussed biostratigraphical correlation of the Tremadocian–Floian stage boundary using acritarchs, and Li *et al.* (2002a, 2010) pointed out the biostratigraphical potential of acritarch morphotypes for correlation of the Floian–Dapingian (Lower–Middle Ordovician) stage boundary. These examples deal mainly with correlations along the margin of Gondwana, including Avalonia, but also touch upon the use of acritarchs to correlate between Gondwana and other palaeocontinents.

The aim of this paper is to assess the First Appearance Data (FADs) of selected acritarch taxa that have the potential to correlate Lower and Middle Ordovician global stage and stage slice boundaries. An ultimate aim is the development of acritarch biozonation schemes to complement the graptolite, conodont and chitinozoan biozonations.

Figure 1 about here

Ordovician acritarch data

A substantial body of published data exists for Ordovician acritarchs; a decade ago, Servais *et al*. (2004a) estimated more than 1000 papers. Much of the data are from Europe, North Africa and North America, i.e. from the palaeocontinents of Baltica, Laurentia and the margins of the supercontinent Gondwana, often referred to as 'Perigondwana' (Fig. 2). A number of investigations have also been carried out on successions in South China (Li *et al.* 2002b) and South America (Rubinstein 2003), particularly in the Gondwanan successions of NW Argentina. In terms of palaeogeography, South China and NW Argentina (excluding the Precordillera) were situated at low to intermediate latitudes on or close to the Gondwanan margin (Fig. 2). In addition, a few publications deal with Lower–Middle Ordovician acritarch assemblages from Australian basins, also Gondwanan and located at low palaeolatitudes (Playford & Martin 1984, Playford & Wicander 1988, Foster *et al.* 2002, Quintavalle & Playford 2006a, b; Foster & Wicander 2016). The geographical coverage is extensive, but there are gaps, both geographically and stratigraphically. Much of the data from North America, for example, are from the Upper Ordovician Series (Sandbian, Katian and Hirnantian stages), with few data from the Lower and Middle Ordovician series.

Figure 2 about here

Acritarchs can be extremely abundant in sedimentary successions and their diversity can be high. The number of acritarch specimens in Lower Palaeozoic sediments can range from a few 10s to 100s or 1000s of individuals per gram of rock (see, for example, Mullins *et al.* 2004), but can reach tens of thousands of specimens depending on lithology and facies. In exceptional circumstances, hundreds of thousands of specimens per gram might be recorded. Dorning (1999), for example, noted that many samples from the Tremadocian Shineton Shales of the Welsh Borderland, UK, yielded more than 100,000 acritarchs per gram. Diversity also varies with sedimentary environment, but under favourable conditions, assemblages may contain 50 species or more.

Acritarch taxa often display a high degree of morphological variability, which in some instances can make it difficult to establish where boundaries lie between species and even between genera (e.g. Stricanne & Servais 2002). Some morphological changes can be interpreted as ecophenotypical responses to fluctuations in palaeoenvironmental factors, such as salinity (Servais *et al*. 2004*b*), and therefore constitute an ecological rather than a biostratigraphical or evolutionary signal. Other morphological changes have more biostratigraphical significance. In particular, the first appearances of new, readily distinguishable, innovative morphotypes, such as those considered here, most probably correspond to genotypic change rather than ecophenotypic adaptation, and consequently identify taxa that have biostratigraphical potential.

Stratigraphical framework

Correlation of the British (Anglo-Welsh), Baltic, Australasian and North America regional divisions with the global series and stages (Fig. 1) follows Cooper & Sadler (2012, fig. 20.9), as does correlation with the stage slices of Bergström *et al.* (2009). Correlation of the Australasian and Anglo-Welsh graptolite zonations, the North Atlantic conodont zonation and the 'North' Gondwanan chitinozoan zonation also follows the correlation shown in Cooper & Sadler (2012, fig. 20.1). The chronostratigraphical divisions adopted here for South China and correlation of the Upper Yangtze graptolite biozones follows Zhang *et al*. (2007, 2010), and the chronostratigraphical divisions for the Mediterranean and 'North' Gondwana are from Bergström *et al.* (2009). 'North Gondwana' has been used by authors to refer to those parts of the Palaeozoic continent of Gondwana that are in the most northerly position at the present day, including parts of southwestern and southern Europe, i.e. Iberia, France (e.g. Armorica, the Massif Central and the Montagne Noire) and Sardinia, North Africa and the Middle East (e.g. Servais & Sintubin 2009). Palaeogeographically, these areas were located at high southern palaeolatitudes and along the margin of SW Gondwana (Fig. 2). In this paper 'North Gondwana' of other authors equates to South Gondwana and West Gondwana (see *Note on palaeogeographical classification* below).

First Appearance Data (FADs) of selected acritarch morphotypes

Selection of genera, species and morphotypes

Brocke *et al.* (1995) discussed the FADs of eight taxa and Li *et al.* (2003) subsequently used the FADs of 17 taxa to correlate Lower and Middle Ordovician Perigondwanan sequences. We build on these earlier papers and discuss the FADs and biostratigraphical usefulness of 19 taxa (species, genera or morphological species groups). All occur on the Gondwanan margin ('Perigondwanan acritarch province') and some are also found on other palaeocontinents. All are easily recognizable with well-constrained morphologies that permit confident determination, and almost all have been subject to a thorough revision of their taxonomy and stratigraphical distribution. Their FADs are here correlated with the standard graptolite biozonations and are plotted against the stage slices of Bergström *et al.* (2009), the time slices of Webby *et al*. (2004) and the global and regional stratigraphical divisions (Fig. 3).

Figure 3 about here

Acritarchs considered in this study include, in alphabetical order, the genera *Ampullula*, *Arkonia*, *Barakella*, *Coryphidium*, *Dasydorus*, *Dicrodiacrodium*, *Frankea*, *Liliosphaeridium*, *Orthosphaeridium*, *Peteinosphaeridium*, *Rhopaliophora*, *Sacculidium* and *Striatotheca*, the species *Arbusculidium filamentosum*, *Aureotesta clathrata simplex*, *Coryphidium bohemicum* and *Dactylofusa velifera*, and the *Veryhachium lairdii* and *Veryhachium trispinosum* groups.

The emphasis in this paper is on elucidating global first occurrences, but we comment also on local FADs, especially where these diverge from the global FAD. The Last Appearance Data (LADs) of the 19 selected taxa are not discussed. Molyneux *et al*. (2006) showed that the LADs of acritarch taxa can be biostratigraphically useful, but the LADs of the taxa considered here are all above the top of the interval of interest.

The acritarchs considered in this paper are discussed in the order of their FADs as shown on Figures 3 and 4.

Note on palaeogeographical classification

The FADs in Figures 3 and 4 are shown in relation to established Ordovician palaeocontinents and other palaeogeographical units. In order to elucidate differences in FADs around the large palaeocontinent of Gondwana, FADs are classified according to whether they are from South Gondwana, West Gondwana or East Gondwana. Following the reconstructions of Ordovician Earth geography by Torsvik & Cocks (2017), South Gondwana is defined here to include regions between a palaeolatitude of 60°S and the Ordovician South Pole, principally North Africa but also including components of the Armorican Terrane Assemblage, notably Bohemia, Saxothuringia and Spain (Iberia). West Gondwana comprises the western margin of Gondwana from 60°S to equatorial regions and includes Saudi Arabia, Oman, Pakistan and Western Australia. Although situated adjacent to the western margin of Gondwana during the Early and Middle Ordovician (Torsvik & Cocks 2017, fig. 6.1), South China is treated as a separate entity. East Gondwana comprises regions on the eastern margin of Gondwana, but data are essentially restricted to those from NW Argentina.

FADs

Dactylofusa velifera (Fig. 5H)

The taxonomy, biostratigraphy and palaeobiogeography of *Dactylofusa velifera* were revised by Wang *et al.* (2015). Molyneux *et al*. (2006) recorded the first downhole occurrence of *Dactylofusa velifera* in cuttings samples from the Tremadocian Mabrouk Member in the Kauther-1H1 well in Oman on the western margin of Gondwana, in an acritarch assemblage that is evidently older than the late Tremadocian *messaoudensis-trifidum* assemblage. This suggests a first occurrence in pre-Tr3 strata, and is indicated by a question mark in Stage Slice Tr1 on Figure 3. It possibly represents the global FAD of the species. Another possible occurrence in pre-Tr3 strata is from the *P. deltifer* conodont Biozone of the Fenghsiang Formation on the Yangtze Platform of South China (Brocke, unpublished Ph.D. thesis, Technische Universität, Berlin, 1998). An occurrence in the *P. deltifer* Biozone would correspond to the uppermost part of Time Slice 1b and to Stage Slice Tr2, but the biostratigraphical dating and correlation require confirmation. Again, this occurrence is indicated by a question mark on Figure 3.

Stratigraphically well-constrained occurrences of *D. velifera* in South China, Avalonia and South Gondwana are in the upper Tremadocian Stage Slice Tr3. In South China, *D.*

velifera has been recorded from the *A. murrayi* graptolite Biozone (Wang *et al.* 2013), and possibly close to the base of the zone, at a level that probably corresponds to Time Slice 1c (Fig. 3). The species is present in *messaoudensis-trifidum* acritarch assemblages from Avalonia (NW England, South Wales and Belgium) and South Gondwana (Spain). In the Lake District of NW England, its FAD is in sub-assemblage 4 of the *messaoudensis-trifidum* assemblage, correlated with a level in the upper part of Stage Slice Tr3 and probably within Time Slice 1d (Molyneux *et al.* 2007; Fig. 3). Occurrences in SW Spain (Servais & Mette 2000) and Belgium (Breuer & Vanguestaine 2004) are from assemblages that are equated with the upper part of sub-assemblage 3 and/or sub-assemblage 4 of the *messaoudensis-trifidum* assemblage in NW England (Molyneux *et al.* 2007), which again suggests correlation with the upper part of Stage Slice Tr3 within Time Slice 1d (Fig. 3). The record from South Wales (Molyneux & Dorning 1989) is considered to be from Stage Slice Tr3, but its exact level is not constrained.

All the records cited above are from either high southern palaeolatitudes (NW England Belgium, South Wales and Spain) or from lower palaeolatitudes on or adjacent to the western margin of Gondwana (Oman, South China). Hitherto, published records of *Dactylofusa velifera* in the Central Andean Basin of NW Argentina, on the eastern margin of Gondwana, suggested a higher FAD, with the oldest recorded occurrences being from the *Tetragraptus akzharensis* graptolite Biozone (de la Puente & Rubinstein 2013, fig. 3), correlated with the upper part of Stage Slice Fl1. Following the adjustment of graptolite zone boundaries in NW Argentina (Toro *et al*. 2015), however, the presence of *Dactylofusa velifera brevis* in the lowest Floian (lower Fl1) *Tetragraptus phyllograptoides* Biozone (Fig. 1) is confirmed, and it is possible that *D. velifera* has its FAD there in the late Tremadocian *Hunnegraptus copiosus* Biozone, corresponding to the upper part of Stage Slice Tr3 (Time Slice 1d). In addition, the occurrence of *D. velifera* in a newly reported *messaoudensis-trifidum* acritarch assemblage (Rubinstein *et al.* in preparation) also suggests a FAD there in the early Floian (Fl1) or possibly late Tremadocian (Tr3?), although there are no graptolites or chitinozoans for independent age control. Consequently, the definite FAD of the species in NW Argentina (East Gondwana) is placed at the base of the Floian on Figure 3, with a tentative FAD in the upper Tremadocian at a level that corresponds to FADs in Avalonia and South Gondwana.

Veryhachium lairdii group (Fig. 5P)

The genus *Veryhachium* can be common in marine palynological assemblages of Ordovician age and younger (Servais *et al.* 2007). Lower and Middle Ordovician forms are generally either rectangular or triangular, and are assigned to the *Veryhachium lairdii* group and *Veryhachium trispinosum* group, respectively (Servais *et al.* 2007; Lei *et al.* 2013). The palaeobiogeographical distribution of *Veryhachium* morphotypes through the Ordovician was discussed by Servais *et al.* (2014), with global first occurrences of both groups at high southern palaeolatitudes of Perigondwana (Gondwana, Avalonia) in the Early Ordovician, followed by spreading to mid southern palaeolatitudes in Baltica and South China by the Middle Ordovician and a global distribution by the Late Ordovician. The diachronous FADs are reflected in Figure 3.

Servais *et al*. (2007) reported the first appearance of the *Veryhachium lairdii* group to be at a depth of 1590 m in the Bir Ben Tartar (Tt-1) Borehole of southern Tunisia (South Gondwana). They further reported graptolites of the *Rhabdinopora flabelliformis* group to occur at the same level, citing unpublished data, and referred to indirect correlation with the *Lagenochitina destombesi* chitinozoan Biozone. Graptolites of the *R. flabelliformis* group (Zalasiewicz *et al.* 2009, fig. 3) and correlation with the *Lagenochitina destombesi* Biozone (Fig. 1; Cooper & Sadler 2012) suggest assignment to Stage Slices Tr1 or Tr2 of Bergström *et al.* (2009) and to Time Slices 1a or 1b of Webby *et al.* (2004). Vecoli & Le Hérissé (2004, fig. 5, taxon number 85) indicated the FAD of *V. lairdii* on the high palaeolatitude ('Northern') Gondwanan margin to be in the middle of the Tremadocian Stage.

