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Acritarchs from the Floian (Early Ordovician) of the Montagne Noire, France: biostratigraphical and palaeobiogeographical implications

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This present study describes the acritarch assemblages from the siltstone and claystone of the Landeyran Formation of southern Montagne Noire, France displaying the Early Ordovician Cabrières Biota, and from the coeval Landeyran section. The moderately to well-preserved organic-walled microfossils allow the identification of a rich and diverse palynoflora bearing different important biostratigraphical and palaeobiogeographical markers. The presence of typical Early Ordovician index species, such as *Coryphidium bohemicum*, *Ampullula* spp., *Barakella* spp., together with the absence of the genera *Arkonia*, *Frankea*, *Orthosphaeridium* and *Dicrodiacrodium*, allow an assignment to the late-middle to early-late Floian (transition Fl2 to Fl3), confirming biostratigraphical data from trilobite and graptolite biozonations. The presence of the genera *Acanthodiacrodium*, *Arbusculidium*, *Coryphidium* and *Striatotheca* enables the attribution of the southern Montagne Noire area to the peri-Gondwana acritarch province in high southern latitudes. The presence of the genus *Ampullula* in the late Floian in the southern peri-Gondwana province allows a modification of its First Appearance Datum in this province where it was previously only recorded from the early Darriwilian. □ *Cabrières Biota, Landeyran Formation, palynology, phytoplankton, early Palaeozoic, peri-Gondwana.*

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The southern part of the Montagne Noire, located in the South of France, is a well-studied area displaying an almost complete geological succession from the early and middle Palaeozoic (Cambrian–Devonian). For almost a century, palaeontological studies in this area have shown the presence of trilobites, molluscs, brachiopods, conodonts, echinoderms, conulariids, graptolites, hyoliths and other groups (Thoral 1935; Ubaghs 1969, 1987, 1998; Courtessole 1973; Capéra *et al.* 1978; Babin *et al.* 1982; Courtessole *et al.* 1983; Vidal 1996; Vizcaïno & Lefebvre 1999; Shergold *et al.* 2000; Vizcaïno *et al.* 2001, 2004; Tortello *et al.* 2006; Štorch & Feist 2008; Kröger & Evans 2011; Devaere *et al.* 2014; Ebbestad *et al.* 2020; Van Iten & Lefebvre, 2020; Dupichaud *et al.* 2023).

The Cabrières Biota was recently discovered in the area of the village of Cabrières, featuring groups already known from either Cambrian or Ordovician Lagerstätten. The Cabrières Biota bears a unique taxonomic composition for the Early Ordovician, dominated by algae and sponges (Li & Reitner, this issue; Vayda *et al.*, this issue). In their first study of the new Lagerstätte, Saleh *et al.* (2024b) mentioned the presence of many other marine fossils (arthropods comprising trilobites and ostracods; brachiopods; cnidarians consisting of conulariids; graptolites; hyolithids; molluscs, comprising cephalopods, gastropods and rostroconchs and vermiform organisms) that are currently being studied in more detail in this issue of *Lethaia* (Gutiérrez-Marco *et al.*, Harper *et al.*, Lefebvre *et al.*; Polechová *et al.*; Van Iten *et al.;* Vannier *et al.*).

Among the different fossil groups, the Cabrières Biota is characterized by a majority of non-biomineralized organisms preserving soft tissues, like algae, bivalves, arthropods, chelicerates, hemichordates, lobopodians, and sponges. Although biomineralized remains without soft-tissue preservation including

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brachiopods, echinoderms, molluscs, and trilobites are also present in lower proportions, the exceptional preservation indicates that the biota corresponds to a Konservat-Lagerstätte (Seilacher 1970; Kimmig & Schiffbauer 2024). Corresponding to the late Early Ordovician (Floian), the Cabrières Biota is present in the lower part of the regional Landeyran Formation, for which different sedimentological studies have been conducted in recent decades (Noffke & Nitsch 1994; Vizcaïno *et al.* 2001; Vaucher *et al.* this issue). At latitudes around 67-68°S according to palaeomagnetic data (Nysaether *et al.* 2002), the Montagne Noire was located on the margin of South Gondwana (*sensu* Manzano *et al.* 2025) during the Middle Ordovician. However, the palaeobiogeographical information provided by different groups in the Cabrières Biota suggests even higher latitude settings (Saleh *et al.* 2024b). These very high latitudes are corroborated by palaeogeographical and palaeontological studies, making the Cabrières Biota one of the very few Lagerstätten typically characteristic of polar ecosystems of the Early Ordovician, similar to the Fezouata (Anti-Atlas, Morocco) and Klabava (Czech Republic) biotas (Saleh *et al.* 2024a). This almost unique Lagerstätte of the Montagne Noire underlines that the Early Ordovician, bearing the Cabrières Biota, should be considered as essential for the understanding of the composition and operation mode of marine ecosystems between the Cambrian 'explosion' and the Ordovician radiations.

Defined by Evitt (1963), the group 'Acritarchs' includes organic-walled microfossils of uncertain origin characterized by a vesicle, displaying variable shapes, with or without different kinds of processes (appendages). Acritarchs of the Early Ordovician are well described in diverse areas of the world, in particular from Bohemia, Czech Republic (e.g. Vavrdová 1965, 1973, 1979, 1986, 1990); Sweden (e.g. Tongiorgi & Ribecai 1990); the British Isles (e.g. Booth 1979; Turner 1985; Molyneux & Dorning 1989; Molyneux 2009); North Africa (e.g. Cramer & Díez 1977; Vecoli & Le Hérissé 2004; Nowak *et al.* 2015, 2016); South America (e.g. de La Puente & Rubinstein 2009, 2013; Toro *et al.* 2010; Rubinstein *et al.* 2019; Kroeck *et al.* 2020); and China (e.g. Li 1989; Li *et al.* 2004; Yan & Li 2010; Yan *et al.*, 2011, 2013).

Ordovician acritarchs have also been described from southern France (e.g. Deflandre 1942, 1945; Martin 1972; Rauscher 1971, 1974; Baudelot & Bessière 1975, 1977; Fournier-Vinas & Donnot 1977; Fournier-Vinas 1978) and to a lesser extent from western France (e.g. Paris & Le Hérissé 1992). However, the area of the Montagne Noire has not been re-investigated since the early 1980s. The study of palynomorphs within this area remains rather complicated because of the strong deformation, recrystallization and metamorphism affecting the rocks of the early Palaeozoic. Different localities have provided variable preservation degrees of palynomorphs, including acritarchs and chitinozoans. Over fifty years ago, moderately well-preserved organic microfossils were described from rocks from the Landeyran Valley, La Roquemaillère (Monts de Cabrières) and the Monts de Pardailhan by several authors (Rauscher 1971; Martin 1972). While Rauscher (1971) mainly discussed the general characteristics of the assemblages (sub-groups and main genera) assigning the microfloras to the Early Ordovician (Tremadocian and Arenigian), Martin (1972) provided a more detailed taxonomic investigation based on samples from the Mont de Cabrières and Mont de Pardailhan areas, describing 17 genera and 56 species, including 15 new species and one new sub-species, from levels attributed to the Early and Middle Ordovician (Tremadocian and Arenigian/Llanvirnian).

This paper is a part of a broader concerted effort to holistically evaluate the Cabrières Biota using palaeontology, sedimentology, biostratigraphy, geochemistry, and palaeoecology. Here, we present a palynological study based on acritarchs, collected from the Cabrières Biota Lagerstätte, as well as from another location (Landeyran section), displaying a complete succession of the Landeyran Formation in the Landeyran Valley, approximately 25 km West-South-West of the village of Cabrières, which can be considered as coeval with the levels including the fossil-bearing horizons of the Cabrières Biota. The main objective of this study is to analyse the biostratigraphical signal present in the acritarch assemblages. In addition, the palaeobiogeographical signature of the assemblage is documented.

Geological setting

The Montagne Noire is a complex tectonostratigraphical unit, formed during the Variscan Orogeny, located in the southern part of the French Massif Central (Fig. 1). Its formation has long been debated, however, the latest studies agreed on a complex process of fold and thrust belts in an important sinistral East-North-East transpressive context linked to the axis of the Cévennes Fault (e.g. Demange 1999; Chardon *et al.* 2020). The presence of sedimentary and metamorphic rocks, and the strong deformation that affected both, allowed a distinction of the Montagne Noire in three main parts: a northern and a southern deformed sedimentary flank, separated by an axial

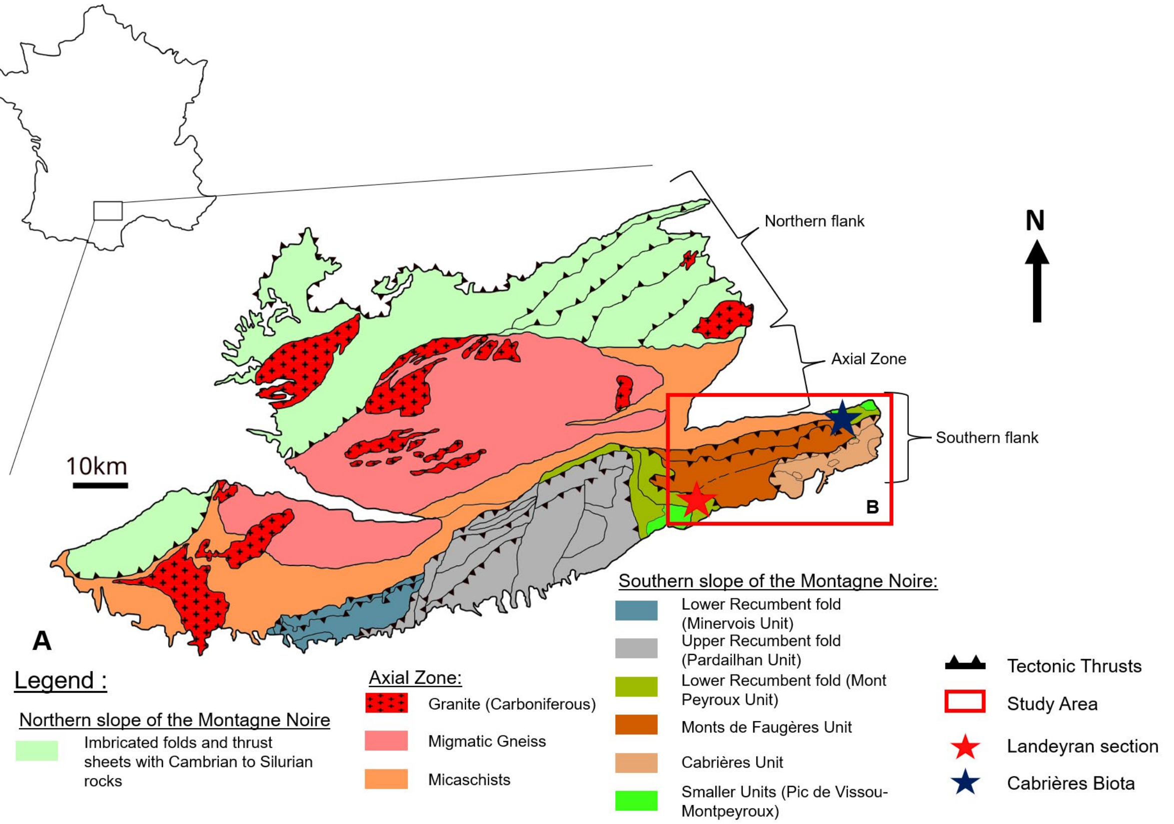

Fig. 1. Geological context of the study area. A, location and geological map of the Montagne Noire (modified from Demange, 1999; Faure *et al.* 2010; Montmartin *et al.* 2021). B, area of the southern slope part of the Montagne Noire, including the Pic de Vissou-Montpeyroux Unit, yielding the Cabrières Biota.

