Biostratigraphy, taxonomic diversity and patterns of morphological evolution of Ordovician acritarchs (organic-walled microphytoplankton) from the northern Gondwana margin in relation to palaeoclimatic and palaeogeographic changes

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Abstract

Acritarchs, the fossilizable, resting cysts of phytoplanktonic algal protists, are the dominant component of marine organic-walled microfossils in the Palaeozoic. The majority of acritarchs show strong similarities with dinoflagellate cysts in morphological and biogeochemical features, as well as distributional patterns in the sediments. The production of these organic-walled microfossils and their distribution and survivorship in the sediments were controlled by differences in ecological tolerances and life cycle (autecology) of the planktonic parent organisms.

Calculation of evolutionary rates and development of a detailed diversity curve at specific level, form the basis for discussing the influence of global palaeoenvironmental perturbations on the evolution of organic-walled microphytoplankton in northern Gondwana during latest Cambrian through Ordovician times. The potential of acritarchs for biostratigraphic correlation at the regional scale (northern Gondwana domain) is much improved by our detailed revision of distributional patterns of 245 acritarch taxa.

The most important Cambro-Ordovician acritarch bio-events are short periods of diversification, which also correspond to introduction of morphological innovations, observed in latest Cambrian and earliest Tremadoc, late Tremadoc, early Arenig, basal Llanvirn, and latest Ashgill, and an important extinction phase in the early Caradoc. Overall, acritarch diversity increased from the basal Ordovician up to the middle Llanvirn, then declined in the early and middle Caradoc. During Ashgill times, the assemblages are poorly diversified at the generic level as a result of a combined effect of sea level drawdown and onset of glacial conditions, but no major extinction event is observed in connection with the end-Ordovician biotic crisis. The peak in acritarch diversity during Middle Ordovician times appears to be correlated to maximum spread of palaeogeographical assembly.

Acritarch dynamics appear largely uncorrelated to second order sea-level oscillations; the primary abiotic controls on acritarch evolution were palaeogeographical and the associated palaeoceanographic changes (especially during Middle Ordovician), and the end-Ordovician palaeoclimatic shift.

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The acritarch fossil record provides important information on the evolution of oceanic primary producers, however, the relationships between acritarch diversity, oceanic productivity, and evolution of invertebrate animals are proving much more complex than previously thought. In particular, the hypothesis of a causal relationship between changes in acritarch diversity and metazoan evolution in the Palaeozoic is not supported by our data.

1. Introduction

During latest Cambrian through Ordovician times, profound biological and environmental changes affected Earth's biosphere and geosphere. The Ordovician fossil record shows evidence of the most rapid, long sustained burst of biotic diversification in the history of marine life on Earth (The Great Ordovician Biodiversification Event, Webby et al., 2004;). Radiation events during Early and Middle Ordovician caused the tripling of marine biodiversity and the establishment of Palaeozoic and Mesozoic evolutionary faunas which have the greater relevance to present-day biotic communities (Miller and Foote, 1996; Droser and Sheehan, 1997; Miller, 1997). The Ordovician ended with a major climatic change, marked by the development of a glaciation centered on the Gondwana supercontinent (Beuf et al., 1971; Brenchley, 1988). The above described ecological changes were associated, throughout the Ordovician, to intense tectonic activity and major re-organization of the plate-tectonic global assembly (Scotese and McKerrow, 1991; Dalziel, 1997). The Ordovician palaeogeographic evolution includes: the fragmentation of the northern margin of Gondwana and subsequent migrations of microcontinents (e.g., Avalonia), the northward drifting of Baltica from high southern latitudes to southern subtropical latitudes, the origination and subduction of short-lived oceanic basins (e.g., the Tornquist Ocean), the shrinking of the Iapetus Ocean, and continental accretions (Berthelsen, 1992; Dalziel, 1997: Winchester et al., 2002).

The parallelism between increased rates of tectonic activity, ecological changes, and patterns of radiations and extinctions has suggested the existence of causative relations between internally driven physical modifications in the geosphere (i.e., geodynamic activity) and biological changes occurring on Earth surface (Miller and Mao, 1995; Dalziel, 1997). In support of such hypotheses, recent analyses of patterns of faunal variation at spatial and temporal scales seem to reveal possible linkages between the Ordovician diversification events and the contemporaneous increased global levels of mountain-building (Miller and Mao, 1995; Miller, 1997).