Specimens of *Veryhachium lairdii*? in a Tremadocian acritarch assemblage from cuttings samples of the Mabrouk Member, in the Kauther-1H1 well of Oman on the western margin of Gondwana (Molyneux *et al.* 2006), are probably also from the lower part of the Tremadocian Stage. Although *V. lairdii* is present in a Darriwilian acritarch assemblage from the same well, the preservation of specimens from the Mabrouk Member suggests that they are *in situ*, not caved. The associated Tremadocian acritarchs further suggest that the assemblage predates Stage Slice Tr3 and Time Slice 1c. The occurrences of the group in Tunisia and Oman are tentatively taken to indicate FADs low in the Tremadocian Stage of South Gondwana and West Gondwana respectively, and are indicated by question marks against Stage Slice Tr1 on Figure 3.

Other Tremadocian occurrences of the *V. lairdii* group from Avalonia and South Gondwana are from the upper Tremadocian Stage Slice Tr3. From Avalonia, specimens of the group have been recorded from sub-assemblage 1 of the *Cymatiogalea messaoudensis-Stelliferidium trifidum* acritarch assemblage in the Lake District of NW England, in the lowest samples collected from the *Araneograptus murrayi* Biozone (Molyneux *et al.* 2007, fig. 3), and are probably from the lower part of Stage Slice Tr3 and Time Slice 1c of Webby *et al*. (2004) (Figs 1, 3).

Specimens also occur in a *messaoudensis-trifidum* acritarch assemblage (Molyneux *et al.* 2007) from core between depths of 3615.8 m and 3835.3 m in the Rügen 5 borehole on the island of Rügen off the northern Baltic coast of Germany (Servais & Molyneux 1997), again part of Avalonia. Chitinozoa from the upper part of the same depth interval in Rügen 5 (3615.8–3794.7 m) were reported to indicate the *Lagenochitina destombesi* Biozone (Samuelsson *et al.* 2000; Servais *et al*. 2001), which is generally correlated with Tr1-Tr2 and with Time Slices 1a and 1b (Fig. 1). Recent investigation of chitinozoan faunas from NW England, however, has shown that *L. destombesi* occurs there at higher stratigraphic levels in the Tremadocian, in Stage Slice Tr3 and the *A. murrayi* Biozone (Amberg *et al*. in press). Based on this evidence, the occurrence of the *V. lairdii* group on Rügen in the *messaoudensis-trifidum* assemblage is considered to indicate a level in Stage Slice Tr3 and Time Slice 1c, equivalent to its FAD in NW England.

Occurrences of the *V. lairdii* group reported by Nowak *et al.* (2015, 2016) from Morocco (South Gondwana) are also placed in the lower part of the *messaoudensis-trifidum* assemblage (Nowak *et al.* 2015, 2016) and correlated with the *A. murrayi* Biozone, Stage Slice Tr3 and Time Slice 1c. Based on the records from NW England, Rügen and Morocco, definite FADs of the *V. lairdii* group on Avalonia and high palaeolatitude South Gondwana are placed at about the base of Stage Slice Tr3 and Time Slice 1c (Fig. 3).

Specimens of the *Veryhachium lairdii* group have been recorded from other upper Tremadocian *messaoudensis-trifidum* acritarch assemblages of Avalonia and South Gondwana. Palynofloras containing the *Veryhachium lairdii* group in the Avalonian successions of Ireland (Connery & Higgs 1999; Todd *et al*. 2000) and Belgium (Vanguestaine & Servais 2002; Breuer & Vanguestaine 2004) and the South Gondwanan succession of Spain (Servais & Mette, 2000) are correlated with the upper part of sub-assemblage 3 and/or the overlying sub-assemblage 4 of the *messaoudensis-trifidum* assemblage of NW England (Molyneux *et al.* 2007). These two sub-assemblages are correlated in turn with the uppermost Tremadocian (Molyneux *et al.* 2007) and therefore with the upper part of Stage Slice Tr3. The associated acritarch assemblage from south Wales (Avalonia; Molyneux & Dorning 1989) suggests correlation with Stage Slice Tr3 undivided, and the associated chitinozoan in Bohemia (South Gondwana; Fatka 1993), *Amphorachitina conifundus*, suggests a late Tremadocian (*murrayi* or *copiosus* graptolite biozones) or possibly earliest Floian age (Paris 1990).

All the occurrences listed above were located at high to intermediate southern palaeolatitudes on the Gondwanan margin (Fig. 2). At lower palaeolatitudes, the first occurrence of the *Veryhachium lairdii* group is apparently in the lowermost Floian Stage or higher (Servais *et al*. 2007). In South China, its first occurrence is in the *Tetragraptus approximatus* graptolite Biozone (Yan *et al*. 2011), equivalent to the lower part of Stage Slice Fl1 (Figs 1, 3). In NW Argentina, on the eastern margin of Gondwana, de la Puente & Rubinstein (2013) recorded its first occurrence in the '*Baltograptus deflexus*' Biozone, equivalent to Stage Slice Fl2, in sections from the Central Andean Basin (Fig. 2). More recently, the *V. lairdii* group has also been found in the Cordillera Oriental, Central Andean Basin, in levels below horizons with *Velachitina veligera* and thus possibly in the Tremadocian (Rubinstein *et al.* in preparation). Based on these records, the FAD in East Gondwana is placed tentatively at the base of the Floian Stage, indicated by a question mark on Figure 3, and definitely at the base of Stage Slice Fl2.

On Baltica, rectangular specimens of *Veryhachium* spp. comparable with *V. lairdii* have been recorded from the Lakity Beds of the Leetse Formation in the Lava River section of the St Petersburg region (Molyneux *et al.* 2007, fig. 5). There they occur in the *T. phyllograptoides* graptolite Biozone (lower part of Stage Slice Fl1), although not in the lowest sample collected from that zone. The Lakity Beds are unconformable on the Nazya Formation, which is correlated with the Varangu Regional Stage, the *Paltodus deltifer* conodont Biozone and Stage Slice Tr2. Consequently, the lower part of the Hunneberg Stage, equivalent to Stage Slice Tr3 and Time Slices 1c and 1d, is missing and the true FAD of rectangular veryhachids in Baltica could be below the Lakity Beds. For now, the FAD of the group is placed at about the base of the Floian Stage on Baltica (Fig. 3).

Rhopaliophora (Fig. 5L)

Li *et al.* (2014) revised the taxonomy and the biostratigraphical and palaeogeographical distribution of the genus *Rhopaliophora*. The FAD of *Rhopaliophora* in North China was recorded (Martin & Yin 1988, text-fig. 2) below the *Adelograptus*-*Clonograptus* with *Kiaerograptus* graptolite 'horizon' but above the *Psigraptus* 'horizon'. The *Adelograptus*-*Clonograptus* with *Kiaerograptus* graptolite 'horizon' has since been replaced in North China by the *Aorograptus victoriae* Biozone (Zhang *et al.* 2004), which is equivalent to the biozone of the same name in Australia (Fig. 1). This implies that the first occurrence of *Rhopaliophora* in North China is in Stage Slice Tr2 or the upper part of Tr1, at a level equivalent to the upper part of Time Slice 1b, and possibly represents its global FAD (Fig. 3).

Rhopaliophora is also reported to be present in the *P. deltifer* conodont Biozone of the Fenghsiang Formation in South China (Brocke, unpublished Ph.D. thesis, Technische Universität, Berlin, 1998). This occurrence, indicated by a question mark on Figure 3, would also correlate with Stage Slice Tr2. A definite FAD in South China is placed at about the base of Stage Slice Tr3 and Time Slice 1c, based on a record low in the *A. murrayi* Biozone (Wang *et al.* 2013).

The FAD of *Rhopaliophora* is similarly placed at about the base of Stage Slice Tr3 and Time Slice 1c in South Gondwana, East Gondwana, Baltica and Laurentia. In South Gondwana, *Rhopaliophora* has been recorded from a *messaoudensis-trifidum* acritarch assemblage low in the *A. murrayi* Biozone of Morocco (Nowak et al. 2016), which justifies the position of the FAD in Figure 3. In East Gondwana, the FAD of *Rhopaliophora* is in the *A. murrayi* Biozone of the Central Andean Basin, NW Argentina (Waisfeld *et al*. 2006; de la Puente & Rubinstein 2009, fig. 2, 2013, fig. 3). In Baltica, *Rhopaliophora* has been recorded from a level in the lower part of the upper Tremadocian *Paroistodus proteus* conodont Biozone on the East European Platform (Paalits & Erdtmann 1993) and at an equivalent level in the Oslo Region (Tongiorgi *et al.* 2003), which again suggests a level low in Stage Slice Tr3 and Time Slice 1c. In Laurentia, the FAD of the genus marks the base of Microflora AU6 of Martin (1992), in the upper massive member of the Survey Peak Formation and the upper part of trilobite zone F (equivalent to the *Rossaspis superciliosa* trilobite Biozone in the upper part of the Stairsian Stage: Ross *et al.* 1997, fig. 10; see also Dean 1989). The upper part of the Stairsian Stage correlates with the lower part of Stage Slice Tr3 (Fig. 1; Cooper & Sadler 2012).

For Avalonia, the FAD of the genus is slightly higher. The first occurrence of *Rhopaliophora* in the *messaoudensis-trifidum* assemblage of NW England is at the base of sub-assemblage 2 in the upper Tremadocian Stage, at a level above the base of the *A. murrayi* graptolite Biozone and therefore above the base of Stage Slice Tr3 (Molyneux *et al.* 2007). Correlation with Time Slices 1c and 1d of Webby *et al*. (2004) is uncertain, but the FAD is certainly above the base of Time Slice 1c and possibly close to the boundary between 1c and 1d (Molyneux *et al.* 2007, fig. 4). This is where its FAD in Avalonia is placed in Figure 3.

Other Tremadocian occurrences of *Rhopaliophora* from Avalonia and South Gondwana are higher. An assemblage with ?*Rhopaliophora* sp. from the Lierneux Member (Jalhay Formation, Salm Group) of Belgium (Breuer & Vanguestaine 2004; Avalonia) is correlated with the uppermost Tremadocian sub-assemblage 4 of the *messaoudensis-trifidum* assemblage (Molyneux *et al.* 2007) and therefore probably with the upper part of Stage Slice Tr3. An occurrence of *Rhopaliophora* in the Barriga Formation of Spain (South Gondwana) is attributed to the top of sub-assemblage 3 or sub-assemblage 4 (Molyneux *et al.* 2007). Nevertheless, it is below a graptolite assemblage containing *H. copiosus* (Servais & Mette 2000) and is therefore perhaps in the uppermost part of Time Slice 1c or in the lower part of 1d. In Bohemia (Fatka 1993; South Gondwana), *Rhopaliophora* is associated with the chitinozoan *Amphorachitina conifundus*, which suggests a late Tremadocian (*A. murrayi* or *H. copiosus* biozones) or possibly an earliest Floian age (Paris 1990), equivalent to Time Slices 1c, 1d or possibly the lowest part of Time Slice 2a.

Peteinosphaeridium (Fig. 5M)

A revision of this widely recorded Ordovician genus, including biometrical studies, is much needed. Of particular interest is the transition to the genus *Rhopaliophora*, as indicated by Li *et al.* (2014). Playford *et al.* (1995) considered the FAD of *Peteinosphaeridium* to be in the uppermost Tremadocian of Alberta, Canada, in the warm-water environments of Laurentia. There, the FAD of *Peteinosphaeridium* coincides with that of *Rhopaliophora* at the base of Microflora AU6 of Martin (1992), in the upper massive member of the Survey Peak Formation and the upper part of trilobite zone F (equivalent to the *Rossaspis superciliosa* trilobite Biozone in the upper part of the Stairsian Stage; Ross *et al*. 1997). The upper Stairsian Stage is correlated with the lower part of Stage Slice Tr3 (Fig. 1; Cooper & Sadler 2012), and the FAD of *Peteinosphaeridium* is therefore shown at the base of Tr3 in Figure 3.

In contrast, Playford *et al.* (1995) considered the first occurrence of *Peteinosphaeridium* in Perigondwanan regions to be in the Floian Stage (Arenig). However, there is now evidence to show that the genus also has first occurrences in the upper Tremadocian Stage Slice Tr3 around Gondwana and possibly also on Baltica.

In South China and East Gondwana (NW Argentina), the FAD of the genus is at the same level as that of *Rhopaliophora* (Fig. 3) at about the base of Stage Slice Tr3 and Time Slice 1c (Wang *et al.* 2013; de la Puente & Rubinstein 2009). In South Gondwana, the FAD of *Peteinosphaeridium* in Bohemia coincides with that of *Rhopaliophora* (Fatka 1993) and is therefore probably late Tremadocian or possibly earliest Floian in age, equivalent to Time Slices 1c, 1d or possibly the lowest part of Time Slice 2a. Nowak *et al.* (2016), however, noted a questionable occurrence low in the upper Tremadocian *A. murrayi* graptolite Biozone of Morocco, at the same level as *Rhopaliophora*. The FAD of the genus in South Gondwana is placed here at the same level as that of *Rhopaliophora*, at about the base of Stage Slice Tr3 (Fig. 3). The genus has been recorded from a *messaoudensis-trifidum* acritarch assemblage of Avalonia in NW England (Molyneux & Rushton 1988), but its first occurrence in sub-assemblage 2 is slightly higher (Fig. 3), probably close to the boundary between Time Slices 1c and 1d (Molyneux *et al.* 2007).

On Baltica, the genus has been recorded from the lower part of the *Paroistodus proteus* conodont Biozone on the East European Platform (Paalits & Erdtmann 1993) and from the Oslo Region (Tongiorgi *et al.* 2003), at levels that correlate with the upper Tremadocian and probably in the lower part of Stage Slice Tr3. The first occurrence of *Peteinosphaeridium* on Baltica is thus consistent with a late Tremadocian Stage Slice Tr3 age and is shown at about the level of the FAD of the genus around Gondwana.