zone (Fig. 1) (Gèze 1949; Arthaud 1970; Montmartin *et al.* 2021; Lefebvre *et al.* 2023). This axial zone is mainly characterized by an elongated dome formed by an association of migmatized orthogneiss, paragneiss and other rocks that experienced a partial melting, and whose protoliths were parautochtonous units of an age ranging from the Ordovician to the earliest Devonian (from 472 Ma to 416 Ma) (Roger *et al.* 2004; Montmartin *et al.* 2021; Lefebvre *et al.* 2023). The southern part of the Montagne Noire is mainly composed of an almost-complete inverted stratigraphic succession of sedimentary layers from the Cambrian to the Devonian, organized in nappes or units that suffered strong deformation (including recumbent folds, sheath folds) during the Carboniferous. Among those different units, the Écailles de Cabrières correspond to very dispersed Ordovician to Carboniferous layers, transported over a wildflysch succession (Gèze 1949). They clearly differ from the other nappes from the southern part of the Montagne Noire (Minervois, Monts de Pardailhan, Mont de Faugères, Mont Peyroux) (Fig.1) by bearing different Ordovician successions and faunas (de Rouville & Delage 1892; Miquel 1894; Thoral 1941; Colmenar *et al.* 2013; Álvaro *et al.* 2016, 2018; Lefebvre *et al.* 2023).

The main palaeogeographical and part of the sedimentological settings of the southern Montagne Noire during the Ordovician have been investigated since the 19th century. Different studies have shown a high to very high latitude setting of the Montagne Noire during the Ordovician. Mainly based on the analysis of Middle or Late Ordovician olistholithic blocks from the Écailles de Cabrières (Nysaether *et al.* 2002; Colmenar *et al.* 2013; Alvaro *et al.* 2016; Lefebvre *et al.* 2023), Nysaether *et al.* (2002) assigned very high latitudes (67-68°S) to the Montagne Noire. More recently, the faunal assemblage of the Cabrières Biota, dominated by sponges and algae, provides a significant signal of polar ecosystems (Saleh *et al.* 2024b) and suggests even higher latitudes than those presented for the Middle or Late Ordovician.

Considering the sedimentological setting of the Ordovician, only the Écailles de Cabrières have shown a preservation of Middle and Late Ordovician sediments. However, their tectonic and sedimentological characteristics make them very different from the other units of the Montagne Noire, suggesting another geological context (Colmenar *et al.* 2013; Álvaro *et al.* 2016, 2018; Lefebvre *et al.* 2023). The sedimentology of the Lower Ordovician of the other nappes, including the Minervois, Mont de Pardailhan, Mont de Faugères, Mont Peyroux and Pic de Vissou-Montpeyroux units, has been investigated in several studies that enabled the identification of different sedimentary formations from the Cambrian to the Early Ordovician (e.g. Noffke & Nitsch 1994; Vizcaïno *et al.* 2001; Álvaro *et al.* 2003; Vaucher *et al.* this issue), from bottom to top: the La Gardie (upper Cambrian), Val d'Homs (Cambrian-Ordovician transition), La Dentelle (Tremadocian), Saint-Chinian (upper Tremadocian/lower Floian), La Maurerie (Floian), Cluse de l'Orb (Floian), Foulon (Floian) and finally the Landeyran (Floian) formations. The facies succession shows different transgressive and regressive phases between the late Cambrian and the end of the Early Ordovician (Noffke & Nitsch 1994; Vizcaïno *et al.* 2001).

Known for bearing a major faunal transition with a diversification of brachiopods, echinoderms, trilobites, and the re-occurrence of several groups from the underlying Saint-Chinian and La Maurerie formations (Vizcaïno *et al.* 2001), the Landeyran Formation corresponds to the upper part of the Lower Ordovician succession that is present in most of the Montagne Noire outcrops. Conformably overlying the Foulon Formation, the Landeyran Formation includes the levels bearing the Cabrières Biota. The section displaying the Landeyran Formation studied in this work corresponds to the Landeyran section, located near the Landeyran river (Fig. 1B). The examination of silty to clayey laminated siltstones in this section, characteristic of the Landeyran Formation across the southern part of the Montagne Noire, allowed assignment of these sediments to distal prodelta to offshore or typical-shelf depositional setting (Vaucher *et al.* this issue).

Material and methods

For this palynological study, a total of 18 samples from two different localities were analysed; 16 samples come from a continuous section in the Landeyran Valley (Landeyran section), located in the Mont Peyroux unit and more precisely within the municipality of Saint-Nazaire-de-Ladarez. The Landeyran valley section (referred to as the Landeyran section in this work) provides a continuous succession through the uppermost part of the Foulon Formation, the transition to the Landeyran Formation and the lower part of the Landeyran Formation (Vaucher *et al.* this issue) allowing a precise placement of the palynological samples along the section (GPS coordinates: 43°29'46.1'N 03°04'38.5'E).

Two additional samples were collected from the small Pic de Vissou-Montpeyroux nappe (Fig. 1). In this small unit, where the Cabrières Biota was described, the samples were more precisely collected from 'La Brouette' and 'La Sangle' sites, in proximity to and east of Valmascle, north-west of the village of Cabrières. The exposure and complexity of these outcrops did not allow any logging of the sections, however their assignment to the lower part of the Landeyran Formation is supported by the associated benthic faunas (Saleh *et al.* 2024b).

The continuity of the Landeyran section allows a study of the distribution of the different acritarch assemblages with the aim of understanding the biostratigraphical evolution of the acritarchs through the Floian succession and their palaeobiogeographical position in relation to the global distribution of late Early Ordovician acritarchs (Fig. 2).

All samples were prepared according to a standard procedure of palynological preparation techniques (e.g. Riding 2021). The sediments collected were first treated with hydrochloric acid in order to eliminate all carbonates. After several rinses to neutral, the samples were then treated with hydrofluoric acid to dissolve the siliciclastic matrix from which the different palynomorphs were extracted. Because this step in the preparation can engender the formation of some fluorosilicate crystals, a final treatment was performed with boiled hydrochloric acid to eliminate the newly formed mineral phases. The palynological preparation was sieved with 51µm and 15µm filter meshes to separate the largest fragments and the main palynological material, respectively. Although generally moderately to well preserved, some of the slides analyzed were also re-oxidized to reduce the opacity of the palynological material by using Schulze's Solution as a bleaching method. All slides were observed under a Zeiss Axio Imager A2 transmitted light microscope (with oil immersion objectives and digital interference contrast), on which was mounted a Zeiss AxioCam ERc5s camera. All pictures were reworked with the software Zeiss 3.11. All studied samples, preparations and slides are stored in the collections of the Evo-Eco-Paleo department of the University of Lille, France.

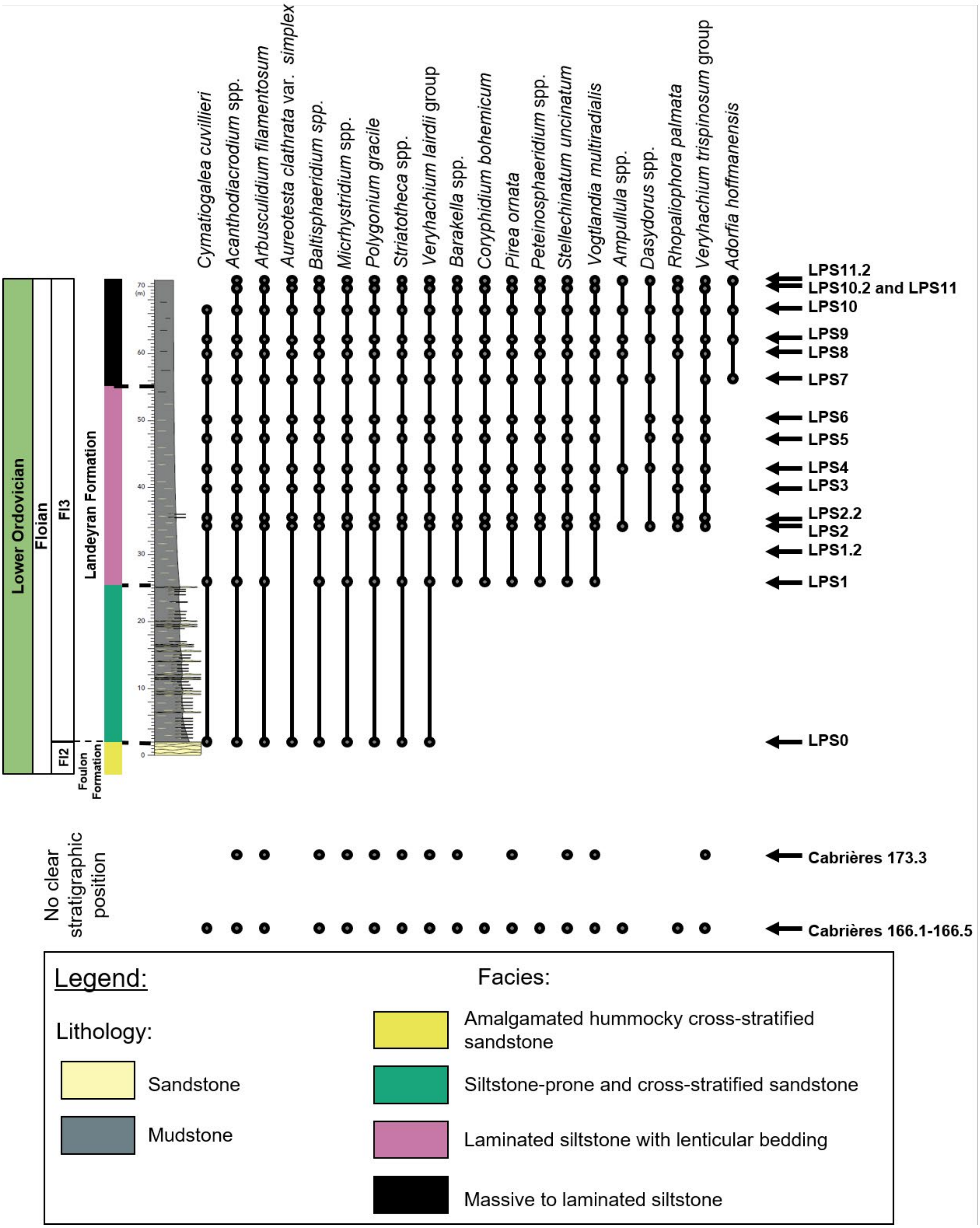

Fig. 2. Stratigraphical column of the Landeyran section recording the uppermost part of the Foulon Formation and the base of the lower part of the Landeyran Formation. The log and the main sedimentary facies are from Vaucher *et al.* (this issue). The position of palynological samples and distribution of acritarch taxa in the Landeyran section are indicated, as well as the taxa present in the samples from the Cabrières Biota from the other localities, of which the precise stratigraphic position within the Landeyran Formation is not clear.

Distribution of the acritarchs

Landeyran section.– From the 16 samples collected from the Landeyran section, only the sample 'SILT1' in the collections of Lille University (named 'LPS1.2' below), located around 25 metres above the base of the Landeyran Formation, shows very few unidentifiable fragments of palynomorphs (Fig. 2). All the samples labelled 'LPS' and 'Point Sup' (named 'LPS10.2' below), and the 'Landeyran Inf' sample in the collections of Lille University (named 'LPS0' below), as well as the samples 'Landeyran' (called 'LPS2.2' below) and 'Landeyran Sup' (called 'LPS11.2' below) bear acritarchs in varying abundance and with different qualities of preservation in the 15 μm < x < 51 μm fraction. The upper fraction with larger palynomorphs (x > 51 μm) mostly contains organic debris and chitinozoans larger than 51 μm, but bears only up to a maximum of 20 acritarchs per palynological slide. On the other hand, the smaller fraction (15 μm < x < 51 μm) allows the identification of at least 150 (and up to more than a thousand) specimens per slide, depending on the preservation, the treatment of the samples, and the abundance of palynomorphs in the sample.

An evolution of the preservation of the organic-walled microfossils and their abundance, from the bottom to the top of the section, can be observed. The samples from the top of the section usually provide more abundant specimens, while those closer to the base of the section, including the samples 'LPS0' and 'LPS1,' show a less diversified and abundant palynoflora. Furthermore, between the base and the top of the Landeyran section, a slight difference in terms of colours of palynomorphs and of their preservation can be observed. At the base of the section, the palynomorphs are in general poorly preserved, often bearing dark central bodies and appearing to be more degraded, with commonly broken processes (appendages) and vesicles, making the identification more difficult and sometimes impossible. At the top of the Landeyran section, the samples are clearly better preserved, being less fragmented (especially the processes) and displaying lighter colours, making the identification of palynomorphs easier. This difference in abundance and preservation of the palynomorphs of the Landeyran section is also found between the two samples collected from the Cabrières Biota locality.

Cabrières area.– Concerning the samples from the Cabrières Biota Lagerstätte, both samples (labelled 'Cabrières 166.1-166.5' and 'Cabrières 173.3') bear a relatively abundant acritarch microflora. However, the latter sample, displaying darker colours and more fragmented palynomorphs in the slides, seems to be more degraded than the first one. This leads to a difference in the abundance of identified specimens between the two samples. While in the sample 'Cabrières 173.3' around 200 specimens were identified in the smaller fraction (15 μm < x < 51 μm), the sample 'Cabrières 166.1-166.5' bears almost four times more identifiable acritarchs in this same fraction. As for the Landeyran section, the upper fraction (x > 51 μm) contains only very few acritarchs while bearing more chitinozoans and other larger organic debris.

Composition of the acritarch assemblages

Although some abundance and preservation differences have been identified between the samples, the composition of the palynomorph assemblages from the Floian of the Montagne Noire remains very similar at all investigated levels. The taxa observed include galeate acritarchs (*Caldariola* Molyneux in Molyneux & Rushton, 1988; *Cymatiogalea* Deunff, 1961 *emend.* Deunff *et al.*, 1974; *Stelliferidium* Deunff *et al.*, 1974; *Priscogalea* Deunff, 1961 *emend.* Rasul, 1974); diacromorphs (e.g. *Acanthodiacrodium* Timofeev, 1958 *emend.* Deflandre & Deflandre-Rigaud, 1962; *Barakella* Cramer & Díez, 1977; *Arbusculidium* Deunff, 1968 *emend.* Welsch, 1986), a few sphaeromorphs, very rare netromorphs, and other genera, such as *Adorfia* Burmann, 1970; *Ampullula* Righi, 1991 *emend.* Yan *et al.*, 2010; *Aureotesta* Vavrdová, 1972 *emend.* Brocke *et al.*, 1997; *Baltisphaeridium* Eisenack, 1958a *emend.* Eiserhardt, 1989; *Coryphidium* Vavrdová, 1972 *emend.* Servais *et al.*, 2008; *Dasydorus* Playford & Martin, 1984; *Micrhystridium* Deflandre, 1937 *emend.* Sarjeant & Stancliffe, 1994; *Petaloferidium* Jacobson, 1978; *Peteinosphaeridium* Staplin *et al.*, 1965 *emend.* Playford *et al.*, 1995; *Pirea* Vavrdová, 1972; *Polygonium* Vavrdová, 1966 *emend.* Le Hérissé, 1988 *emend.* Sarjeant & Stancliffe, 1994; *Pterospermella* (Eisenack, 1972); *Rhopaliophora* Tappan & Loeblich, 1971 *emend.* Li *et al.,* 2014; *Stellechinatum* Turner, 1984; *Striatotheca* Burmann, 1970 *emend.* Sarjeant & Stancliffe, 1994, but see Servais 1997; *Tectitheca* Burmann, 1968; the *Veryhachium lairdii* and *Veryhachium trispinosum* groups of the genus *Veryhachium* Deunff, 1954 emended by Sarjeant & Stancliffe, 1994; but see Servais *et al.* 2007) and *Vogtlandia* (Burmann, 1970). A comprehensive list including all genera and species recorded is provided in Table 1.

Selected taxa with biostratigraphical, palaeobiogeographical and palaeoecological significance are illustrated in Figures 3 and 4. For some taxa the identification at the species level is possible due to detailed taxonomical revisions made in recent years (e.g. Servais 1993, 1997; Servais *et al.* 1996, 2003, 2007,

Table 1. List of all taxa observed in the samples from the Floian of the southern Montagne (Cabrières Biota and Landeyran section)

List of taxa
Acanthodiacrodium angustizonale (Rauscher, 1974) *non* Burmann, 1968
Acanthodiacrodium angustum (Downie, 1958) Combaz, 1967
Acanthodiacrodium sp.
Adorfia hoffmanensis (Cramer *et al*., 1974) Ottone in Ottone *et al*., 1992
Ampullula crassula (Vavrdová, 1990) *comb. et emend*. Yan *et al*., 2010
Arbusculidium sp.
Arbusculidium filamentosum (Vavrdová, 1965) Vavrdová, 1972 *emend*. Fatka & Brocke, 1999
Aureotesta clathrata var. *clathrata* Vavrdová, 1972 *emend*. Brocke *et al*., 1997
Aureotesta clathrata var. *simplex* (Cramer *et al*., 1974) Brocke *et al*., 1997
Baltisphaeridium klavabense (Vavrdová, 1965) Kjellström, 1971
Barakella felix Cramer & Díez, 1977
Barakella sp.
Caldariola spp.
Coryphidium bohemicum Vavrdová, 1972 *sensu strictu*
Coryphidium elegans Cramer & Díez, 1976
Coryphidium minutum Cramer & Díez, 1976
Cymatiogalea cuvillieri (Deunff, 1961) Deunff, 1964
Cymatiogalea deunffii Jardiné *et al*., 1974
Cymatiogalea granulata Vavrdová, 1966
Cymatiogalea messaoudensis Jardiné *et al*., 1974
Dasydorus sp.
Eupokilofusa spp.
Leiosphaerida spp.
Michrystridium spp.
cf. *Petaloferidium florigerum* (Vavrdová, 1977) Fensome *et al*., 1990
Peteinosphaeridium sp.
Peteinosphaeridium armatum Playford *et al*., 1995
Peteinosphaeridium robustiramosum Playford *et al*., 1995
Pirea ornata (Burmann, 1970) Eisenack *et al*., 1976
Pirea sp.
Poikilofusa spp. Staplin *et al*., 1965
Polygonium gracile Vavrdová, 1966 *emend*. Jacobson & Achab, 1985 *emend*. Sarjeant & Stancliffe, 1996
Priscogalea spp.
Pterospermella sp.
Rhopaliophora sp.
Rhopaliophora palmata Combaz & Péniguel, 1972 *emend*. Playford & Martin, 1984
Stellechinatum sicaforme Molyneux in Molyneux & Rushton, 1988
Stellechinatum uncinatum (Downie, 1958) Molyneux, 1987
Stelliferidium trifidum (Rasul, 1974) Fensome *et al*., 1990
Striatotheca principalis var. *parva* Burmann, 1970
Tectitheca additionalis Burmann, 1968
Veryhachium trispinosum group
Veryhachium lairdii group
Vogtlandia cf. *flosmaris* (Deunff, 1977) Molyneux, 1987
Vogtlandia multiradialis Burmann, 1970