Striatotheca (Fig. 5O)

Servais (1997) revised the 'veryhachid' taxa *Arkonia* and *Striatotheca*. Both genera are characteristic of the Perigondwanan acritarch province.

Striatotheca has its FAD on Avalonia in the lowest samples that have yielded the *messaoudensis-trifidum* acritarch assemblage from NW England (Molyneux *et al.* 2007). These are from the *Araneograptus murrayi* graptolite Biozone and probably close to the bases of Stage Slice Tr3 and Time Slice 1c of Webby *et al*. (2004) (Figs 1, 3). Rare specimens of *Striatotheca* were also recorded by Servais & Molyneux (1997) from the *messaoudensis-trifidum* acritarch assemblage in core between depths of 3615.80 m and 3796.40 m in the Rügen 5 borehole on the island of Rügen. As with the *Veryhachium lairdii* group, the Rügen 5 occurrences are probably close to the base of the *A. murrayi* Biozone and the base of Tr3 on Avalonia. Occurrences of *Striatotheca* recorded by Nowak *et al.* (2016) from Morocco are also low in the *A. murrayi* Biozone. These occurrences are used to position the FAD of *Striatotheca* at the base of Stage Slice Tr3 and Time Slice 1c for Avalonia and South Gondwana in Figure 3.

Other late Tremadocian occurrences from Avalonia and South Gondwana are from higher stratigraphical levels. *Striatotheca* has been recorded from upper Tremadocian *messaoudensis-trifidum* acritarch assemblages of South Wales (Molyneux & Dorning 1989) and Belgium (Vanguestaine & Servais 2002; Breuer & Vanguestaine 2004), both on Avalonia, and from Spain (Servais & Mette 2000), South Gondwana. The palynofloras from Belgium and Spain are correlated with the upper part of sub-assemblage 3 and/or the overlying sub-assemblage 4 of the *messaoudensis-trifidum* assemblage of NW England (Molyneux *et al.* 2007), and therefore with the upper part of Stage Slice Tr3 and with a level in Time Slice 1d. Correlation of the beds containing *Striatotheca* in South Wales is with Stage Slice Tr3.

The upper Tremadocian occurrences of *Striatotheca* from Avalonia and South Gondwana are all from high southern Early Ordovician palaeolatitudes. At lower palaeolatitudes, *Striatotheca* has not yet been recorded from the Tremadocian Stage in South China. The first recorded occurrence of the genus there is at the base of the Floian Stage (Yan *et al*. 2011), equivalent to the bases of Stage Slice Fl1 and Time Slice 2a (Fig. 3). First occurrences of *Striatotheca* in the Central Andean Basin of NW Argentina, situated at middle palaeolatitudes on the eastern margin of Gondwana, are higher still, in the '*Baltograptus deflexus*' Biozone (Ottone *et al*. 1992; Rubinstein & Toro 1999, 2001; Rubinstein *et al.* 1999; de la Puente & Rubinstein 2013), and are correlated with Stage Slice Fl2 (Figs 1, 3). The relatively high FAD of *Striatotheca* in NW Argentina could be a consequence of either lack of samples from lower levels or environmental control on its distribution and occurrence, but as no specimens have been recorded from *messaoudensis-trifidum* associations in Argentina (e.g. de la Puente & Rubinstein 2009), it is possible that the progressively higher FADs of the genus in South China and NW Argentina resulted from protracted migration of the genus around the northern promontory of Gondwana (Fig. 2).

Coryphidium (Fig. 5G)

The genus *Coryphidium*, reviewed by Servais *et al.* (2008), is a common component of acritarch assemblages from the Floian to Darriwilian stages of Perigondwana, but its first occurrence is in the uppermost Tremadocian. The genus has not been recorded from Baltica or Laurentia (Servais & Fatka 1997) and is one of the taxa used to define the Perigondwanan acritarch province (Li 1989; Servais *et al*. 2003; Molyneux *et al*. 2013).

Coryphidium was reported by Fang (1986) from the Tremadocian Tangchi Formation of South China, although the precise age of this record remains problematical. Wang *et al.* (2013), however, recorded *Coryphidium* sp. from the Ningkuo Formation of the Jiangnan Slope in South China, at the base of their Assemblage Zone C in the middle of the *A. murrayi* Biozone. This is possibly its FAD in South China. It might also represent its global FAD and is placed within Stage Slice Tr3 at about the base of Time Slice 1d on Figure 3.

In East Gondwana (NW Argentina), *Coryphidium*? sp. occurs in beds corresponding to the *A. murrayi* Biozone (Stage Slice Tr3, Time Slices 1c to lower 1d), and *Coryphidium* sp. (positive assignment) in beds corresponding to the *H. copiosus* Biozone (upper Stage Slice Tr3, Time Slice 1d) (de la Puente & Rubinstein 2009, 2013). The former is indicated on Figure 3 by a question mark at about the base of Time Slice 1d, and the latter by a definite FAD within the time slice.

In Avalonia, the first occurrence of *Coryphidium* in NW England is in the upper part of sub-assemblage 3 of the *messaoudensis-trifidum* assemblage, corresponding to the upper part of Stage Slice Tr3 and probably at a level within Time Slice 1d (Molyneux *et al*. 2007). Other Avalonian occurrences of *Coryphidium* at about the same level are from southern Ireland (Connery & Higgs 1999; Todd *et al.* 2000) and Belgium (Vanguestaine & Servais 2002; Breuer & Vanguestaine 2004), and the genus is also present at about the same level in the *messaoudensis-trifidum* acritarch assemblage from the graptolitic Barriga Formation of SW Spain (Servais & Mette 2000). It also occurs in possible transitional 'latest Tremadoc-earliest Arenig' samples from south and SE Turkey (Martin 1996). The occurrences in Ireland, Spain and Belgium are all probably from the upper part of Stage Slice Tr3 and within Time Slice 1d (Molyneux *et al.* 2007, fig. 4). The first occurrence of *Coryphidium* throughout the Perigondwana region is thus in the upper part of Stage Slice Tr3.

Veryhachium trispinosum group (Fig. 5S)

The first occurrence of triangular veryhachid acritarchs of the *V. trispinosum* group post-dates that of the rectangular morphotypes of the *V. lairdii* group (Servais *et al.* 2007). The global FAD is possibly from Avalonia, where the *V. trispinosum* group has its first occurrence in sub-assemblage 3 of the *messaoudensis-trifidum* acritarch assemblage of NW England (Molyneux *et al.* 2007), in the upper part of Stage Slice Tr3 and probably in the lower part of Time Slice 1d (Fig. 3). Its first occurrence in Belgium (Vanguestaine & Servais 2002; Breuer & Vanguestaine 2004), also part of Avalonia, is in a *messaoudensis-trifidum* assemblage comparable with sub-assemblage 4 in the Lake District, again in the upper part of Stage Slice Tr3 and probably in the middle of Time Slice 1d.

The first occurrence of the group in Bohemia (Fatka 1993), part of the Armorican Terrane Assemblage of South Gondwana, is in either the upper part of Tremadocian Stage Slice Tr3 or possibly the lowermost part of the Floian Stage Slice Fl1. This occurrence is broadly correlated with sub-assemblages 3–5 of the *messaoudensis-trifidum* assemblage in

NW England, and is therefore possibly at about the same level as in Avalonia or slightly higher (Fig. 3). However, the group was not recorded by Nowak *et al*. (2016) from the upper Tremadocian of Morocco, and Vecoli & Le Hérissé (2004) placed the FAD of *V. trispinosum* at the base of the Floian Stage in their review of Ordovician acritarchs from the 'North' Gondwanan margin.

At lower palaeolatitudes, FADs of the *V. trispinosum* group around Gondwana are currently post-Tremadocian. In South China, the *V. trispinosum* group, like the *V. lairdii* group, has its FAD at the base of the Floian Stage, in the *Tetragraptus approximatus* Biozone (Fig. 3; Xu 2001; Yan, unpublished Ph.D. thesis, Nanjing Institute of Geology and Palaeontology 2007; Yan *et al*. 2011). In NW Argentina (East Gondwana), the *V. trispinosum* group first appears at the base of Stage Slice Fl3 (de la Puente & Rubinstein 2013), so far its highest first occurrence around Gondwana (Fig. 3). Achab *et al* (2006) recorded the group from the Suri Formation of unspecified Floian age in the Perigondwanan volcanic arc of the Famatina System in NW Argentina, but Ottone *et al.* (1992) and Rubinstein *et al.* (1999) recorded the lowest occurrences of *V. trispinosum* from the *Didymograptus bifidus* graptolite Biozone in the Central Andean Basin, which equates with Fl3 (Fig. 3).

Although the *Veryhachium trispinosum* group is generally common and widespread across palaeocontinents in the later Ordovician, its first occurrence on Baltica is apparently much later than on the Perigondwanan margin (Servais *et al*. 2014). The oldest record appears to be from the undivided Kunda Stage (B_{III}), equivalent to upper Stage Slice Dw1 and Stage Slice Dw2, in the Rapla Borehole of Estonia (Uutela & Tynni 1991). The group's FAD on Baltica is placed at the base of Stage Slice Dw2 (Fig. 3). There are no records at the Tremadocian–Darriwilian level from Laurentia, but this could reflect a lack of data as much as a real absence.

Barakella (Fig. 5E)

The genus *Barakella* was described originally from the late Arenig of Morocco (Cramer & Díez 1977). It has since been reported widely around the Gondwanan margin, from high to low Ordovician palaeolatitudes.

First definite occurrences of the genus on Avalonia and South China are in the lower–middle Floian Stage. In South China, the FAD of the genus is placed in Stage Slice Fl1 in the lower or middle Floian, in the lower part of Time Slice 2b or possibly in 2a (Yan *et al*., in press). On Avalonia, Molyneux (1987) recorded the genus from the upper part of the

Moridunian Stage of the Arenig Series in South Wales, approximately equivalent to Time Slice 2b (Fig. 1). FADs in both areas are placed at the base of Time Slice 2b (Fig. 3), with a question mark indicating its possible occurrence in Time Slice 2a in South China. However, it is possible that the FAD of the genus is lower in Avalonia, based on a record of *Barakella*? sp. at about the same level as the FAD of *Coryphidium* in NW England (Molyneux 2009). This is in the upper part of sub-assemblage 3 of the *messaoudensis-trifidum* assemblage, corresponding to the upper part of Stage Slice Tr3 and probably at a level within Time Slice 1d (Molyneux *et al*. 2007).

Elsewhere around Gondwana, first occurrences of the genus tend to be in the middle or upper Floian, or higher. The FAD of the genus in NW Argentina is in the '*B. deflexus*' graptolite Biozone (de la Puente & Rubinstein 2013), which correlates with Stage Slice Fl2 in the middle Floian and the upper part of Time Slice 2b (Fig. 1). Records from Pakistan (Tongiorgi *et al*. 1994; Quintavalle *et al.* 2000) are slightly higher, from the *Azygograptus suecicus* graptolite Biozone, which correlates with the upper part of Stage Slice Fl3 and the lowermost Dapingian Stage Slice Dp1 (Fig. 1). The FADs for East Gondwana and West Gondwana shown on Figure 3 are based on these records respectively, at the base of Stage Slice Fl2 and the base of Stage Slice Dp1. However, given that there is another possible middle Floian record from the Zard-Kuh Formation in the Zagros Basin of Iran (Ghavidel-syooki 1996), although in this case correlation with global stages and stage slices is imprecise, it is also possible that the FAD in West Gondwana is also at a level in the Floian Stage.

Vecoli & Le Hérissé (2004) indicated the FAD of *Barakella fortunata* on the 'northern Gondwanan margin' (corresponding largely to South Gondwana as defined herein) to be at the base of the *Desmochitina ornensis* chitinozoan Biozone, which correlates approximately with the base of the Dapingian (Stage Slice Dp1) and the base of Time Slice 3a (Fig. 1). The FAD in South Gondwana is therefore placed at the base of the Dapingian Stage.

The occurrence of the genus on other palaeocontinents is unconfirmed. *Barakella*? sp. was recorded from Sweden (Baltica) by Ribecai & Tongiorgi (1995), where its FAD is in the Hunderum Substage of the Kunda Stage, which correlates with a level in the Darriwilian (upper Dw1–lower Dw2; Fig. 1). A questionable FAD is placed at about the base of Stage Slice Dw2.

Figure 4 about here

Aureotesta clathrata simplex (Fig. 5C)

Recorded as *Marrocanium simplex* before its taxonomic reassignment by Brocke *et al*. (1998), *A. clathrata simplex* is easily recognizable. It was first described from Morocco (South Gondwana; Cramer *et al*. 1974) at a level that is now correlated with the *Desmochitina bulla* chitinozoan Biozone (Soufiane & Achab 1993) and therefore with the lower Darriwilian Dw1 Stage Slice (Fig. 1). However, the first occurrence of *Aureotesta clathrata simplex* in NW England (Avalonia) is in sub-assemblage 5 of the *messaoudensis-trifidum* assemblage, considered to be of early Floian age (Molyneux *et al.* 2007) and correlated with Stage Slice Fl1. Molyneux *et al.* (2007) considered the FAD of *A. clathrata simplex* in NW England to be close to the base of the *T. phyllograptoides* Biozone. The first occurrence of *A. clathrata simplex* in South China is also in the early Floian, in the *T. approximatus* graptolite Biozone (Yan, unpublished Ph.D. thesis, Nanjing Institute of Geology and Palaeontology 2007; Yan *et al*. 2011), and is therefore close to its FAD in NW England. These records are the criteria used to place the FAD of *A. clathrata simplex* at the base of the Floian Stage in both Avalonia and South China (Fig. 4).