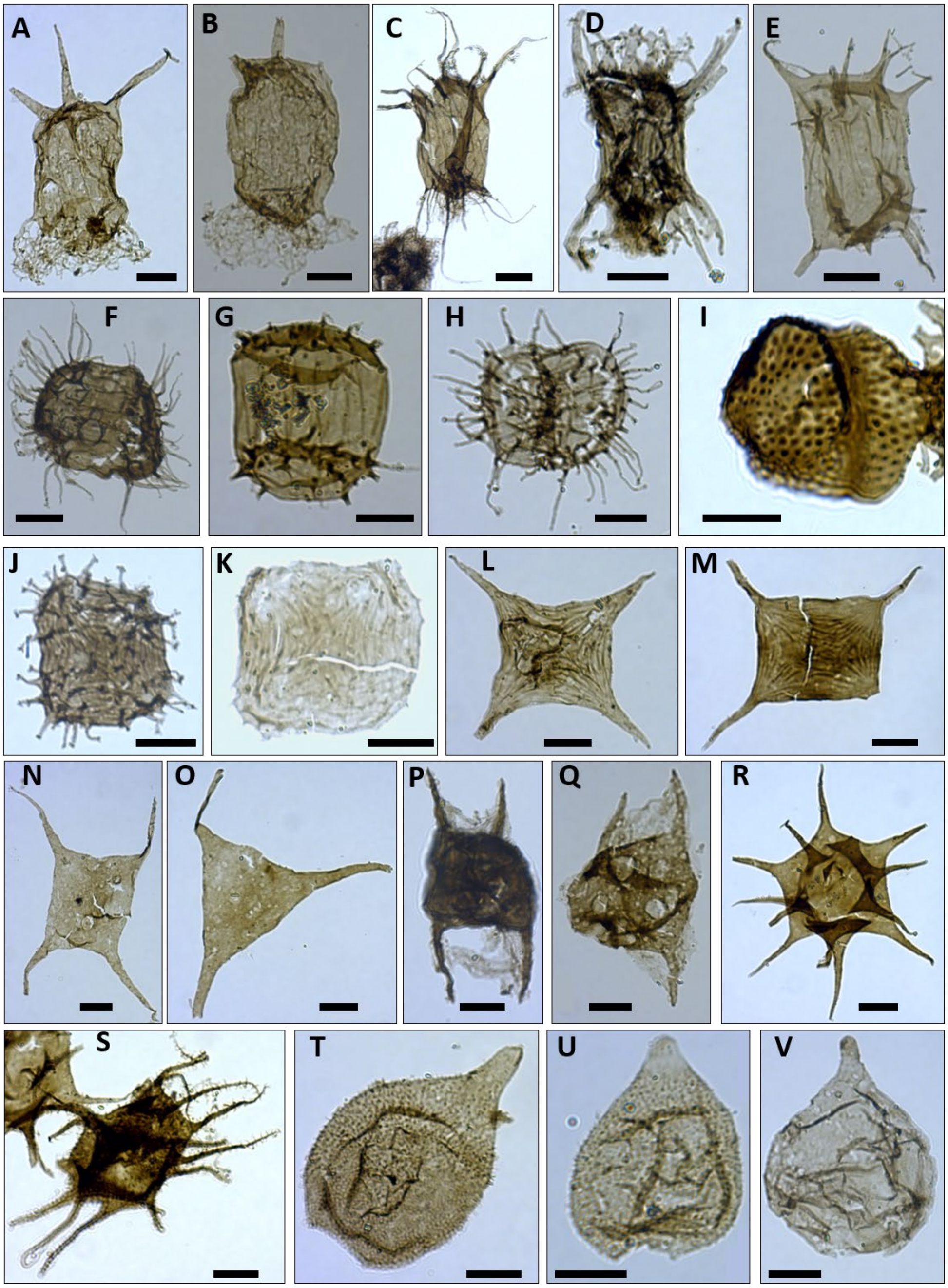

Fig. 3. Specimens of selected taxa from the Ordovician of the Landeyran Valley and Cabrières Biota, Montagne Noire, France. For each illustrated specimen, the following information is given: slide label, England Finder coordinates. For example, LPS11, R48-3 refers to slide LPS11, England Finder coordinates R48-3. Scale bar = 10 µm. A, *Arbusculidium filamentosum* (Vavrdová, 1965) Vavrdová, 1972 *emend.* Fatka & Brocke, 1999, LPS3, 15 µm < x < 51 µm, E64. B, *Arbusculidium filamentosum*, (Vavrdová, 1965) Vavrdová, 1972 *emend.* Fatka & Brocke, 1999, LPS6, 15 µm < x < 51 µm, H66-2. C, *Arbusculidium* sp., LPS11.2 15 µm < x < 51 µm, S64. D, *Barakella* sp., Cabrières 166,1-166,5, 15 µm < x < 51 µm, J53. E, *Barakella* cf. *felix* Cramer & Díez, 1977, LPS8, 15 µm < x < 51 µm, X53. F, *Acanthodiacrodium* sp., LPS11.2, 15 µm < x < 51 µm, E57-4. G, *Acanthodiacrodium* cf. *angustizonale*, Rauscher, 1974 (*non* Burmann, 1968), LPS10, 15 µm < x < 51 µm, W54-2. H, *Acanthodiacrodium* sp., LPS11.2 15 µm < x < 51 µm, S60. I, *Acanthodiacrodium angustum* (Downie, 1958) Combaz, 1967, LPS10, 15 µm < x < 51 µm, L48. J, *Coryphidium bohemicum*, Vavrdová, 1972 *sensu stricto*, LPS11.2, 15 µm < x < 51 µm,S52-2. K, *Coryphidium minutum*, Cramer & Díez, 1976, LPS10, 15 µm < x < 51 µm, F64-4. L, *Striatotheca principalis* var. *parva*, Burmann, 1970, LPS6, 15 µm < x < 51 µm, G64-2. M, *Striatotheca principalis* var. *parva*, Burmann, 1970, LPS2, 15 µm < x < 51 µm, M64-2. N, *Veryhachium lairdii* group, LPS11.2, 15 µm < x < 51 µm,R55-1. O, *Veryhachium trispinosum* group, LPS10, 15 µm < x < 51 µm, H67-1. P, *Aureotesta clathrata* var. *simplex*, (Cramer *et al.*, 1974) Brocke *et al.*, 1998, LPS11.2, 15 µm < x < 51 µm, F64. Q, *Aureotesta clathrata* var. *simplex* (Cramer *et al.*, 1974) Brocke *et al.*, 1998, LPS3, 15 µm < x < 51 µm, U71-3. R, *Polygonium gracile*, Vavrdová, 1966 *emend.* Jacobson & Achab, 1985 *emend.* Sarjeant & Stancliffe, 1996, LPS11, 15 µm < x < 51 µm, O60-3. S, *Stellechinatum uncinatum*, (Downie, 1958) Molyneux, 1987, LPS8, 15 µm < x < 51 µm, M71-2. T, *Pirea ornata* (Burmann, 1970) Eisenack *et al.*, 1976, LPS8, 15 µm < x < 51 µm,N72. U, *Pirea ornata* (Burmann, 1970) Eisenack *et al.*, 1976, LPS10, 15 µm < x < 51 µm,Y72-1. V, *Pirea* sp., LPS11.2, 15 µm < x < 51 µm,R62-1

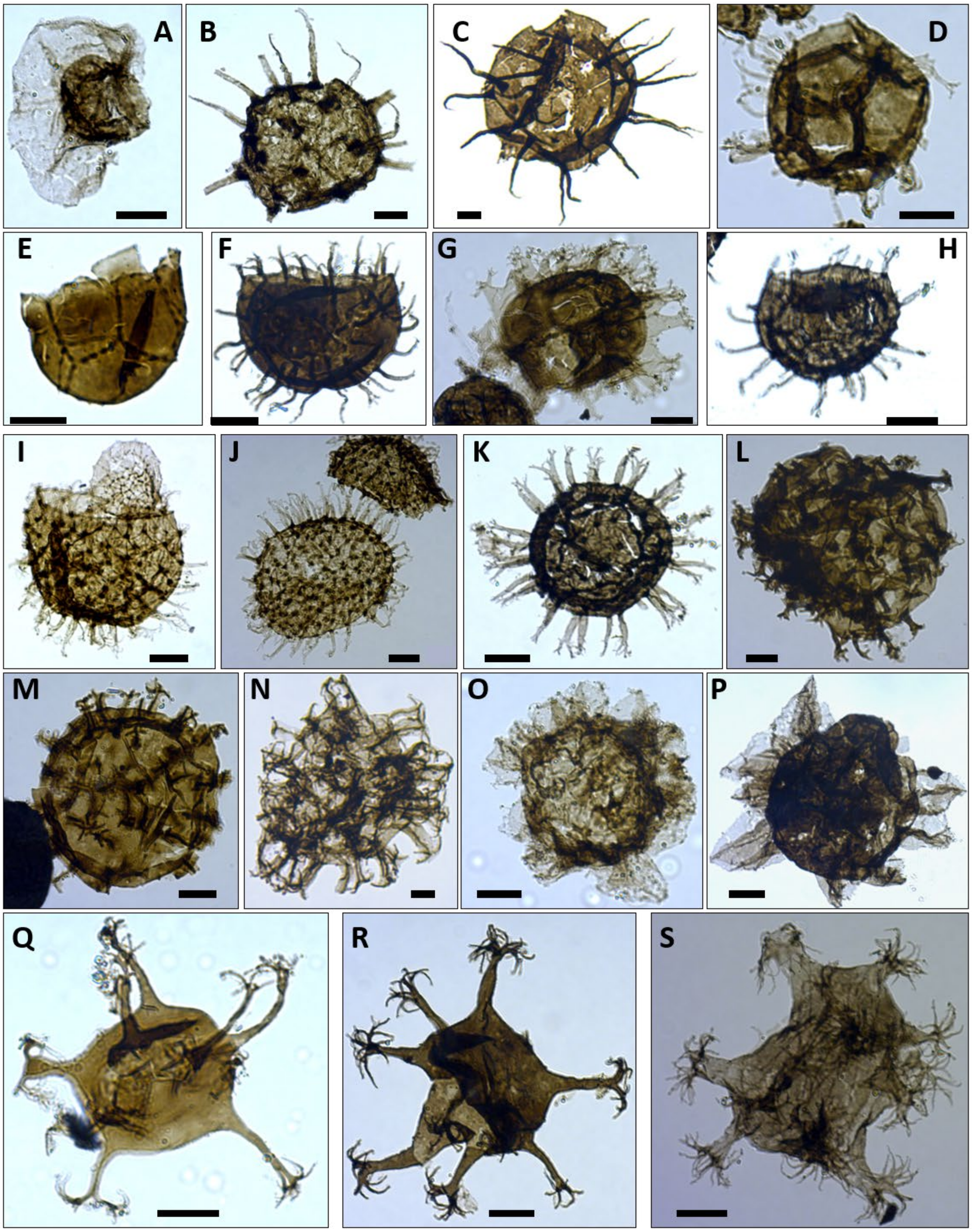

Fig. 4. Specimens of selected taxa from the Ordovician of the Landeyran Valley and Cabrières Biota, Montagne Noire, France. For each illustrated specimen, the following information is given: slide label, England Finder coordinates. For example, LPS11, R48-3 refers to slide LPS11, England Finder coordinates R48-3. Scale bar = 10 µm. A, *Pterospermella* sp., LPS11.2 15 µm < x < 51 µm, T64. B, *Baltisphaeridium klabavense* (Vavrdová, 1965) Kjellström, 1971, LPS5, 15 µm < x < 51 µm, O57. C, *Baltisphaeridium* sp., LPS11, x > 51 µm, V73-1. D, *Cymatiogalea* cf. *granulata* Vavrdová, 1966, LPS4, 15 µm < x < 51 µm, X51-3. E, *Cymatiogalea cuvillieri* (Deunff, 1961) Deunff, 1964, LPS10, 15 µm < x < 51 µm, Q58-3. F, *Cymatiogalea* cf. *granulata* Vavrdová, 1966, LPS11.2, 15 µm < x < 51 µm, G50-3. G, *Cymatiogalea messaoudensis* Jardiné *et al.,* 1974 LPS10.2, 15 µm < x < 51 µm, M63-4. H, *Cymatiogalea* cf. *granulata* Vavrdová, 1966, Cabrières 166,1-166,5, 15 µm < x < 51 µm, K48-2. I, *Stelliferidium* cf. *trifidum* (Rasul, 1974) Fensome *et al*., 1990, LPS4, 15 µm < x < 51 µm,T56-3. J, *Stelliferidium* sp., LPS4, 15 µm < x < 51 µm, L51. K, *Stelliferidium* sp., Cabrières 166,1-166,5 15 µm < x < 51 µm, R69. L, *Ampullula* cf. *crassula* Vavrdová, 1990 *comb. et emend.* Yan *et al.*, 2010, LPS8, 15 µm < x < 51 µm, X68-1. M, *Peteinosphaeridium armatum* Playford *et al*., 1995, LPS9, 15<x<51, L59-1. N, *Peteinosphaeridium robustiramusum* Playford *et al*., 1995, LPS11, x > 51 µm, K70-1. O, *Rhopaliophora palmata* Combaz & Péniguel, 1972 *emend.* Playford & Martin, 1984, LPS10.2, 15<x<51, P51. P, *Rhopaliophora* cf. *palmata* Combaz & Péniguel, 1972 *emend.* Playford & Martin, 1984, LPS11.2, 15 µm < x < 51 µm, F49-4. Q, *Vogtlandia* cf. *multiradialis* (Burmann, 1970), LPS10.2, 15 µm < x < 51 µm, M72-4. R, *Vogtlandia multiradialis* (Burmann, 1970) LPS11.2, 15 µm < x < 51 µm, U52-3. S, cf. *Adorfia hoffmanensis* (Cramer *et al*., 1974) Ottone *in* Ottone *et al.*, 1992, LPS11.2, 15 µm < x < 51 µm, Q59.

2008, 2014; Brocke *et al.* 1997; Fatka & Brocke 1999; Stricanne & Servais 2002; Yan *et al.* 2010, 2017; Li *et al.* 2014). For others, the taxonomy remains unclear, and the identification is made at the genus level only, with either one (sp.) or several (spp.) species of the genus being present.

The different acritarch taxa show variations in their relative abundance, between the site of the Cabrières Biota and the Landeyran section, and also within the latter locality. These variations will be discussed in the frame of palaeoecological interpretations in a separate paper focusing on the palaeoecology of the Cabrières Biota (Lefebvre *et al.* this issue). On the other hand, even the rare or very rare presence of specimens of particular taxa can be of great significance, for example some index taxa, although very rare, can be biostratigraphically or palaeobiogeographically useful. In the present study the terms very rare, rare, common, very common, dominant are used. They respectively refer to relative abundance: extremely rare: <0.5%; very rare: 0.5-1%; rare: 1-5%; common: 5-10%; very common: 10-30%; dominant: >30%

Across the whole section, one of the predominant acritarch sub-groups is the polygonomorph group, representing around 30% of the specimens in the assemblages. It is mainly represented by different species of the genus *Polygonium,* such as *P. gracile* Vavrdová, 1966 *emend.* Jacobson & Achab, 1985 *emend.* Sarjeant & Stancliffe, 1996 (Fig. 3R). The assemblages from the southern Montagne Noire comprise also extremely rare and scarce occurrences of *Petaloferidium*, with *P. florigerum* (Vavrdová, 1977) Fensome *et al.*, 1990, and very rare to rare occurrences of *Tectitheca,* including *T. additionalis* Burmann, 1968, and of *Stellechinatum,* including *S. uncinatum* (Downie, 1958) Molyneux, 1987 (Fig. 3S) and *S. sicaforme* Molyneux *in* Molyneux & Rushton, 1988.

The galeate group is also predominant at the base of the Landeyran section (~35%). However, their proportion tends to diminish towards the top of this section (~12%). The palaeoenvironmental significance of this trend observable in all four genera (*Caldariola, Priscogalea, Cymatiogalea* and *Stelliferidium*) is discussed in the paper of Lefebvre *et al.* (this issue). The latter two genera are the most abundant representatives of the galeate group, with *Cymatiogalea* (10% in LPS0 to 4% in LPS11.2) (Fig. 4D-H) being slightly more present than *Stelliferidium* (8% in LPS0 to 4% in LPS11.2) (Fig. 4I-K). Among the galeate acritarchs, the species *Cymatiogalea messaoudensis* Jardiné *et al.*, 1974 (Fig. 4G) and *C. deunffii* Jardiné *et al.*, 1974 are extremely rare, whereas other species like *C. cuvillieri* (Deunff, 1961) Deunff, 1964 (Fig. 4E) and *C. granulata* Vavrdová, 1966 (Fig. 4H) are respectively rare to very rare and very common to rare. In contrast to the polygonomorph group, which appears only in the smaller fraction (15µm < x < 51µm), a few specimens (2-5) of galeate taxa (*Stelliferidium and Cymatiogalea*) are also observable within the larger fraction (x > 51 µm) of well-preserved samples from the middle or top of the section.

The relative abundance of the galeate group progressively diminishes as other genera appear, like the spinose *Baltisphaeridium* and the veryhachid group, which includes the genus *Veryhachium* as well as striated rectangular-shaped acritarchs attributed to *Striatotheca*. Two different subgroups of *Veryhachium* have been identified within the sediments of the Montagne Noire: the *Veryhachium lairdii* group (Fig. 3N), and the *V. trispinosum* group (Fig. 3O). The genus *Striatotheca* (Fig. 3 L-M) is almost absent from the lowest 27m of the section. However, the abundance of this genus increases towards the top of the section (from 0.3% in LPS0 to ~6% in LPS11.2). Finally, baltisphaerids, present in both fractions (x > 51 µm and 15 µm < x < 51 µm) and represented by different species, such as *Baltisphaeridium klavabense* (Vavrdová, 1965) Kjellström, 1971 (Fig. 4B), common at the base of the section, become very common at the top.

Diacromorphs are also rare to common across the whole section. Although their proportion slightly varies (from 4 to 9%) from one sample to another, no clear trend in these changes has been observed across the section. This rare to common group is, however, represented by a diversity of genera and species, some of which are biostratigraphically useful. The diacromorphs present in the samples include *Arbusculidium filamentosum* (Vavrdová, 1965) Vavrdová, 1972 *emend.* Fatka & Brocke, 1999 (Fig. 3 A,B); *Barakella felix* Cramer & Díez, 1977; see Yan *et al.*, 2017(Fig. 3E) and different species of *Acanthodiacrodium* (Fig. 3 F-I), such as *A. angustizonale* Rauscher, 1974 (*non* Burmann, 1968) (Fig. 3G) and *A. angustum* (Downie, 1958) Combaz, 1967 (Fig. 3I).

The sphaeromorphs, mostly represented by specimens of *Leiosphaeridia,* also display a more or less constant relative abundance (~5-6%) across the section with only slight variations depending on the samples.

Following the same evolution of proportions as the galeate group, the genus *Micrhystridium*, usually represented by small specimens (< 20 µm), shows approximately the same proportions (~6%) as the sphaeromorphs at the bottom of the section, becoming increasingly less abundant upwards and being almost absent at the top of the studied section (~1.5% in LPS11.2). Following the complete opposite trend of *Micrhystridium*, the biostratigraphically significant genus *Coryphidium* represented by different species, including very rare to common *C. bohemicum* Vavrdová, 1972 *sensu stricto* (Fig. 3J), and very rare *C. minutum* Cramer & Díez, 1976 (Fig. 3K) and *C. elegans* Cramer & Díez, 1976, becomes more abundant up section (1.5% in LPS0 to 5.5% in LPS11.2).

Other forms are rare to very rare in the Landeyran section, as well as in the Cabrières Biota samples, like the genus *Pirea* (mean ~1.9%) (Fig. 3T, U, V), represented by different species, including *P. ornata* (Burmann, 1970) Eisenack *et al.*, 1976 (Fig. 3T), and the genus *Dasydorus* (mean ~0.1%) (Fig. 3U). Other rare taxa include some of the genera showing complex process structures, such as *Peteinosphaeridium* (with low proportions, mean ~1.2%) (Fig. 4M, N); *Rhopaliophora* (mean ~0.2%) (Fig. 4O, P), including possible representatives of the species *Rhopaliophora palmata* Combaz & Péniguel, 1972 *emend.* Playford & Martin, 1984 (Fig. 4P); *Ampullula* (mean ~0.2%); *Vogtlandia* (mean ~0.9%), with as the main representatives *V. multiradialis* Burmann, 1970 (Fig. 4 Q-R) and *V. flosmaris* (Deunff, 1977) Molyneux, 1987 (Fig. 4S), and *Adorfia* (mean ~0.1%).

Finally, both varieties of the biostratigraphically useful species *Aureotesta clathrata*, i.e., *A. clathrata* var. *clathrata* Vavrdová, 1972 *emend.* Brocke *et al.*, 1997 (mean ~0.1%) and *A. clathrata* var. *simplex* (Cramer *et al.*, 1974) Brocke *et al.*, 1997 (mean ~0.1%) (Fig. 3P-Q), have also been observed very rarely through the Landeyran section.

It can be concluded that there is only a single assemblage present in the Landeyran section, displaying varying proportions of the different acritarch taxa present. Both samples from the Cabrières Biota bear the same assemblage with similar proportions to those in the Landeyran Section. Although small differences in the abundance of the main groups from the Landeyran section have been observed in the samples of the Cabrières Biota, a correlation of both of these samples with levels within the Landeyran section had been attempted. While the relative abundance of *Baltisphaeridium* in the Cabrières samples (12 and 14%) is close to the 10 to 16% from samples LPS7 to LPS11.2 of the top of the Landeyran section, the relative abundances of the galeates (20 and 21%), the polygonomorphs (29 and 26%) and of the *Veryhachium lairdii* group (~10%) in the layers of the Cabrières Biota are closer to those from the middle part of the Landeyran section and especially from the samples LPS5 (respectively 23%, 28% and 12%), and Landeyran (respectively 17%, 32% and 10%). According to Figure 2 and the study of the presence and absence of the taxa through the section, it can be concluded that the palynofloras from the samples 'Cabrières 166.1-166.5' (from the 'La Brouette' site) and from the sample 'Cabrières 173.3' (from the 'La Sangle' site) possess taxa present that also occur in the samples LPS2. As a consequence, the palynomorphs from both Cabrières' samples can be compared to those from the samples LPS2 to LPS7.

Discussion

Biostratigraphy

Age of the palynomorph assemblages.– Although acritarchs are not yet used as standard index fossils in Palaeozoic biostratigraphy to define global series and stage boundaries, a few clearly established biozonation schemes, correlating different sedimentary basins across the globe, have been published, allowing precise age assignments for some early Palaeozoic time intervals. In addition, the group has often been used by palaeontologists and stratigraphers in attempts to provide a first age identification for sedimentary successions, in particular when the investigated areas do not contain some of the classical stratigraphical index fossils, like graptolites, conodonts and chitinozoans, or when the rocks are deformed and/or have been subject to low-grade metamorphism, with acritarchs being the only fossil remains preserved (e.g. Benachour 2020).

For the Early-Middle Ordovician, acritarchs currently display a high correlation potential, following detailed reviews of the biostratigraphy of several easily recognizable acritarch taxa. Servais *et al.* (2018) established the basis of a possible biozonation scheme for the Early and Middle Ordovician of the Gondwana area by determining the First Appearance Data (FADs) of selected acritarch taxa. Among the 19 different taxa selected by Servais *et al.* (2018), 12 have been identified in the samples from the southern Montagne Noire (Fig. 5). The presence of these biostratigraphically useful index taxa provides precise information concerning the stratigraphical position of the studied section from the lower part of the Landeyran Formation and from the Cabrières Biota.

As indicated above, the composition of the acritarch associations is approximately the same through the whole Landeyran section, with no clear first appearance being identified, and no indication of a succession of biozones in the investigated section. Some taxa are only present higher in the section, but this is rather an indication of palaeoenvironmental changes (with higher diversities towards the top of the section) than the result of biostratigraphical changes with first occurrences of species within the section, because all taxa identified belong to the same time interval.