The FAD of *A. clathrata simplex* in South Gondwana is uncertain, but based on a record from the *Corymbograptus v-similis* graptolite Biozone (Vavrdová 1993) of Bohemia it is likely to be in the Floian Stage. The *C. v-similis* Biozone is low in the Arenig Klabava Formation of Bohemia and has been correlated with the *Pseudodidymograptus balticus* Biozone of Baltica (Paris & Mergl 1984, table 1), which in turn is correlated with Time Slice 2b (Webby *et al*. 2004). The FAD of *A. clathrata simplex* in South Gondwana is placed at the base of Time Slice 2b (Fig. 4), but this does not exclude the possibility that the true FAD is lower and at about the same level as in Avalonia or South China.

The first occurrence of *A. clathrata simplex* in NW Argentina (East Gondwana) is higher (Fig. 4), in the '*Baltograptus deflexus*' graptolite Biozone (Rubinstein *et al.* 2007; de la Puente & Rubinstein 2013), which is correlated with Stage Slice Fl2 (Fig. 1). In common with other taxa, *A. clathrata simplex* appears to have had a later first occurrence on the eastern Gondwanan margin than at high southern palaeolatitudes.

A. clathrata simplex has not been reported from Baltica and so remains an indicator of the 'Perigondwanan' acritarch bioprovince (Li 1989; Servais *et al*. 2003; Molyneux *et al.* 2013).

Arbusculidium filamentosum (Fig. 5B)

Arbusculidium filamentosum is another characteristic species of the Perigondwanan acritarch province and has its FAD in the middle Floian around Gondwana. In Avalonia, the FAD of the species is in sub-assemblage 5 of the *messaoudensis-trifidum* assemblage of NW England, between beds that are correlated with the *Tetragraptus phyllograptoides* and *Corymbograptus varicosus* graptolite biozones (Molyneux *et al.* 2007). This level is within Stage Slice Fl1 and probably equates with the lower part of Time Slice 2b (Figs 1, 4). The FAD of *Arbusculidium filamentosum* in Bohemia (Armorican Terrane Assemblage) is in the *Corymbograptus v-similis* graptolite Biozone (Vavrdová 1993), which is correlated with Time Slice 2b (see *Aureotesta clathrata simplex*). Based on these records, the FAD of *A. filamentosum* in both Avalonia and South Gondwana is placed here at the base of Time Slice 2b (Fig. 4).

The FAD of *Arbusculidium filamentosum* might be slightly higher at lower palaeolatitudes and on the eastern margin of Gondwana. Studies in South China (Yan, unpublished Ph.D. thesis, Nanjing Institute of Geology and Palaeontology 2007; Yan *et al*. 2011) have established that its first occurrence there is in the *Didymograptus eobifidus* graptolite Biozone, which is correlated with Stage Slice Fl2 and the upper part of Time Slice 2b. In NW Argentina (East Gondwana), the first occurrence of *A. filamentosum* is correlated with the '*B. deflexus*' graptolite Biozone (Rubinstein & Toro 2001; Rubinstein *et al*. 2007; de la Puente & Rubinstein 2013), which is again correlated with Stage Slice Fl2 and the upper part of Time Slice 2b. The FAD of the species is placed here at the base of Stage Slice Fl2 in both areas (Fig. 4).

Coryphidium bohemicum (Fig. 5F)

Coryphidium bohemicum, the type species of the genus, has been reported from many localities around the margin of Gondwanan and is one of the characteristic species of the Perigondwanan acritarch assemblages (Li 1989). It has not been recorded from other palaeocontinents. FADs of the species around Gondwana are in the Floian Stage, and within Time Slice 2b.

Cooper *et al.* (1995) defined the *Stelliferidium trifidum-Coryphidium bohemicum* assemblage in the upper part of the Hope Beck Formation in NW England, overlain by beds that contain the *Coryphidium bohemicum* assemblage in the Loweswater Formation. The incoming of *C. bohemicum* in the *trifidum-bohemicum* Biozone is above the highest *T. phyllograptoides* Biozone graptolite faunas, but below the lowest *C. varicosus* Biozone faunas (Molyneux *et al.* 2007). Correlation of this interval is with the middle and upper parts of Stage Slice Fl1 and the lower part of Time Slice 2b (Fig. 1). The FAD of *C. bohemicum* in NW England is above that of *A. filamentosum* so is shown above the base of Time Slice 2b on Figure 4, but still in its lower part and therefore in the upper part of Stage Slice Fl1.

The FAD of *C. bohemicum* in Bohemia, representing South Gondwana, is at the same level as the FADs there of *Aureotesta clathrata simplex* and *Arbusculidium filamentosum*, in the *Corymbograptus v-similis* graptolite Biozone (Vavrdová 1993), and is similarly placed here at the base of Time Slice 2b (Fig. 4). The oldest records of *C. bohemicum* from South China are from the *A. filiformis* graptolite Biozone (Yan *et al*. 2011), which also corresponds to the lower part of Time Slice 2b and the upper part of Stage Slice Fl1, and the FAD there is again placed at the base of Time Slice 2b (Fig. 4). The specimen of '*C. bohemicum*' recorded by Xu (1999) from the *T. approximatus* graptolite Biozone of the Sandu area in South China does not belong to the species.

Comparable forms have a slightly higher first occurrence on the east Gondwanan margin in NW Argentina. There, *Coryphidium* cf. *bohemicum* has its first occurrence in the '*B. deflexus*' Biozone (Rubinstein & Toro 1999, 2001; Rubinstein *et al*. 2007; de la Puente & Rubinstein 2013), correlated with Stage Slice Fl2 and the upper part of Time Slice 2b. Its FAD in East Gondwana is placed at the base of Stage Slice Fl2 (Fig. 4).

Sacculidium (Fig. 5N)

Sacculidium has been recorded from around Gondwana, from South China and from Baltica. Its global FAD is in South China, where it is present in the *Acrograptus filiformis* graptolite Biozone (Yan *et al*. 2013). This establishes the global FAD of *Sacculidium* in the Floian Stage, equivalent to the upper part of Stage Slice Fl1 and the lower part of Time Slice 2b (Fig. 1), and it is placed herein at the base of Time Slice 2b (Fig. 4). However, the genus is not widespread below the Dapingian Stage.

Sacculidium is common in the Middle Ordovician Volkhov and Kunda regional stages of Baltica. The lowest recorded occurrence in Baltica is from the Langevoja Substage of the Volkhov Stage in Sweden (Ribecai & Tongiorgi, 1995, recorded as '*Peteinosphaeridium macropylum*'; Ribecai *et al.* 2002), which correlates with the uppermost Dapingian to lowest Darriwilian stages (top Dp3–lower Dw1 stage slices, top 3b–lower 4a time slices; Fig. 1).

The FAD of the genus in Baltica is placed at the base of Stage Slice Dw1 (Fig. 4). Other records from Baltica are from around the same level. Those from Estonia (Uutela & Tynni 1991; Ribecai *et al.* 2002), Baltic Russia (St Petersburg region: Ribecai *et al.* 2002) and Arctic Russia (Arkhangelsk region: Ribecai *et al.* 2002; Raevskaya *et al.* 2006) are reported to be from the upper Volkhov Stage. In Norway, *Sacculidium* has been recorded from the Hunderum Substage of the Kunda Stage (Ribecai *et al.* 1999; Ribecai *et al.* 2002; Tongiorgi *et al.* 2003), corresponding to the upper Dw1–basal Dw2 stage slices and the upper 4a Time Slice (Fig. 1).

Around Gondwana, the genus is also present in the Llanvirn Series (Darriwilian Stage) of North Africa (Ribecai *et al.* 2002, previously recorded as *'Peteinosphaeridium macropylum* s.l.' in Tunisia). In the Canning Basin of Australia (Fig. 2), Quintavalle & Playford (2006a, b) recorded it from the *C. setarium* Biozone, correlated with the upper Dapingian and lower Darriwilian stages, and from overlying zones. In NW Argentina, Achab *et al.* (2006) recorded *Ammonidium* [*Sacculidium*] cf. *A. aduncum* Playford & Martin 1984, from the Molles Formation in the Famatina System, probably equivalent to the Dapingian *Baltoniodus navis* conodont Biozone. Based on these records, FADs are placed respectively at the base of Stage Slice Dw2 (base Llanvirn Series) in South Gondwana, the base of the Darriwilian Stage in West Gondwana, and the base of the Dapingian Stage in East Gondwana.

Dasydorus (Fig. 5I)

First described from the Middle Ordovician of Australia by Playford & Martin (1984), the genus *Dasydorus* has since been cited from other parts of Gondwana and from other palaeocontinents, including Baltica. The genus is present on the Gondwanan margin from low palaeolatitudes (Australia) to high palaeolatitudes. Examples of the latter include its occurrences in the *Bergamia rushtoni* trilobite Biozone (regional Fennian Stage, equivalent to the Dapingian and lower Darriwilian stages) of South Wales (Molyneux 1987) and the Llanvirn Series of Tunisia (Vecoli 1999). Le Hérissé *et al*. (2007) recorded the genus from the early Middle Ordovician of Saudi Arabia.

Li *et al.* (2003) indicated the first occurrences of *Dasydorus* in South China to be close to the Dapingian–Darriwilian boundary. Revision of Ordovician sequences in South China, however, has shown that the genus is common in the *A. suecicus* graptolite Biozone (Floian–Dapingian boundary), but that its first occurrence is in the *D. eobifidus* graptolite Biozone

(Yan, unpublished Ph.D. thesis, Nanjing Institute of Geology and Palaeontology 2007; Yan *et al*. 2011). The *D. eobifidus* Biozone correlates with the middle Floian Stage Slice Fl2 (Fig. 1), and the FAD of the genus in South China is accordingly positioned at the base of Fl2 (Fig. 4).

On Baltica, Raevskaya *et al.* (2004) indicated the occurrence of *Dasydorus* in the *O. evae* conodont Biozone of the Billingen Stage in the St. Petersburg area, which again suggests a mid to late Floian age, equivalent to Stage Slice Fl2 or Fl3 (Fig. 1). Based on this evidence, the FAD of *Dasydorus* in Baltica is again placed at the base of Stage Slice Fl2, although it could be higher (Fig. 4).

A specimen attributed to *Dasydorus* sp. was illustrated by Vavrdová (1993, plate 1.1) from the *Corymbograptus v-similis* graptolite Biozone in the Klabava Formation of the Prague Basin, Bohemia. Based on this specimen, the FAD of *Dasydorus* in Bohemia, representing South Gondwana, is placed at the same level there as the FADs of *Aureotesta clathrata simplex*, *Arbusculidium filamentosum* and *Coryphidium bohemicum*, at the base of Time Slice 2b in Stage Slice Fl1 (Fig. 4).

The FADs of *Dasydorus* on Avalonia and at lower palaeolatitudes on the western margin of Gondwana are higher. On Avalonia, the record from middle of the upper Arenig Fennian Stage of South Wales correlates approximately with the base of the Darriwilian Stage (Fig. 1), and the FAD is therefore placed at that level (Fig. 4). In the Canning Basin of Western Australia, the FAD of *Dasydorus* is in the *Aremoricanium solaris* acritarch Biozone, which is correlated with the upper *D. artus* and *D. murchisoni* graptolite biozones of the Llanvirn Series (Quintavalle & Playford 2006b), and in Saudi Arabia is at the base of the Llanvirn Hanadir Member in well QSIM-801 (Le Hérissé *et al*. 2007). Based on the occurrences from Western Australia and Saudi Arabia, the FAD of *Dasydorus* in West Gondwana is placed at the base of Stage Slice Dw2, correlating with the base of the Llanvirn Series (Figs 1, 4).

Ampullula (Fig. 5A)

The genus *Ampullula* was first described by Righi (1991) and subsequently revised by Brocke (1997) and Yan *et al.* (2010). The first occurrence of *Ampullula* in South China (Yan *et al.* 2010, fig. 3; Yan *et al.* 2011) is in the *D. eobifidus* graptolite Biozone of the Yangtze Platform (Stage Slice Fl2, upper Time Slice 2b), and the FAD is placed herein at the base of Fl2 (Fig. 4). The first occurrence of the genus in Argentina could be at about the same level.

In the Famatina System of NW Argentina, the first occurrence of the genus is in the upper Suri Formation in beds containing chitinozoans of the *Eremochitina brevis* Biozone and correlated with the *Oepikodus evae* conodont Biozone (Achab *et al.* 2006). Achab *et al.* (2006) suggested that the presence of *Ampullula* in the upper Suri Formation indicated a probable latest Early Ordovician age, corresponding to Time Slice 2c, but correlation with the *O. evae* conodont Biozone and the *E. brevis* chitinozoan Biozone does not rule out equivalence to the upper part of Time Slice 2b. The FAD for East Gondwana is therefore placed tentatively at the base of Stage Slice Fl2 and more definitely at the base of Time Slice 2c (Fig. 4).

The first occurrence of the genus in Baltica is also in the upper Floian Stage, in Norway (Tongiorgi *et al.* 2003, Billingen Stage, *O. evae* conodont Biozone), Poland (Raevskaya *et al*. 2004, Billingen Stage, *Phyllograptus angustifolius elongatus* graptolite Biozone, uppermost Floian Stage) and Baltic Russia (Raevskaya *et al*. 2004, Billingen Stage, *O. evae* conodont Biozone). The *P. angustifolius elongatus* Biozone correlates with the upper part of Time Slice 2c (Webby *et al.* 2004, fig. 2.1) so the occurrence of *Ampullula* in Poland is later than its first occurrence in South China. Correlation of the other records with the *O. evae* Biozone, while establishing late Floian ages, is insufficiently precise to establish whether they are coeval with or younger than the first occurrence in South China. A definite FAD of *Ampullula* in Baltica is therefore placed in the middle of Time Slice 2c, at about the base of the *P. angustifolius elongatus* Biozone, and a tentative FAD at the base of Stage Slice Fl2, coinciding with the base of the *O. evae* Biozone (Figs 1, 4).

On the western margin of Gondwana, *Ampullula* has been recorded from the *Azygograptus suecicus* graptolite Biozone of Pakistan (Quintavalle *et al.* 2000), correlated with the upper part of Floian Stage Slice Fl3 and Time Slice 2c and the lowermost part of Dapingian Stage Slice Dp1 and Time Slice 3a (Fig. 1). The FAD is placed here at about the base of Time Slice 3a in the uppermost Floian Stage. At higher palaeolatitudes on the Gondwanan margin, the FAD seems to have been later. The species *Ampullula suetica*, for example, was shown by Vecoli & Le Hérissé (2004, fig. 5) as having its first occurrence in the Darriwilian *Cyathochitina calix* chitinozoan Biozone, at the base of the regional Llanvirn Series (bases of Stage Slice Dw2 and Time Slice 4b). The FAD of the genus in South Gondwana is therefore placed at the base of Dw2 (Fig. 4).

Liliosphaeridium (Fig. 5K)

Liliosphaeridium is closely related to *Peteinosphaeridium*. Both possess laminate processes, but those of *Liliosphaeridium* are modified distally in the form of a more or less distinct calyx. Although these distally elaborated processes might be an expression of ecophenotypic controls within the peteinoid acritarch plexus (see also Bagnoli & Ribecai 2001), *Liliosphaeridium* appears to have independent biostratigraphical value and its global FAD is later than that of *Peteinosphaeridium*.

Playford *et al.* (1995, fig. 8) indicated the FAD of *Liliosphaeridium* to be in the Middle Ordovician of Baltica. There, *Liliosphaeridium* has been recorded from the Volkhov and Kunda stages. The genus has been recorded from the Langevoja Substage of the Volkhov Stage in Sweden (Ribecai & Tongiorgi 1995; Bagnoli & Ribecai 2001), correlated with the uppermost Dapingian to lowest Darriwilian stages (top Dp3–lower Dw1 stage slices, top 3b–lower 4a time slices; Fig. 1). The earliest occurrence in NW Russia (Arkhangelsk: Raevskaya *et al.* 2006) is also reported to be from the upper Volkhov Stage, and that in Estonia (Uutela & Tynni 1991) is from an undivided Volkhov Stage, but probably also from the upper part of the stage (Langevoja Substage: compare with records of *Sacculidium macropylum* in Ribecai *et al.* 2002). In Norway, *Liliosphaeridium* has been recorded from the uppermost *Didymograptus hirundo* graptolite Biozone and the *Asaphus expansus* trilobite Biozone, both correlated with the Hunderum Substage of the Kunda Stage (Ribecai *et al.* 1999; Pärnaste *et al.* 2013, fig. 3) and corresponding to the upper Dw1–basal Dw2 stage slices and the upper 4a Time Slice. Based on these records, the FAD of *Liliosphaeridium* in Baltica is placed at the base of the Darriwilian Stage (Fig. 4).

Liliosphaeridium also has its first appearance in the Middle Ordovician of North Africa and other high latitude Perigondwanan areas, and its FAD was placed at about the base of the Darriwilian Stage by Vecoli & Le Hérissé (2004, fig. 5). It is accordingly placed here at the same level for South Gondwana (Fig. 4). Its FAD in West Gondwana is placed slightly higher, at the base of Stage Slice Dw2 (Fig. 4), based on records of *Peteinosphaeridium intermedium* from middle–upper Darriwilian Stage strata of Oman (Rickards *et al*. 2010), but this might also reflect the lack of suitable lower Darriwilian facies meaning that its true FAD in West Gondwana could be lower.

In contrast, *Liliosphaeridium* has been recorded from the *D. eobifidus* graptolite Biozone (Yan, unpublished Ph.D. thesis, Nanjing Institute of Geology and Palaeontology 2007; Yan *et al*. 2011) of South China, indicating a first occurrence in the middle Floian Stage Slice Fl2 and the upper part of Time Slice 2b. Its FAD in South China is here placed at the base of Stage Slice Fl2 (Fig. 4).

The first occurrence of *Liliosphaeridium* might be at a similar level in East Gondwana, where *Peteinosphaeridium trifurcatum intermedium* was recorded by Ottone *et al.* (1992) and Rubinstein & Toro (2001) from the '*B. deflexus*' graptolite Biozone of NW Argentina. However, de la Puente & Rubinstein (2013, fig. 3) placed the FAD of *Liliosphaeridium intermedium* at the base of the Darriwilian Stage (base of Stage Slice Dw1 and Time Slice 4a) in the Central Andean Basin, and Rubinstein *et al*. (2011) placed the FAD of the same species at about the same level in the Capillas Formation of the Sierras Subandinas. Hence, the FAD of *Liliosphaeridium* in East Gondwana is placed tentatively at the base of Stage Slice Fl2 and more definitely at the base of Stage Slice Dw1 (Fig. 4).

The genus might therefore be an indicator for the middle Floian in low to intermediate palaeolatitude Perigondwanan regions, with a first appearance in Stage Slice Fl2 and the upper part of time-slice 2b, but with a wider biogeographical distribution including Baltica and high palaeolatitude Perigondwana from the late Dapingian onwards.

Frankea (Fig. 5J)

Servais (1993) revised the genus *Frankea* and reviewed its stratigraphical occurrence. More recently, Wang et al. (in press) revised its taxonomy. *Frankea* is a distinctive genus that commonly occurs in assemblages from the Dapingian onwards at high to mid palaeolatitudes on the western margin of Gondwanan, including Avalonia (Servais *et al*. 2003). It has not been recorded from low palaeolatitudes of West Gondwana, or from South China, or from East Gondwanan assemblages of NW Argentina. Nor has it been recorded from other palaeocontinents. It is possibly a temperature-sensitive genus that is restricted to the margin of Gondwana at higher palaeolatitudes (Fig. 2).

A rare early occurrence of *Frankea* is known from the Avalonian succession on the Isle of Man in the British Isles, where a single specimen was recorded from an upper *messaoudensis-trifidum* or *trifidum-bohemicum* assemblage (Molyneux 1999). Correlation of this occurrence is with the *Tetragraptus phyllograptoides* or low *Corymbograptus varicosus* graptolite Biozone and with an interval in the lower Floian Stage Slice Fl1 (Molyneux 1999). Based on this, the FAD of the genus on Avalonia is provisionally indicated at about the base of Time Slice 2b (Fig. 4). Another possible Floian occurrence on Avalonia is from the Abbaye de Villers Formation in Belgium. The formation is considered to be of late Dapingian to earliest Darriwilian age (Herbosch & Verniers 2014), but chitinozoans recorded by

Samuelsson & Verniers (2000), which include *Eremochitina brevis*, point to a possible older, late Floian age (Fig. 1) for at least part of the formation (but see below).

Most records of the genus from Avalonia and elsewhere are from Dapingian or younger successions. Cooper *et al.* (1995) indicated that their *Frankea hamata-Striatotheca rarirrugulata* assemblage in NW England originated in the *I. gibberulus* graptolite Biozone but above its base, so probably within Time Slice 3b. Based on these records, a definite FAD of the genus on Avalonia is placed at about the base of Stage Slice Dp3 (Fig. 4).

Other occurrences on Avalonia are from South Wales and Belgium. The recorded occurrence of *Frankea* in the Arenig succession of South Wales is in the middle of the Fennian Stage (Molyneux 1987), in the upper part of the *Stapeleyella abyfrons* trilobite Biozone. This level is also above the base of the *I. gibberulus* graptolite Biozone (Fortey & Owens 1987, figs 5, 11), so is probably at about the same level as the FAD of the genus in NW England. On the Brabant Massif of Belgium, *Frankea* is present in several formations below the lower Llanvirn *Didymograptus artus* graptolite Biozone (Servais 1991; Servais *et al.* 1993), including the Abbaye de Villers Formation at the base of the Rebecq Group (Herbosch & Verniers 2014). The Abbaye de Villers Formation rests unconformably on the Tremadocian Chevlipont Formation, so records from this formation do not help to establish the global FAD of *Frankea*. Although as noted above chitinozoans have been interpreted as suggesting a possible Floian age for the Abbaye de Villers Formation, the acritarch assemblage from the formation corresponds to the late Dapingian to earliest Darriwilian *F. hamata-S. rarirrugulata* assemblage of NW England (Vanguestaine & Wauthoz 2011).

The lowest records of *Frankea* from South Gondwana are of late Arenig age, for example from Morocco (Cramer & Diez 1977; Deunff 1977; Elaouad Debbaj 1984) and Bohemia (Vavrdová 1977, 1993), while Vecoli & Le Hérissé (2004) placed the first occurrence of the genus at about the base of the Darriwilian Stage. The lowest recorded occurrence on the Arabian Plate (West Gondwana) is also probably of late Arenig age, from the Saq Formation of Saudi Arabia (Le Herisse *et al*. 2007). Based on these records, the FAD of *Frankea* is placed at about the base of the Darriwilian Stage in South Gondwana and West Gondwana (Fig. 4).

Arkonia (Fig. 5D)

Servais (1997) noted the occurrence of *Arkonia* in the upper Arenig Series (Dapingian–lower Darriwilian stages), but more recent work has established its presence in lower Arenig successions. In South China, for example, *Arkonia tenuata* has been recorded from the *C. deflexus* graptolite Biozone (Yan & Li 2005; Yan *et al*. 2011), from the lower parts of Floian Stage Slice Fl3 and Time Slice 2c (Fig. 1). The FAD of the genus in South China is therefore placed here at the base of Fl3, representing its global FAD.

There are also possible upper Floian records of *Arkonia* from East Gondwana. The first verified occurrences of *Arkonia* (*A. tenuata*) in NW Argentina are at the base of the Capillas Formation in the Sierras Subandinas (Rubinstein *et al.* 2011), interpreted as being Darriwilian in age (Stage Slice Dw1), and at the base of the Darriwilian Stage (base Dw1) in the Central Andean Basin (de la Puente & Rubinstein 2013, fig. 3). However, *Striatotheca triangulata*, originally *Rugulidium triangulata* Cramer *et al*., 1974, but recombined as *Striatotheca triangulata* by Eisenack *et al.* (1976) and then as *Arkonia triangulata* by Vavrdová (1978), was recorded by Ottone *et al.* (1992) and Rubinstein & Toro (2001) from the *D. bifidus* graptolite Biozone. The graptolite zone is correlated with the upper Floian Stage Slice Fl3 and with Time Slices 2c to basal 3a (Fig. 1). A tentative FAD is placed at the base of Stage Slice Fl3, and a more definite FAD at the base of Dw1 (Fig. 4).

The FAD of the genus in South Gondwana is probably within the Dapingian Stage (Fig. 4). Vavrdová (1990) recorded *Arkonia tenuata* from the *Azygograptus ellesi-Tetragraptus reclinatus abbreviatus* graptolite Biozone of Bohemia, which is probably of Dapingian and possibly earliest Darriwilian age (e.g. Kraft & Kraft 2003, fig. 1b). The FAD of the genus in South Gondwana is therefore placed at the base of the Dapingian Stage (Fig. 4), although with some uncertainty over its exact level. The specimens of *Rugulidium triangulata* recorded by Cramer *et al.* (1974) from the Tadla Basin of Morocco are from levels attributed to the *D. bulla* chitinozoan Biozone (Soufiane & Achab 1993), which correlates with Darriwilian Stage Slice Dw1 and Time Slice 4a (Fig. 1).

On Avalonia, *Arkonia* is questionably present in assemblages from the late Arenig Kirkstile and Buttermere formations of NW England, correlated with the *Isograptus gibberulus* and *Aulograptus cucullus* graptolite biozones, with Stage Slices Dp2–Dw1 and with Time Slices 3b and 4a, and is definitely present in the Llanvirn Tarn Moor Formation, correlated with Stage Slices Dw2–lower Dw3 and Time Slices 4b–lower 4c (Molyneux 2009). A tentative FAD is placed at the base of Stage Slice Dw1, and a definite FAD at the base of Stage Slice Dw2 (Fig. 4).

Dicrodiacrodium (Fig. 5Q)

Servais *et al.* (1996) revised the taxonomy of *Dicrodiacrodium* and reviewed its stratigraphical distribution. The genus was first described from the Llanvirn of Germany by Burmann (1970), and has subsequently been used as a stratigraphical index fossil for upper Arenig–lower Llanvirn successions (Servais *et al.* 1996, fig. 4). Most records of the genus, however, are from strata that lack independent age control.

Brocke *et al.* (2000) reported the first occurrence of the genus to be at the base of the *Undulograptus sinodentatus* graptolite Biozone in South China. These data were used by Li *et al.* (2003) to indicate its first occurrence in the upper part of the Dapingian Stage (Time Slice 3b). Investigations by Yan (unpublished Ph.D. thesis, Nanjing Institute of Geology and Palaeontology 2007) and Yan *et al.* (2011) now indicate a first occurrence of the genus to be at about the base of the *A. suecicus* graptolite Biozone in South China, and therefore its FAD to be in the upper part of Stage Slice Fl3 and the upper part of Time Slice 2c (Figs 1, 4).