Besides some long-ranging taxa, several acritarch taxa present provide stratigraphic information, allowing relatively precise positioning of the samples from the southern Montagne Noire in terms of biostratigraphy and international correlation. The abundance of taxa belonging to the genera *Acanthodiacrodium*, *Stelliferidium*, and *Cymatiogalea*, which all appear around the Cambrian-Ordovician transition (e.g. Vecoli & Le Hérissé 2004), is a first indication that the Landeyran Formation displays a typical Early Ordovician palynoflora. Other more common taxa in the Ordovician are also present, such as the long-ranging species *Polygonium gracile* and *Stellechinatum uncinatum*, which are commonly present in sediments from the late Cambrian to the Late Ordovician, and a display large morphological variability.

In addition, the occurrence in the assemblages of the Montagne Noire of easily identifiable taxa with clearly distinguishable morphologies and well-known FADs provides a more precise age of the investigated samples (Fig. 5). The presence of the *Veryhachium lairdii* and *V. trispinosum* groups, as well as that of the genera *Rhopaliophora* (including the species *R. palmata*), *Peteinosphaeridium, Striatotheca,* and *Coryphidium* indicates that the lower boundary of the Landeyran section must be of late Tremadocian/early Floian or younger age, excluding an early or middle Tremadocian age. Furthermore, the presence of age-diagnostic taxa, such as *Ampullula, Arbusculidium filamentosum, Aureotesta clathrata* var. *simplex, Barakella, Coryphidium bohemicum,* and *Dasydorus*, implies a middle Floian or younger age according to the first FADs identified by Servais *et al.* (2018) at a global scale, because these taxa have never been recorded in older rocks (Fig. 5). Among these taxa, most are commonly found in localities of the southern Gondwana margin, with *Arbusculidium filamentosum, Coryphidium bohemicum,* and *Striatotheca* being diagnostic for the peri-Gondwana province during the Arenigian (Floian–early Darriwilian) (see below). In addition, the presence of *Vogtlandia flosmaris*, previously recorded from the Arenig (Floian) to late Darriwilian (Martin 1978; Molyneux 2009), and *Adorfia hoffmanensis*, so far only known from the late Arenig (Floian) (Tongiorgi *et al.* 1994) to late Darriwilian to early Sandbian (Aráoz 2009), also implies at least a Floian age (or younger) for the sediments. Although the FADs of these two latter species have not yet been clarified, most of their occurrences have been recorded from the middle-late Arenig, which corresponds to a late Floian to an early Dapingian age.

Of particular importance is the fact that typically younger acritarch taxa are missing in the investigated sedimentary succession. This constitutes a further indication, although not proof, of a middle Floian age. Some of the younger age-diagnostic taxa that appear later elsewhere, such as *Arkonia, Dicrodiacrodium, Frankea, Orthosphaeridium* and *Sacculidium* (see Servais 1993, 1997*;* Servais *et al.* 1996; Navidi-Izad *et al.* 2020); have not been recorded in the present study. All these taxa appear typically during the latest Floian or the Middle Ordovician (Dapingian and Darriwilian). Even if their absence in our samples does not provide clear evidence in biostratigraphical terms, the fact that they are all missing in all the samples from the Montagne Noire is an indication that helps to constrain the age of the Landeyran Formation in both the Landeyran section and the Cabrières Biota to an interval that most probably corresponds to the middle-late Floian (Top of Fl2- Base Fl3) (Fig. 5).

Comparison of the age of the palynomorph assemblages with other established biozonations in the Montagne Noire

In the lower Palaeozoic sedimentary successions from the southern Montagne Noire, different studies based on trilobites (Vizcaïno & Álvaro 2003) have assigned two trilobite biozones to the Landeyran Formation: the *Apatokephalus incisus* Biozone for its lower part and the *Hangchungolithus primitivus* Biozone for its upper part. Both of these biozones allow assignment of a late Floian age to the Landeyran Formation.

Moreover, in a study based on graptolites, the biozones of this group are correlated with Floian biozonations around the world, allowing a suggestion of a more precise age (Gutiérrez-Marco *et al.,* this issue). The results indicate the assignment of the levels containing the Cabrières Biota, and by extension the probable age of the samples studied in our study, to the *Baltograptus minutus* graptolite Biozone, which correlates to the late Floian of southern Scandinavia (Maletz 2023).

Both studies on trilobites and graptolites seem to be roughly in concordance with the age assigned to the Landeyran section and the Cabrières Biota by the palynomorphs recorded in the present study. However, slight differences have to be noted. While the graptolite study seems to show clearly a late Floian age, the age range by the palynomorphs assigned to the Cabrières Biota is clearly wider, encompassing the late-middle part of the Floian and the earliest part of the late Floian. Indeed, the absence of genera such as *Arkonia*, *Frankea*, and *Dicrodiacrodium* suggests a minimum age from the samples corresponding to the early part of the Fl3 time slice, although this does not provide strong evidence. Biozonations based on

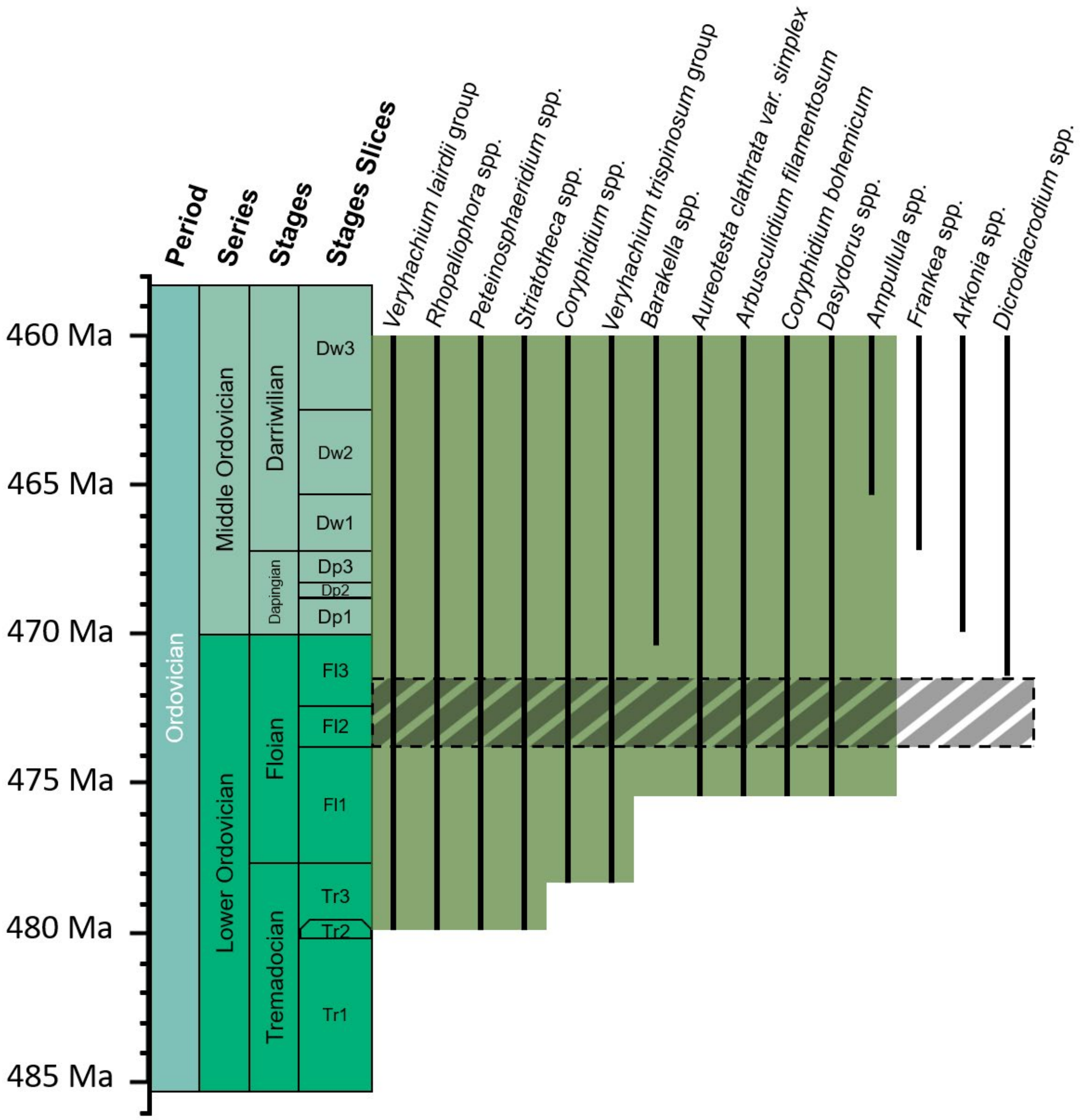

Fig. 5. Age of the samples (band of hatched shading) from the Landeyran section and the Cabrières Biota based on the acritarchs content and the First Appearance Data (FADs) of selected taxa (Figure based and modified from Servais *et al.* (2018). The green shaded area represents the global age range of the taxa identified within the southern Montagne Noire samples, whereas the black lines represent their first occurrences and age range in the South Gondwana province. The first occurences in South Gondwana of the three genera *Frankea*, *Arkonia*, *Dicrodiacrodium* are represented with black lines without any shading as they are all absent from the samples of the present study.

acritarchs remain very rare and therefore the remaining problems in the classification of many taxa and the current knowledge on acritarch biostratigraphy do not enable us for the moment to provide more precise age indications of the sediments based on the palynomorph association alone. In addition to the acritarchs, a biostratigraphical investigation of the chitinozoans would therefore be useful.

A new FAD of Ampullula *in southern peri-Gondwana*

The work of Servais *et al.* (2018) forms a basis for a biostratigraphical scheme, based on the FAD of different genera. However, this database remains incomplete, and the analysis of newly discovered assemblages might change some FADs in the future. In the present study, the presence of *Ampullula* in the samples from the Cabrières Biota and the Landeyran section, from levels that can be attributed to the middle-late Floian, would change the first occurrence of this genus in the southern part of Gondwana. Although *Ampullula* has already been known from the middle Floian elsewhere in the world, its earliest occurrence in the southern part of Gondwana is so far only from the Dapingian at Mýto near Rokycany in Bohemia, Czech Republic (Vavrdová 1990).

The genus *Ampullula* Righi, 1991, was revised by Yan *et al.* (2010), allowing the distinction of six species, including some new combinations: *A. calix* (Quintavalle & Playford, 2008); Yan *et al.*, 2010*, A. composita* (Yin *et al.*, 1998) Yan *et al.*, 2010; *A. crassula* (Vavrdová, 1990) Yan *et al.*, 2010*; A. erchunensis* (Fang, 1986), Brocke, 1997 *emend. nov.* Yan *et al.*, 2010*, A. princeps* (Brocke, 1997) and *A. suetica* Righi, 1991. Found in Baltica and all around the peri-Gondwana province, the genus is present in a wide range of climatic zones from tropical zones, warm-temperate and even cold-temperate water environments during the late-Early and Middle Ordovician. Its palaeoenvironmental range along the continental margin is also wide, making it a eurytopic microfossil (Yan *et al.* 2010). The records of the genus remain rare in the Mediterranean subprovince ('southern' Gondwana), being only represented by the species *A. crassula* in the Dapingian of Bohemia. The lack of records of the genus from other localities is surprising, because this would suggest that the genus is present in the southernmost part of the Gondwanan margin for the first time only around 6 to 7 Myrs after its appearance in all other palaeobiogeographical provinces (Eastern and Western Gondwana, South China and Baltica). Indeed, the first peri-Gondwana appearance of the genus is recorded from the middle Floian in the Yangtze Platform, while in Argentina, Pakistan, Russia, Poland and even Turkey this taxon appeared in the late Floian (Yan *et al.* 2010). The presence of the genus in the assemblages of the Montagne Noire in this study is thus significant for biostratigraphical considerations.