At higher palaeolatitudes around South Gondwana, Vecoli & Le Hérissé (2004) placed the FAD of the genus in the *E. brevis* chitinozoan Biozone of Paris (1990), which corresponds to the upper part of the Floian Stage, spanning most of Stage Slices Fl2 and Fl3 (Fig. 1). The FAD of the genus in South Gondwana is placed at the same level in the upper Floian Stage Slice Fl3 as in South China (Fig. 4).

For Avalonia, Servais *et al*. (1996, fig. 4) indicated FADs based on graptolite control at the base of the Llanvirn Series, for example in successions in the British Isles and Belgium, but with possible upper Arenig occurrences in Belgium based on the associated acritarchs. From this, the FAD of *Dicrodiacrodium* in Avalonia is placed tentatively at the base of the Dapingian Stage, and with more certainty at the base of Stage Slice Dw2, correlated with the base of the Llanvirn Series (Figs 1, 4).

Orthosphaeridium (Fig. 5R)

The genus *Orthosphaeridium* was described by Eisenack (1968) and comprises several species. Burmann (1970) later described the morphologically similar genus *Baltisphaera*. The two genera are probably synonymous, although the taxonomy has yet to be revised. The genus is commonly found in Llanvirn strata (middle Darriwilian Stage) of Germany, Belgium (e.g. Burmann 1976; Servais 1991) and Saudi Arabia (Le Hérissé *et al*. 2007).

The first occurrence of *Orthosphaeridium* in South China is in the *Expansograptus hirundo* graptolite Biozone, correlated with the upper part of Dapingian Stage Slice Dp1 and the overlying Dp2, and with the upper Time Slice 3a and lower Time Slice 3b (Yan *et al.*

2011; Fig. 1). The FAD of the genus in South China is placed within this interval, at the base of Time Slice 3b (Fig. 4).

Records of the *Orthosphaeridium-Baltisphaera* complex elsewhere also suggest first occurrences at about the same level, in the upper Arenig Series, but are correlated less precisely. For Avalonia, Molyneux (1987) recorded *Orthosphaeridium* from the regional Fennian Stage of the upper Arenig Series in South Wales, equivalent to the Dapingian–lower Darriwilian stages (Dp1–Dw1), and Cooper *et al.* (1995) recorded *Orthosphaeridium bispinosum* in the upper part of the *Frankea hamata-Striatotheca rarirrugulata* acritarch assemblage in NW England, also of late Arenig age and probably from the upper Dapingian–lower Darriwilian stages (Dp2–Dw1). In neither succession are there records of the genus below these levels. The FAD of the genus in Avalonia is placed at the base of Stage Slice Dw1 (Fig. 4).

In Saxothuringia, part of the Armorican Terrane Assemblage (Torsvik & Cocks 2017) and therefore included here in South Gondwana, Heuse *et al.* (1994) recorded *Baltisphaera* cf. *quadrinata* and *Baltisphaera* sp. from the Griffelschiefer in the Schwarzburg Anticline, for which they indicated a late Arenig *hirundo* Zone (equivalent to the *A. cucullus* Biozone) or possibly slightly older age. The *A. cucullus* Biozone is correlated with the lower Darriwilian Stage Slice Dw1 (Fig. 1), so the FAD in South Gondwana is again placed at the base of Dw1 (Fig. 4).

Also in South Gondwana, Elaouad Debbaj (1984) recorded *Orthosphaeridium ternatum* (as '*Baltisphaeridium ternata*') from the upper Arenig–Llanvirn Tachilla Formation of Morocco, and Paris *et al.* (2007) recorded *O. ternatum* (as '*Baltisphaeridium ternatum*') from the TAR2 assemblage of southern and SE Turkey. The TAR2 assemblage seems to range through the entire Dapingian and Darriwilian stages, based on chitinozoan dating of samples, from the *Belonechitina henryi* chitinozoan Biozone to the *Linochitina pissotensis* Biozone (Fig. 1). There is no indication of where *Orthosphaeridium* first occurs in the Dapingian–Darriwilian interval in either Morocco or Turkey.

A further Dapingian–lower Darriwilian record is from Sweden and provides the FAD of *Orthosphaeridium* in Baltica. The precise levels at which Ribecai & Tongiorgi (1995) recorded *Orthosphaeridium densiverrucosum* and *O. ternatum* in Sweden are unknown, but the relevant section spans the interval from the Langevoja Substage of the Volkhov Stage to the Hunderum or possibly Valaste substages of the Kunda Stage. This interval correlates with the upper Dapinigian (top Dp3) to middle Darriwilian (lower Dw2) (Fig. 1). The FAD of the genus in Baltica is placed at the base of the Darriwilian Stage.

Recognition of Lower and Middle Ordovician stage slices and stage boundaries

Tremadocian Stage Slice Tr3

The FADs of *Coryphidium*, *Peteinosphaeridium*, *Striatotheca* and the *Veryhachium trispinosum* group are potentially important for correlation of Tremadocian Stage Slice Tr3. Of these, *Coryphidium* and *Peteinosphaeridium* have widespread first occurrences in the stage slice. *Coryphidium* is restricted to the margin of Gondwana (Perigondwana), including derived terranes such as Avalonia, but ranges from high southern palaeolatitudes northwards to South China and eastwards to NW Argentina. Its first occurrence is in Tr3 throughout its biogeographical range, and probably in the upper part of Tr3. The first occurrence of *Peteinosphaeridium* is also in Tr3 on the Gondwanan margin, from high southern palaeolatitudes to South China and NW Argentina, and furthermore is in Tr3 on Baltica and Laurentia, suggesting a potential for correlation between palaeocontinents.

Striatotheca has only been recorded from Perigondwana and not below Stage Slice Tr3. Its FAD is probably at the base of Tr3 at high palaeolatitudes, for example in NW England and on the island of Rügen (northern Germany), but its first recorded occurrence is in the lower Floian (Fl1) in South China and in the middle Floian (Fl2) in NW Argentina. First occurrences of the *Veryhachium trispinosum* group are also in Stage Slice Tr3 on the high palaeolatitude Gondwanan margin, but higher than that of *Striatotheca* and possibly in the upper part of Tr3. As with *Striatotheca*, FADs of the *V. trispinosum* group are in the Floian in South China (Fl1) and NW Argentina (Fl3). In addition, the *Veryhachium trispinosum* group became more widespread during later Ordovician stages (Servais *et al*. 2014), with a FAD during the Darriwilian on Baltica (Estonia) and subsequently on Laurentia. The diachronous FADs of these taxa limit their use in long-distance correlation, but nevertheless they might be used to distinguish the latest Tremadocian stage slice (Tr3) from older divisions at high palaeolatitudes.

Dactylofusa velifera, *Rhopaliophora* and the *Veryhachium lairdii* group are also generally characteristic of later Tremadocian assemblages, although all appear to have FADs that are below Tr3. The global FAD of the *Veryhachium lairdii* group is possibly in the lower

Tremadocian in North Africa and Oman (Stage Slice Tr1 or Tr2), but the group was more common and widespread during Tr3, in *messaoudensis-trifidum* acritarch assemblages at high palaeolatitudes. Its first recorded occurrences in South China and possibly Baltica (St Petersburg region) are higher, in the lower Floian (Fl1). The *V. lairdii* group might also have a lower Floian FAD in NW Argentina, although there is some uncertainty over the exact level. Previous published records had the FAD in the middle Floian (Fl2). Like the *Veryhachium trispinosum* group, the *V. lairdii* group became widespread during the later Ordovician (Servais *et al*. 2014). First occurrences of *Dactylofusa velifera*, another species restricted to Perigondwana, are mostly in Tr3, albeit with some uncertainty in NW Argentina, but possibly lower in South China (Tr2?) and Oman (Tr1-Tr2?). The distribution of *Rhopaliophora* resembles that of *Peteinosphaeridium*, with first occurrences in Tr3 on the Gondwanan margin, from high southern palaeolatitudes to South China and NW Argentina, and also on Baltica (Norway) and Laurentia (Alberta). As with *Peteinosphaeridium*, this suggests a potential for intercontinental correlation, except that *Rhopaliophora* has possible slightly older FADs in South China (Tr2?) and North China (upper Tr1–Tr2).

The Tremadocian–Floian stage boundary and Floian stage slices

As noted above, the FADs of *Striatotheca*, the *Veryhachium lairdii* group and the *V. trispinosum* group are higher in South China and/or NW Argentina than at high southern latitudes on the margin of Gondwana. The FADs of *Striatotheca*, the *Veryhachium lairdii* group and the *V. trispinosum* group are all in the lower Floian Stage Slice Fl1 in South China and so distinguish Floian from Tremadocian strata there. The *Veryhachium lairdii* group is also present in Stage Slice Fl1 on Baltica (St Petersburg region), although it remains uncertain whether this represents its FAD there because of a stratigraphical hiatus below its first occurrence. The FADs of *Striatotheca*, the *Veryhachium lairdii* group and the *V. trispinosum* group are higher in NW Argentina, in the middle Floian (Fl2) for *Striatotheca* and the *V. lairdii* group and the upper Floian (Fl3) for the *V. trispinosum* group. They might be useful as local markers for successive Floian stage slices.

Aureotesta clathrata simplex, *Arbusculidium filamentosum* and *Coryphidium bohemicum* are all restricted to Perigondwanan assemblages and all have FADs in the lower to middle Floian Stage. They serve to distinguish Floian successions from the upper Tremadocian Stage Slice Tr3 around Gondwana. *Aureotesta clathrata simplex* has its FAD at about the base of Stage Slice Fl1 in NW England and South China. The FADs of *A. filamentosum* and *C. bohemicum* are above the base of the Floian Stage in both areas, either in the upper part of Stage Slice Fl1 or in Stage Slice Fl2. The FADs of all three species are in Fl2 in NW Argentina (*C*. cf. *bohemicum* in NW Argentina), replicating the Tremadocian pattern of taxa having later FADs there.

Ampullula, *Dasydorus*, *Liliosphaeridium* and *Sacculidium* comprise a group of genera that occur in Floian successions from South China, East Gondwana and Baltica, and distinguish Floian from Tremadocian successions there. All have global FADs in South China in the Floian Stage, where that of *Sacculidium* is in Stage Slice Fl1 and those of the other genera are in Stage Slice Fl2. *Ampullula*, *Dasydorus* and possibly *Liliosphaeridium* also have FADs in Floian Stage Slices Fl2–Fl3 in East Gondwana (*Ampullula*, possibly *Liliosphaeridium*) and/or Baltica (Norway: *Ampullula*; St Petersburg region: *Ampullula*, *Dasydorus*). Their FADs suggest some potential as markers for the middle–upper Floian Stage in South China, East Gondwana and/or Baltica, depending on their respective distributions. *Sacculidium*, however, has not been recorded from NW Argentina below the Dapingian Stage, and *Dasydorus* has not been recorded there at all. *Liliosphaeridium* and *Sacculidium* both have first occurrences in Baltica in the uppermost Dapingian or lowest Darriwilian and are important components of acritarch assemblages there, making them potential local markers for later stages and stage slices. With the possible exception of *Dasydorus*, none of these genera have been reported from high palaeolatitude Perigondwanan successions below the Darriwilian (Fig. 4).

Arkonia, *Barakella* and *Dicrodiacrodium* have first definite occurrences in Floian successions on the margin of Gondwana. Floian occurrences of *Arkonia* are in Stage Slice Fl3 in South China (lower Fl3) and possibly East Gondwana (NW Argentina). First occurrences at higher palaeolatitudes in South Gondwana and Avalonia are in the Dapingian and/or lower Darriwilian stages. *Barakella* has been reported from the lower–middle Floian Stage of South Wales, South China and East Gondwana (NW Argentina). Records from South Gondwana and West Gondwana are generally higher, from the Dapingian Stage upwards. Apart from an uncertain record from the Darriwilian of Sweden (upper Dw1–lower Dw2), all records of *Barakella* are from the margin of Gondwana. *Dicrodiacrodium* has FADs in the upper Floian Stage of South China and South Gondwana.

Lower–Middle Ordovician series (Floian–Dapingian stage) boundary

Frankea and *Orthosphaeridium* are potential markers for the Dapingian Stage. There is an exceptionally early and very rare record of *Frankea* from the lower Floian Stage on the Isle of Man (Molyneux 1999), but the first common appearance of *Frankea*, so far only recorded from high palaeolatitudes, is placed in the upper Dapingian Stage (Stage Slice Dp3) in NW England and in the undivided Dapingian–lower Darriwilian (Dp1–Dw1) of Morocco, Saudi Arabia and South Wales. *Orthosphaeridium* is distributed more widely on the Gondwanan margin, where it occurs in the lower–middle Dapingian (Dp1–Dp2) of South China, the undivided Dapingian–lower Darriwilian (Dp1–Dw1) of NW England and South Wales, and the undivided Dapingian–Darriwilian (Dp1–Dw3) of Morocco and Turkey. *Orthosphaeridium* also occurs on Baltica but at a higher level, in the uppermost Dapingian to lower Darriwilian (top Dp3-lower Dw1) of Sweden.

Conclusions

The acritarch genera and species considered in this paper comprise morphotypes that are easily recognizable using transmitted light microscopy. Their FADs have the potential to aid correlation of Lower and Middle Ordovician stages, stage slices and time slices, but the degree to which this applies varies. Some genera and species considered here have widespread FADs at about the same level throughout their biogeographical range and are useful for long-distance and intercontinental correlation. Others have diachronous FADs, and this needs to be taken into account when using them for correlation. They may be useful for correlation within basins and perhaps also between basins that are in proximity to each other, but on currently available evidence, care is needed when using them for correlation over longer distances.

Among the genera and species that have widespread FADs at about the same level are *Coryphidium* and *Peteinosphaeridium*, but whereas *Coryphidium* is restricted to Perigondwana, *Peteinosphaeridium* also occurs in Baltica and Laurentia, suggesting a potential for correlation between palaeocontinents. The distribution of *Rhopaliophora* resembles that of *Peteinosphaeridium* and again suggests a potential for intercontinental correlation around the Tr2–Tr3 Stage Slice boundary. *Dactylofusa velifera* is a potential marker for the upper Tremadocian Stage (Tr3) throughout most of its biogeographical range, but is again restricted to Perigondwana. *Arbusculidium filamentosum*, *Aureotesta clathrata simplex* and *Coryphidium bohemicum* are similarly restricted to Perigondwana and their FADs are in the lower–middle Floian Stage throughout their biogeographical range. Other genera restricted in their biogeographical distribution to Perigondwana include *Dicrodiacrodium*, which has FADs in the upper Floian Stage of South Gondwana and South China, and *Frankea*, with FADs in the Dapingian–lower Darriwilian at high palaeolatitudes. *Orthosphaeridium* has FADs in the Dapingian to lower Darriwilian of Perigondwanan regions and a FAD at about the same level on Baltica. *Orthosphaeridium* is distributed widely in the Upper Ordovician, including records from Laurentia.

Although FADs of these genera and species are generally at about the same level throughout their ranges, there is nevertheless a degree of diachronism in their first appearances. Diachronism is more marked in the other genera and species considered, and some recurring patterns are evident. *Striatotheca*, the *Veryhachium lairdii* group and the *V. trispinosum* group, for example, all have FADs in the Tremadocian Stage on Avalonia and in South Gondwana and West Gondwana, but in the Floian Stage of South China and East Gondwana. *Striatotheca*, unlike the other two, is restricted to Perigondwana whereas the *Veryhachium* spp. spread to Baltica and ultimately more widely.

The other genera discussed herein, *Arkonia*, *Ampullula*, *Barakella*, *Dasydorus*, *Liliosphaeridium* and *Sacculidium*, have markedly diachronous FADs throughout their biogeographical ranges, although in the case of *Arkonia*, *Ampullula*, *Liliosphaeridium* and *Sacculidium*, the global FAD is apparently in South China and/or East Gondwana, followed by slow dispersal to other regions.

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Figures and Captions

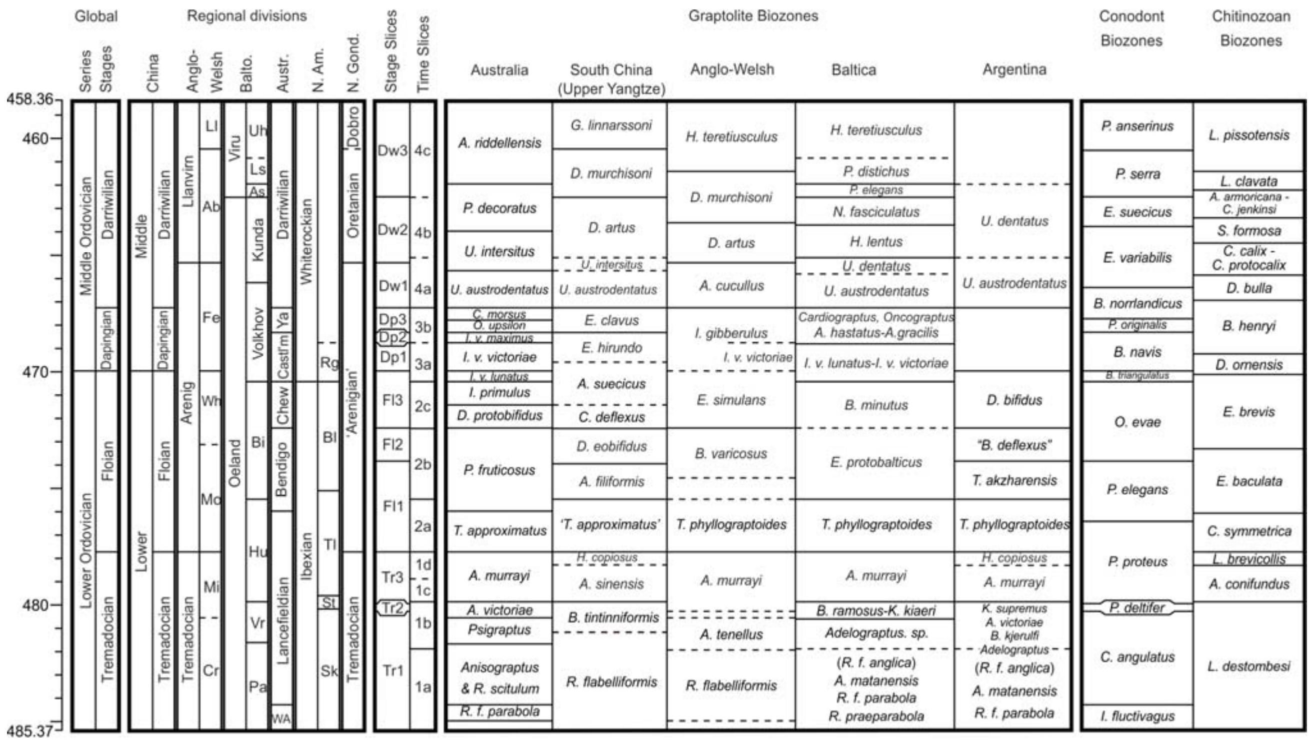

Fig. 1. Correlation of global Lower and Middle Ordovician series and stages, regional series and stages, stage slices (Bergström *et al.* 2009), time slices (Webby *et al.* 2004), and graptolite, conodont (North Atlantic zonation) and chitinozoan ('North Gondwana' zonation) biozones. The South Chinese graptolite zonation is from Zhang *et al.* (2007, 2010), the Baltic graptolite zonation is from Cooper *et al.* (2004), and the Argentinian graptolite zonation is from de la Puente & Rubinstein (2013, based on Toro & Maletz 2007, and Albanesi *et al.* 2008). All other correlations are from TSCreator (2014; see also Cooper & Sadler 2012). Abbreviations: Anglo-Welsh stages: Cr, Cressagian; Mi, Migneintian; Mo, Moridunian; Wh, Whitlandian; Fe, Fennian; Ab, Abereiddian, Ll, Llandeilian. Baltoscanian stages: Pa, Pakerort; Vr, Varangu; Hu, Hunneberg; Bi, Billingen; As, Aseri; Ls, Lasnamagi; Uh, Uhaku. Australasian stages: WA, Warendan; Bendigo, Bendigonian; Chew, Chewtonian; Castl'm, Castlemainian; Ya, Yapeenian. North American stages: Sk, Skullrockian; St, Stairsian; Tl, Tulean; Bl, Blackhillsian; Rg, Rangerian. North Gondwanan stages: Dobro, Dobrotivian.

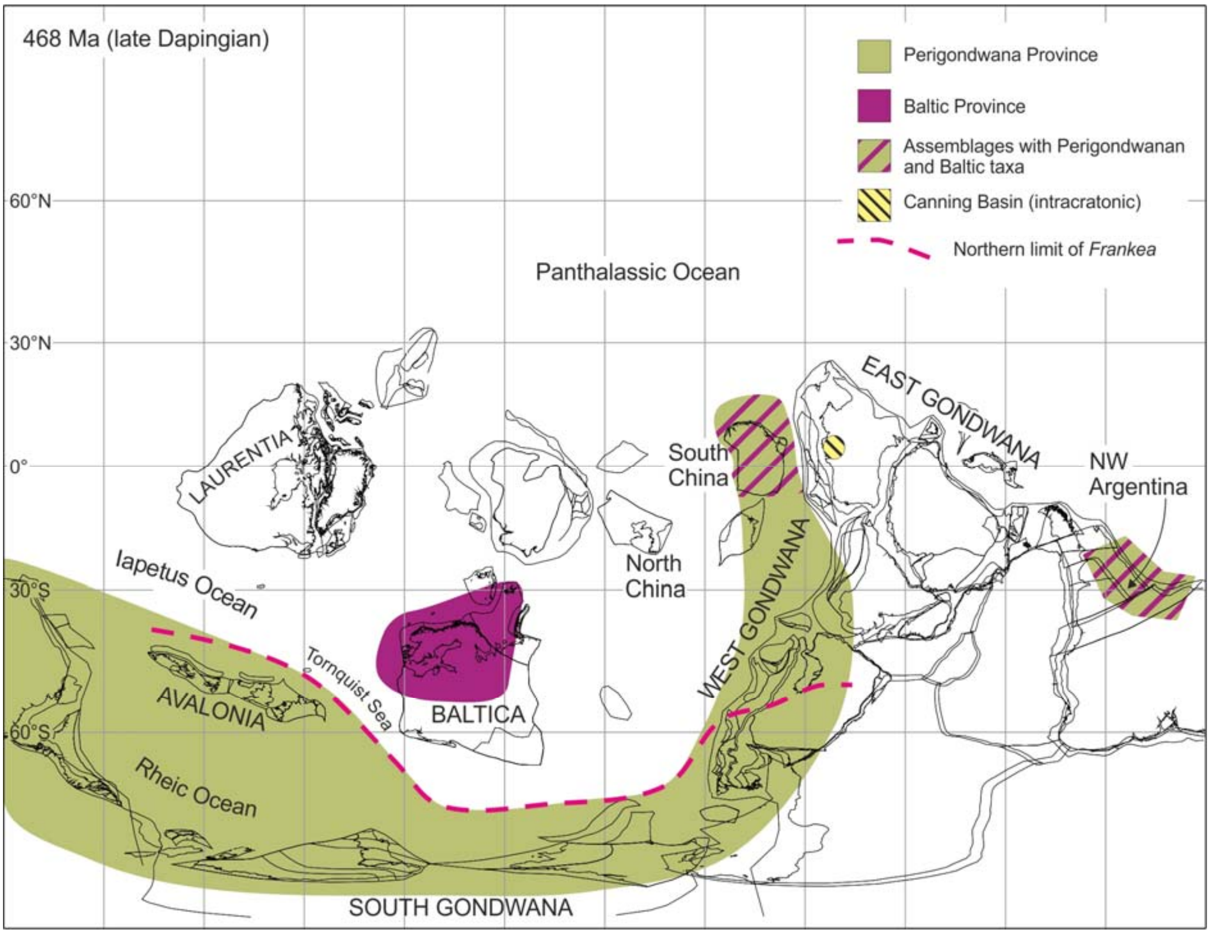

Fig. 2. Palaeogeographical reconstruction (Galls projection, using BugPlates software [http://www.geodynamics.no/bugs/SoftwareManual.pdf]) for the Middle Ordovician (upper Dapingian Stage, 468Ma) showing the distribution of the Perigondwana and Baltic acritarch provinces, palaeocontinents and other regions mentioned in the text. See also Torsvik & Cocks (2017) and Molyneux *et al.* (2013).

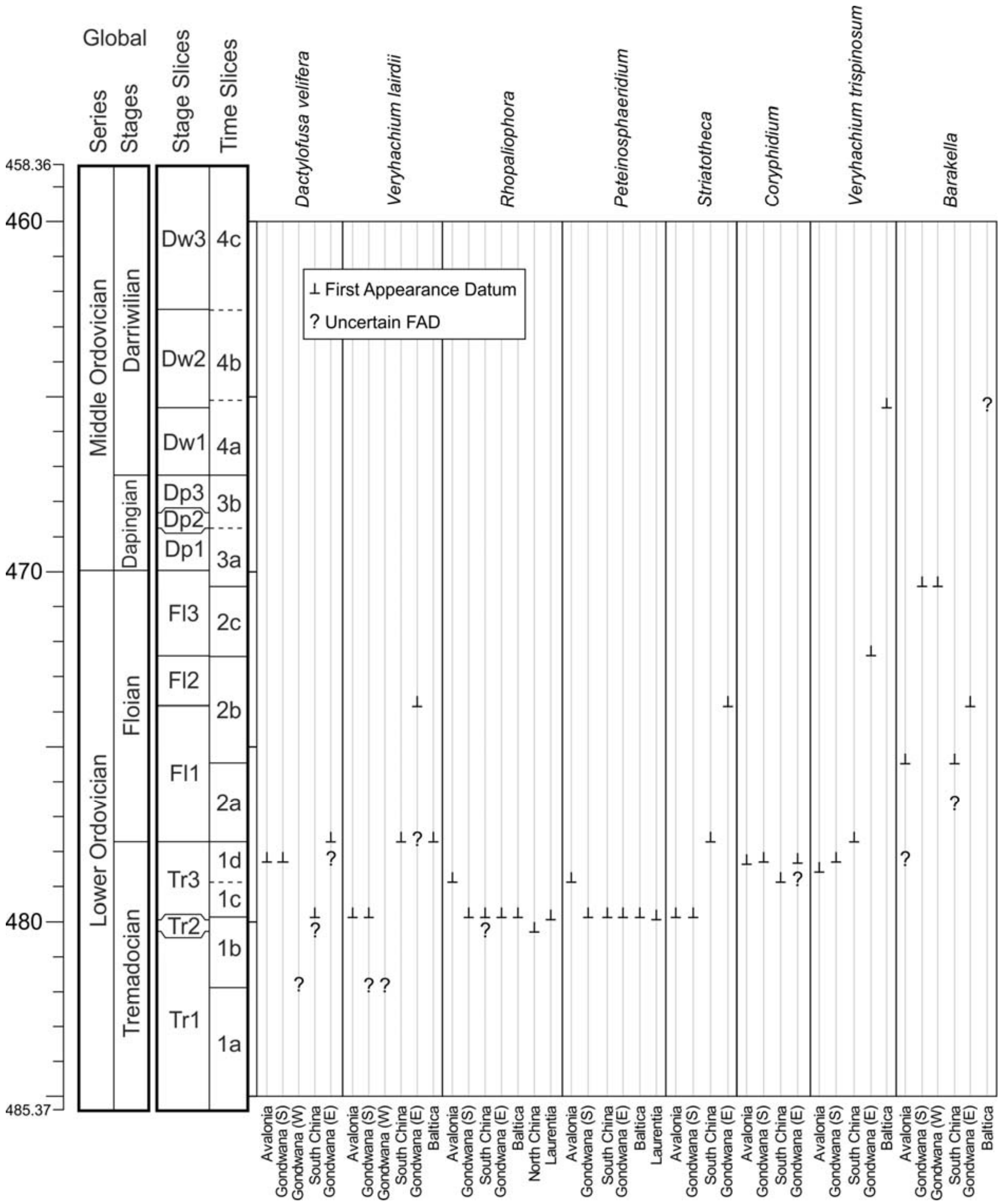

Fig. 3. First Appearance Data (FADs) of acritarch morphotypes with FADs in the Tremadocian Stage plotted against the global Lower–Middle Ordovician series and stages, the stage slices of Bergström *et al.* (2009) and the time slices of Webby *et al.* (2004). Dates are from GTS2012 (Cooper & Sadler 2012).