Ampullula crassula has been recovered from the Yangtze Platform in South China (Yan *et al.* 2010); the Łeba area in Poland (Baltica) (Raevskaya *et al.* 2004); Pakistan (East Gondwana) (Quintavalle *et al.* 2000) and Argentina (West Gondwana) (Achab *et al.* 2006); but also from southern Gondwana in the Mýto area (Bohemia, Czech Republic) (Vavrdová 1990). In all areas where it has been previously recorded, except from Bohemia, the species appeared during the late Floian, in the *deflexus* or *suecicus* graptolite biozones, and even earlier (Fl2) in South China. Thus, the observation of the species *A. crassula* in the middle to late Floian of the southern Montagne Noire and thus in the south peri-Gondwana province conforms to its global FAD (middle Floian). The presence of *Ampullula* in southern France in the middle to late Floian thus strengthens the biostratigraphical significance of the genus, with a high potential for global correlation.

Comparison with previous palynomorph studies in the Montagne Noire

Although first publications on acritarchs from the Montagne Noire date from the 1940s, with the first studies by Deflandre (1942, 1945), papers describing palynomorph assemblages from the southern and northern Montagne Noire in more detail were only published during the 1970s and early 1980s (Martin 1972; Rauscher 1971, 1974; Fournier-Vinas & Donnot 1977; Fournier-Vinas 1978), documenting assemblages from the Cambrian-Ordovician boundary to the Middle Ordovician.

Among the samples studied by Martin (1972), those from Col de Sainte Colombe in the Mont de Pardailhan Unit are from sections bearing the Cambrian *Paradoxides* sandstone and the Tremadocian red layers with *Euloma* (Boyer & Guiraud 1964) that helped to locate the Cambrian-Ordovician boundary in the area. Despite being highly degraded and poorly diverse, with only 13 species identified in total (8 maximum per sample), these Cambrian-Ordovician assemblages from the Montagne Noire were dominated by *Micrhystridium*, *Priscogalea* and *Acanthodiacrodium*. The sedimentary layers from this period are characterized by an important transition from slope deposits to sandy shoals in the southern Montagne Noire (Álvaro *et al.* 2003). However, the Mont de Pardailhan Unit is considered to have been at that time rather in a distal setting (Álvaro *et al.* 2003, 2008). The high degradation might be a reason for a loss of much acritarch data because they are either too opaque or too deteriorated. To date, the description of Cambrian-Ordovician boundary interval palynomorphs remains rare in the southern Montagne Noire.

Most of the other assemblages described from the southern Montagne Noire were collected from the Écailles de Cabrières (Roquemaillère, Roque de Bandies, Mougno, Castelec, Grange du Pin, Sainte Cécile) by Martin (1972) and Rauscher (1971, 1974) and were assigned to the Tremadocian. Despite the presence of long-ranging taxa in the previously described Tremadocian assemblages and in the newly studied Floian samples, significant differences were identified between Tremadocian and Floian associations by these authors in the 1970s. Tremadocian palynofloras are characterized by a strong domination of diacromorphs with significant abundance and diversity of species of the genus *Acanthodiacrodium*, such as *A. angustum*, *A. simplex*, *A. hamatum* and *A. ubui*. This observation is characteristic of the Tremadocian in France in general (Rauscher 1974). Abundant *Micrhystridium*, *Priscogalea*, common *Cymatiogalea*, *Stelliferidium*, very rare to absent *Veryhachium*, and rare *Baltisphaeridium*, *Goniosphaeridium*, *Cymatiosphaera*, *Dasydiacrodium*, and sphaeromorphs were also identified. Based on a palynoflora from the Montagne Noire, Rauscher (1974) characterized the Tremadocian Stage with genera either found later in the Floian, like *Acanthodiacrodium*, *Cymatiogalea*, *Stelliferidium*, or with genera not found in the samples from the present study, such as *Vulcanisphaera* and *Impluviculus*. Although the Écailles de Cabrières are known for bearing fossil assemblages that differ from those of other units of the Montagne Noire (Colmenar *et al.* 2013, Álvaro *et al.* 2016, 2018; Lefebvre *et al.* 2023), suggesting a different geological context, the presence of rather diverse and abundant forms of *Acanthodiacrodium* specimens in the samples from the Tremadocian of the Écailles de Cabrières and the Floian of the Mont Peyroux and Pic de Vissou units implies that both localities studied were part of the peri-Gondwana province during the Early Ordovician (see palaeobiogeography section below).

In this study, the Floian samples were collected from the section bearing the Cabrières Biota, and from the Landeyran section which had already been partly studied by Rauscher (1971, 1974). Therefore, our work can be considered as an update to the knowledge of the acritarch assemblages from the Floian (corresponding more or less to the earlier parts of the Arenigian) in the southern part of the Montagne Noire. The common occurrence of *Striatotheca*, rectangular and triangular *Veryhachium*, *Polygonium gracile*, *Baltisphaeridium* including *Baltisphaeridium klavabense*, the presence of *Peteinosphaeridium* and diacromorphs like *Arbusculidium*, the identification of *Coryphidium* (*Coryphidium bohemicum*), and the rarity of netromorphs and galeates are the most important features identified by Rauscher (1971, 1974) to characterize the 'Arenigian' of the southern Montagne Noire. All these main features have been identified in the samples investigated in the present study, thus confirming the observations made by Rauscher (1971, 1974). Furthermore, Rauscher (1971, 1974) had already noted in the 1970s the strong similarities between the Floian assemblages from the Montagne Noire and those described in Bohemia (Vavrdová 1965). Our study also confirms these affinities with the Bohemian assemblages described by Vavrdová in numerous papers (Vavrdová 1965; 1973; 1997).

However, in his description of the section within the Landeyran Valley, Rauscher (1971) documented only a single assemblage without showing any evolution of acritarch associations as highlighted in the present study. The reason is possibly that Rauscher's (1971) material was not very well preserved and did not allow counts of hundreds of specimens per slide. It is not clear where exactly the samples from Rauscher (1971) were collected in the formation. Common features between the results from the present study and that of Rauscher (1971) are the presence of abundant *Baltisphaeridium* and *Polygonium*, as well as the record of the characteristic taxa *Arbusculidium filamentosum* and *Cymatiogalea*, and abundant *Striatotheca* and *Veryhachium*. The common presence of *Baltisphaeridium*, *Veryhachium* and *Striatotheca*, as well as the rarity of galeates and netromorphs, noted by Rauscher (1971), is characteristic of the samples of the upper part of the Landeyran section. As a consequence, the samples described by Rauscher (1971) possibly come from the upper part of the Landeyran section as investigated here, or from even higher levels not studied in the present work (uppermost part of the *A. incisus* trilobite zone or *H. primitivus* trilobite zone).

Although some samples from the Écailles de Cabrières were assigned a late Arenigian to Llanvirnian age by Martin (1972), their compositions are different from those of our study, with occurrences of the genus *Dicrodiacrodium*, absent from all the samples of the present study. The FAD of this genus is in the latest Floian (Servais *et al.* 2018), suggesting that the samples from the Cabrières area described by Martin (1972) are slightly younger than those studied in the present work, probably coming from another tectonic unit.

Palaeobiogeography

The study of acritarch diversity during the early Palaeozoic has allowed the identification of different phases within the evolution of organic-walled phytoplankton. Although affected by possible sampling bias around the end of the Middle Ordovician, the Dapingian has been identified as the period with the highest phytoplanktonic diversity of the Palaeozoic, following an especially strong diversification between the late Cambrian and the Middle Ordovician (Kroeck *et al.* 2022; Shan *et al.* 2022). However, the assemblages from this period not only revealed a high diversity but also a strong provincialism of the microfloras that seems to be at its maximum during the Early– Middle Ordovician. Acritarch provincialism and the separation into different palaeobiogeographical units appear to be less pronounced during the Cambrian and decreased again during the Late Ordovician (Servais *et al.* 2003; Molyneux *et al.* 2013; Manzano *et al.* 2025). Different palaeogeographical and palaeoenvironmental factors, such as oceanic currents, water chemistry, nutrient availability, sea-level change and the distribution of the different continental masses have been identified as possible drivers for the distribution of acritarch assemblages and taxa (Molyneux *et al.* 2013; Manzano *et al.* 2025).

Because palaeobiogeographical provinces, as all palaeobiogeographical units, are based on the degree of endemism of the taxa present, their definition depends also on the data available. As a consequence, areas that are not or only poorly sampled will not bear enough data to provide any relevant palaeobiogeographical information, and thus might be neglected. Two very well recognized palaeobiogeographical provinces have been established thanks to an important sampling, the Baltic and the peri-Gondwana province (Servais *et al.* 2003; Vecoli & Le Hérissé 2004; Molyneux *et al.* 2013), but hypotheses of other palaeobiogeographical units for the acritarchs of the Early-Middle Ordovician have emerged (Servais *et al.* 2003; Molyneux *et al.* 2013; Manzano *et al.* 2025). The Baltic province has been defined as a province of mixed cold and warm-water environments located in medium to high southern latitudes (between 30°S and 60°S). The peri-Gondwana province is currently considered as a very large palaeoprovince extending around the margin of Gondwana from Argentina to South China, including many localities from South America, eastern Newfoundland, North Africa, central and southern Europe, southern Turkey, Jordan, Iran, Pakistan, and others (Servais *et al.* 2003, fig. 2; Molyneux *et al.* 2013, fig. 23.5; Kroeck *et al.* 2020, fig. 4).