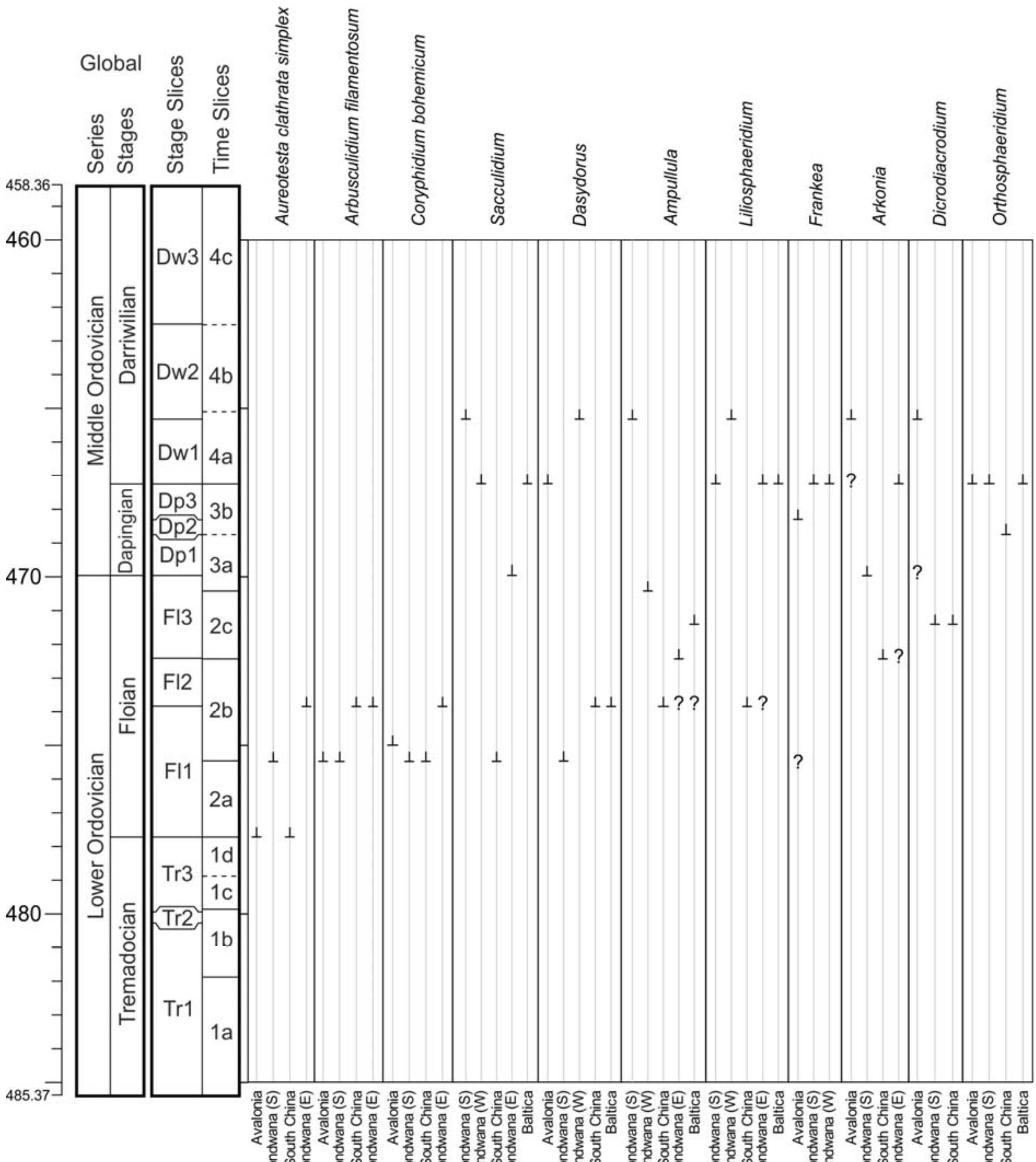

Fig. 4. First Appearance Data (FADs) of acritarch morphotypes with FADs in the Floian, Dapingian and Darriwilian stages plotted against the global Lower–Middle Ordovician series and stages, the stage slices of Bergström *et al.* (2009) and the time slices of Webby *et al.* (2004). Dates are from GTS2012 (Cooper & Sadler 2012).

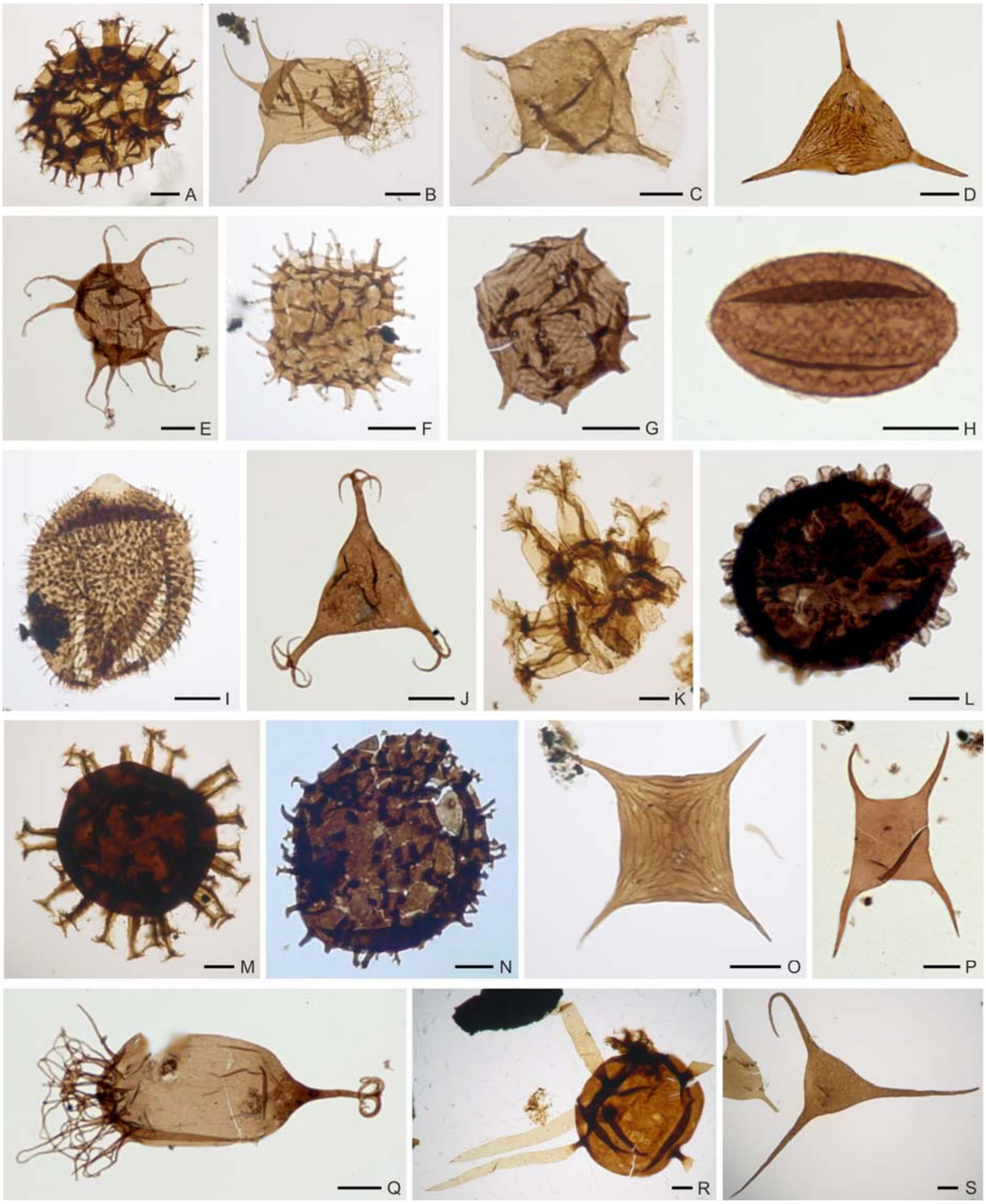

Fig. 5. Microphotographs of the selected acritarch taxa. Taxonomic names are followed by the palynological slide number and the England Finder coordinates. The scale bar indicates 10 µm. All specimes are housed in the collections of the Nanjing Institute of Geology and Palaeontology, Nanjing, China, except specimens D, E, J and Q, that are housed in the collections of the Evo-Eco-Paleo department, CNRS-University of Lille, France.

A. *Ampullula erchunensis* (Fang, 1986) Yan et al. 2010, modified from Yan et al. (2010), Pl. 2, Fig. 4, Dawan Formation (Huanghuachang section), Yichang, Hubei, China, Sample

HHDW10, Slide 3, EF: L51; B. *Arbusculidium filamentosum* (Vavrdová 1965) Vavrdová 1972 emend. Fatka & Brocke, 1999, Meitan Formation (Honghuayuan section), Tongzi, Guizhou, China, Sample AFI1033, Slide 1, EF: V47; C. *Aureotesta clathrata* var. *simplex* (Cramer et al 1974) emend. Brocke *et al*. 1998, Meitan Formation (Honghuayuan section), Tongzi, Guizhou, China, Sample AFI1039, Slide 3, EF: N37/3; D. *Arkonia tenuata* Burmann, 1970, Borehole BJ109m Morocco, -464m, Slide 1, EF: W35/1; E. *Barakella felix* Cramer & Díez 1977, modified from Yan et al. (in press), Pl. I, Fig. 15, Borehole BJ109m Morocco, -404m, Slide 2, EF: P33/3; F. *Coryphidium bohemicum* Vavrdová 1972, Meitan Formation (Honghuayuan section), Tongzi, Guizhou, China, Sample AFI1033, Slide 1, EF: S36/1; G *Coryphidium* sp., Fenghsiang Formation (Xiangshuidong section), Songzi, Hubei, China, Sample AGO297, Slide 1, EF: Q51; H. *Dactylofusa velifera* Cocchio, 1982, Hungshihyen Formation (Erchun section), Kunming, China, Sample AGC8, Slide 6, EF: K40; I. *Dasydorus cirritus* Playford & Martin, 1984, Meitan Formation (Honghuayuan section), Tongzi, Guizhou, China, Sample AFI1033, Slide 1, EF: W46/2; J. *Frankea breviuscula* Burmann, 1970, Borehole BJ109, Morocco, -464m, Slide 1, EF: H29/1; K. *Liliosphaeridium kaljoi* Uutela & Tynni, 1991 emend. Playford et al., 1995, Dawan Formation (Daping section), Yichang, Hubei, China, Sample AFI4017, Slide 1, EF: O46/4; L. *Rhopaliophora palmata* (Combaz & Peniguel, 1972) emend. Playford & Martin 1984, Fenghsiang Formation (Xiangshuidong section), Songzi, Hubei, China, Sample AGO297, Slide 1, EF: M43/1; M. *Peteinosphaeridium robustriramosum* Tongiorgi et al., 1995, Dawan Formation (Huanghuachang section), Yichang, Hubei, China, Sample HHDW11, Slide 1, EF: L43/3; N. *Sacculidium macropylum* (Eisenack, 1995) Ribecai et al., 2002, Dawan Formation (Daping section), Yichang, Hubei, China, Sample AFI4016, Slide 1, EF: U51; O. *Striatotheca pricipalis* var. *parva* Burmann 1970, Meitan Formation (Honghuayuan section), Tongzi, Guizhou, China, Sample AFI1030, Slide 4, EF: F38/4; P. *Veryhachium lairdii* group, Hungshihyen Formation (Erchun section), Kunming, China, Sample AGC8, Slide 1, EF: S46/1; Q. *Dicrodiacrodium ancoriforme* Burmann, 1968 emend Servais et al., 1996, Borehole BJ109, Morocco, -464m, Slide 1, EF: G53/4; R. *Orthosphaeridium* sp. Dawan Formation (Huanghuachang section), Yichang, Hubei, China, Sample HHDW28, Slide 2, EF: M40; S. *Veryhachium trispinosum* group, Meitan Formation (Honghuayuan section), Tongzi, Guizhou, China, Sample AFI1039, Slide 2, EF: M47/2.