In addition to these two main Early-Middle Ordovician palaeobiogeographical provinces, three possible 'warm-water' provinces have been identified by Playford *et al.* (1995): North America (Laurentia), North China and Australia. These were regrouped into one main warm-water province by Volkova (1997) based on different data. The latter definition of the 'warm-water' province was based on the presence of genera like *Aryballomorpha, Athabascaella*, *Corollasphaeridium, Goniomorpha,* and *Lua* during the latest Tremadocian (Volkova 1997), while the identification of the subdivisions of this warm-water province was based on the recognition of particular *Peteinosphaeridium* species from the Arenigian to the Caradoc and the absence of diacromorphs (Playford *et al.* 1995). The existence of this Tremadocian province is currently questioned, as it was actually based on the occurrence of taxa of which the distribution remains poorly known. *Corollasphaeridium* is actually not phytoplanktonic, but can now be related to the Small Carbonaceous Fossils (SCFs), being possibly a loricate protist (Green *et al.* 2025). *Goniomorpha* is also clearly related to the SCFs, representing the teeth of priapulid worms (Shan *et al.* 2023). Both *Corollasphaeridium* and *Goniomorpha* are thus not acritarchs *sensu stricto* (displaying a central vesicle), and should not be related to the phytoplankton, and thus not to phytoplanktonic provinces. In addition, they remain rarely described and they are not just present in areas related to the warm-water environments of the Tremadocian, but appear to be much more cosmopolitan (Shan *et al.* 2023; Green *et al.* 2025). Similarly, *Aryballomorpha* is currently under revision and this genus appears also to be more widespread than previously thought, with occurrences in high latitudes. The main characteristic features of *Aryballomorpha* are similar to those of *Athabascaella*. This latter genus has been found in southern Gondwana and thus in high latitudes by Vecoli & Le Hérissé (2004), after being considered for a long time as typical of warm-water environments, following the definition of the 'warm-water' province by Volkova (1997). The peteinoid acritarchs also need a complete revision. It is difficult to discern the different species and subspecies, which possibly cannot serve as palaeobiogeographical markers (Kroeck *et al.* 2021) as a consequence, and the recognition of species of *Peteinosphaeridium* considered as diagnostic for different sub-units of a warm-water province, as suggested by Playford *et al.* (1995), is today questionable.

The Baltic (Baltica) province was first defined by Vavrdová (1974) and then redefined by Tongiorgi & Di Milia (1999). This province seems to be lacking clear typical (endemic) acritarch taxa. Bearing many cosmopolitan species and genera, the Baltic province was considered to contain no diacromorph acritarchs and to display specific taxa of the genus *Peteinosphaeridium*, such as *P. bergstroemii* and *P. hymeniferum* (but see above for the limited use of peteinoid acritarchs for palaeobiogeography), as well as species of the genus *Pachysphaeridium*, as possible marker species (Vecoli & Le Hérissé 2004).

Finally, the peri-Gondwana province, originally described as the 'Mediterranean Province' (limited to only southern and central Europe) by Vavrdová (1974), bears as major palaeobiogeographic markers the genera *Arbusculidium, Coryphidium,* and *Striatotheca* (Li 1989), and an important diversity of diacromophs, such as *Acanthodiacrodium and Dasydiacrodium* (Albani 1989). This province was long considered to be of 'cold-water' environments in high latitudes (but see discussion in Li & Servais 2002).

The presence of different species of *Acanthodiacrodium*, *Arbusculidium*, *Coryphidium* and *Striatotheca* is a very clear indicator for an attribution of the Montagne Noire samples to the palaeobiogeographical peri-Gondwana province (Albani 1989; Li 1989; Servais *et al.* 2003; Molyneux *et al.* 2013; Manzano *et al.* 2025). The plotting of the province on a palaeogeographic reconstruction of the Floian clearly confirms that the Montagne Noire belongs to this palaeobiogeographical unit (Fig. 6).

Most interestingly, Playford *et al.* (1995) proposed a subdivision of the peri-Gondwana province into three subprovinces: the 'Mediterranean' (corresponding to the primary definition of the province by Vavrdová 1974), the 'South America,' and the 'South China' subprovinces. In order to define precisely this 'Mediterranean' subprovince, Vavrdová (1997) subsequently identified 16 diagnostic taxa from an assemblage from the 'Arenigian' of Bohemia, called the '*Coryphidium bohemicum* assemblage.' Among these 16 taxa, most are identified in the samples from the Montagne Noire, including: *Adorfia hoffmanensis, Arbusculidium filamentosum, Aureotesta clathrata* var. *clathrata, A. clathrata* var. *simplex* (formerly *Marrocanium simplex*), *Coryphidium bohemicum, Cymatiogalea granulata, Pirea, Striatotheca principalis,* and *Vogtlandia multiradialis*. These findings clearly allow assignment of the palynoflora from the late Early Ordovician from the Cabrières Biota and the base of the Landeyran Formation to the Mediterranean subprovince within the peri-Gondwana acritarch palaeoprovince. However, most of these taxa, such as *Coryphidium bohemicum*, *Cymatiogalea granulata*, *Aureotesta clathrata* var. *clathrata* and *A. clathrata* var. *simplex* (Brocke *et al.* 1997), have now also been found all around peri-Gondwana (from Argentina to South China) reducing the relevance of the identification of such an assemblage to identify specifically the very high palaeolatitudes of the peri-Gondwana province. Among the different subprovinces from the peri-Gondwana province, the South America and South China subprovinces are also known to bear a mix of acritarchs with different palaeobiogeographical affinities. Although the peri-Gondwana acritarchs are the main representatives of these subprovinces, Baltic and Australian influences have been identified in significant proportions (Molyneux *et al.* 2013). The Baltic and Australian representatives listed by Molyneux *et al.* (2013) have, however, for most of them, not been identified in the samples from the

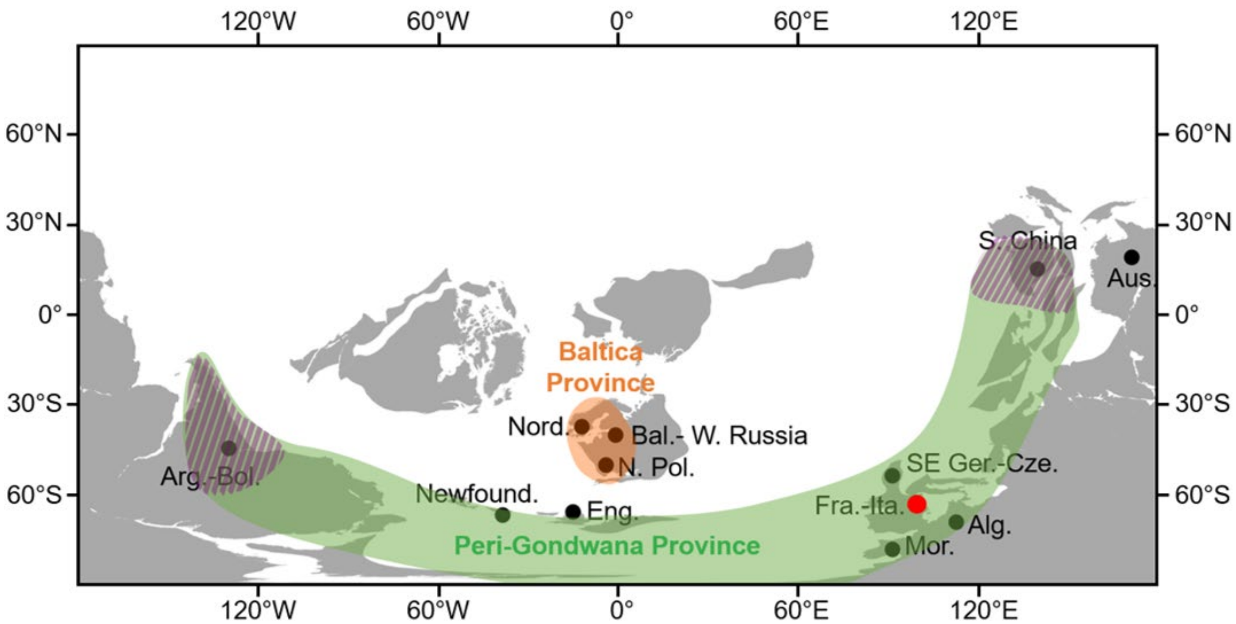

Fig. 6. Floian (475 Ma) palaeogeographical reconstruction with the location of the Baltica Province (Nord.: Norway, Denmark, Sweden; Bal.-W. Russia: Estonia, St. Petersburg area, Finland; N. Pol.; northern Poland), and the peri-Gondwana Province, including Eastern Gondwana (Arg.-Bol.: Argentina, Bolivia, Columbia), Western Gondwana (S. China: southern China), Northern Gondwana (Aus.: Australia), and the 'southern peri-Gondwana subprovince' (Newfound.: Newfoundland; Eng.: England, Wales, Ireland; Fra.-Ita.: southern France, Sardinia.; SE Ger.-Cze: south-eastern Germany and the Czech Republic; Mor.: Morocco; Alg.: Algeria) Reconstruction based on the PALEOMAP project (Scotese & Wright, 2018).

Montagne Noire. In conclusion, the Montagne Noire assemblage investigated in this study seems to be typical for the high palaeolatitude 'Mediterranean' subprovince (central and southern Europe, Turkey, but also Belgium, Germany and southern Britain).

In addition, although the genera *Ampullula* and *Rhopaliophora*, that are both found in the Montagne Noire, were long considered to be more typical of warm-water environments and therefore lower latitudes (Li & Servais 2002; Achab *et al.* 2006), the subsequent revisions of both taxa, respectively made by Yan *et al.* (2010) and Li *et al.* (2014), have highlighted their presence in a very wide area, including the 'Mediterranean' subprovince. Therefore, the presence of *Rhopaliophora palmata* and *Ampullula crassula* is not that surprising. *Rhopaliophora palmata* had prior records from Baltica (Raevskaya *et al.* 2004), South China (Brocke *et al.* 2000; Li *et al.* 2010), Australia (Playford & Martin 1984; Quintavalle & Playford 2006) and in a wide range of localities from the peri-Gondwana province, including Bohemia (Fatka 1992) and North Africa (Vecoli 1999; Vecoli & Le Hérissé 2004). *Ampullula crassula*, on the other hand, was recorded so far from South China (Yan *et al.* 2010), South America (Argentina) (Achab *et al.* 2006) and the Mediterranean (Bohemia) subprovince (Vavrdová 1990), but also from Baltica (Poland) (Raevskaya *et al.* 2004). The presence of these taxa in the samples from the Landeyran section and from the Cabrières Biota does therefore not necessarily imply a warm-water environment or a low-latitude setting for the assemblage of the Montagne Noire.

Conclusions

Our study of the palynomorphs from the Landeyran section and the Cabrières Biota in the southern Montagne Noire (France) allows a number of conclusions. First, the diverse, abundant and fairly well-preserved acritarch microflora described provide important biostratigraphical information. The presence of typically Lower-Middle Ordovician taxa like *Arbusculidium filamentosum, Barakella felix, Coryphidium bohemicum, Peteinosphaeridium, Rhopaliophora, Striatotheca,* the *Veryhachium lairdii* and *V. trispinosum* groups, associated with the absence of genera such as *Arkonia, Frankea* and *Orthosphaeridium*, allows assignment of a middle to late Floian age (Fl2-Fl3) to the levels studied. This confirms the age information provided by graptolites and trilobites. Moreover, the presence of *Ampullula* in the samples suggests a new First Appearance Datum of this genus in the southern Gondwana area (central and southern Europe).

In terms of palaeobiogeography, the diverse assemblages are typical of the peri-Gondwana acritarch province, with the presence of diagnostic taxa such as *Arbusculidium, Coryphidium, Striatotheca* and abundant *Acanthodiacrodium*. More precisely, the samples contain the presence of almost all the typical taxa of the 'Mediterranean' subprovince. Indeed, the present study has shown that the assemblages from Bohemia and Montagne Noire are very similar.

Not studied for over four decades, the palynomorph assemblages from southern France also provide up-to-date middle to late Floian acritarch data and therefore a better understanding of the evolution of this palynoflora in this area.

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