Early Palaeozoic biodiversity, speciation, and extinction trends have been thoroughly investigated and accurately described for many of the major groups of marine invertebrate metazoans (e.g., Barnes et al., 1996). Much less is known about the dynamics of biodiversification of ancient phytoplanktonic associations, represented in the fossil record by organic-walled microfossils including acritarchs and other microalgal groups contained in Palaeozoic marine sedimentary rocks. The acritarchs are *incertae sedis* by definition. In spite of uncertainties regarding their precise biological alliances, acritarchs are now considered to represent, in their majority, the resting cysts of algal protists (Tappan, 1980; Martin, 1993; Colbath and Grenfell, 1995; Strother, 1996). Morphological characteristics, biogeochemical properties (Moldowan and Talyzina, 1998) and mode of occurrence in the marine sedimentary record of the acritarchs are very close to those of the dinoflagellate cysts. Other organic walled microfossils generally associated with the acritarchs (also called ''allied forms'') have been assigned to the phycomata stages of various chlorophycean algae, e.g., hydrodictyaceae and Prasinophyta (Colbath and Grenfell, 1995). As such, acritarchs and allied forms provide indirect but valuable information about the marine primary producers which, together with cyanobacteria, were at the base of the marine trophic web during Proterozoic and Palaeozoic times. The impact of marine photosynthetic algae on production of atmospheric oxygen, total biomass accumulation, and the global carbon cycle was probably much higher in Cambrian to Ordovician times than in following periods, since emerged lands

were almost devoid of vegetation cover. Oscillations in the density of marine microphytoplankton were probably not only responsible for the fluctuations of food availability for the higher-level organisms within the global trophic chain, but also influenced global climatic changes, indirectly regulating the accumulation of greenhouse gases in the atmosphere.

Only a few published studies are devoted to the analysis of acritarch diversity. Tappan and Loeblich (1973) plotted the number of described species of acritarchs per geological period, showing their predominance among major phytoplanktonic groups during Palaeozoic times, their increasing diversity from Precambrian to Silurian followed by a marked decrease at the Devono-Carboniferous boundary, and their replacement by the dinocysts from the late Triassic to the present. The complete catalogue of acritarch species for all the geological epochs compiled by Fensome et al. (1990) was used by Strother (1996) to plot the number of all validly published genera per million year. This distribution of genera over time confirmed the general temporal trend already described by Tappan and Loeblich (1973). Strother (1996) also plotted the number of acritarch species versus time (Cambrian to Devonian) using the old dataset of Downie (1984) on the distribution of acritarchs in the British Isles. In this case, he obtained a non-normalized curve showing two distinct diversity peaks in the Llanvirn (Middle Ordovician, 70 species) and in the Wenlock (Early Silurian, 90 species), and two main periods of very low specific diversity in the Ashgill (latest Ordovician, 10 species) and at the base of the Downtonian (latest Silurian, ca. 20 species). These data must be treated with some circumspection taking account of their large degree of synthesis and because they were derived from obsolete sources. A more recent work on acritarch diversity by Vidal and Moczydlowska-Vidal (1997) concerned Proterozoic and Cambrian global acritarch biodiversification trends. A further short paper by Kaljo et al. (1995) briefly described Middle to Late Ordovician acritarch and chitinozan diversity patterns derived from the study of a single sedimentary succession (Rapla borehole) in Estonia.

Under the IGCP 410 project, preliminary results of a study aiming at the complete survey of Ordovician acritarch diversity did not lead to the construction of a reliable acritarch global diversity curve due to prob-

lems encountered in assembling, correlating, and interpreting geographically sparse, stratigraphically poor-constrained, and taxonomically inconsistent data (Servais et al., 2004). Therefore, one of the recommendations issued by the ''acritarch clade'' of the IGCP 410 project was that before attempting to elaborate a global picture of Early Palaeozoic microphytoplankton diversification, emphasis should be placed in the study of regional trends of acritarch diversification, at least at the level of single palaeobiogeographic provinces. In addition, recent studies by Miller and Mao (1995) and Miller (1997) showed that organismal diversity trajectories can be strongly dependent by geological processes acting on restricted areas so that biotic diversification phenomena are better analyzed on the basis of palaeogeographically and palaeoenvironmentally homogeneous datasets rather than on global compendia.

In the present study (based primarily on original investigations and complemented with selected published data), we attempt to reconstruct the Ordovician diversification history of acritarchs from the northern Gondwana margin (Figs. 1 and 2). This region includes the stable cratonic basins of North Africa (North Sahara Platform), and a series of microcontinents (''terranes'') of Gondwanan affinity (e.g., with a Pan-African consolidated crystalline basement), plus Turkey and Saudi Arabia. We propose: (1) an up-to-date, synthetic acritarch diversity curve for the Ordovician of the region; (2) a description of the main phases of acritarch evolution based on the identification of successive origination (introduction of new species and innovative morphologies) and extinction events; and (3) a discussion of possible palaeoecological meaning of such diversification patterns.

2. Palaeobiogeographic setting

2.1. Palaeogeography

During Ordovician times, North Africa constituted a vast intracratonic platform forming an integral part of the huge Gondwana continent (Figs. 1 and 2). The Ordovician palaeogeographical position of North Africa is known with a good degree of precision, especially if compared with other portions of Gondwana (e.g., South China). Apart from minor discrep-

c) Early Ashgill, ca. 445 M.y.

b) Early Llanvirn, ca. 465 M.y.

a) Early Tremadoc, ca. 490 M.y.
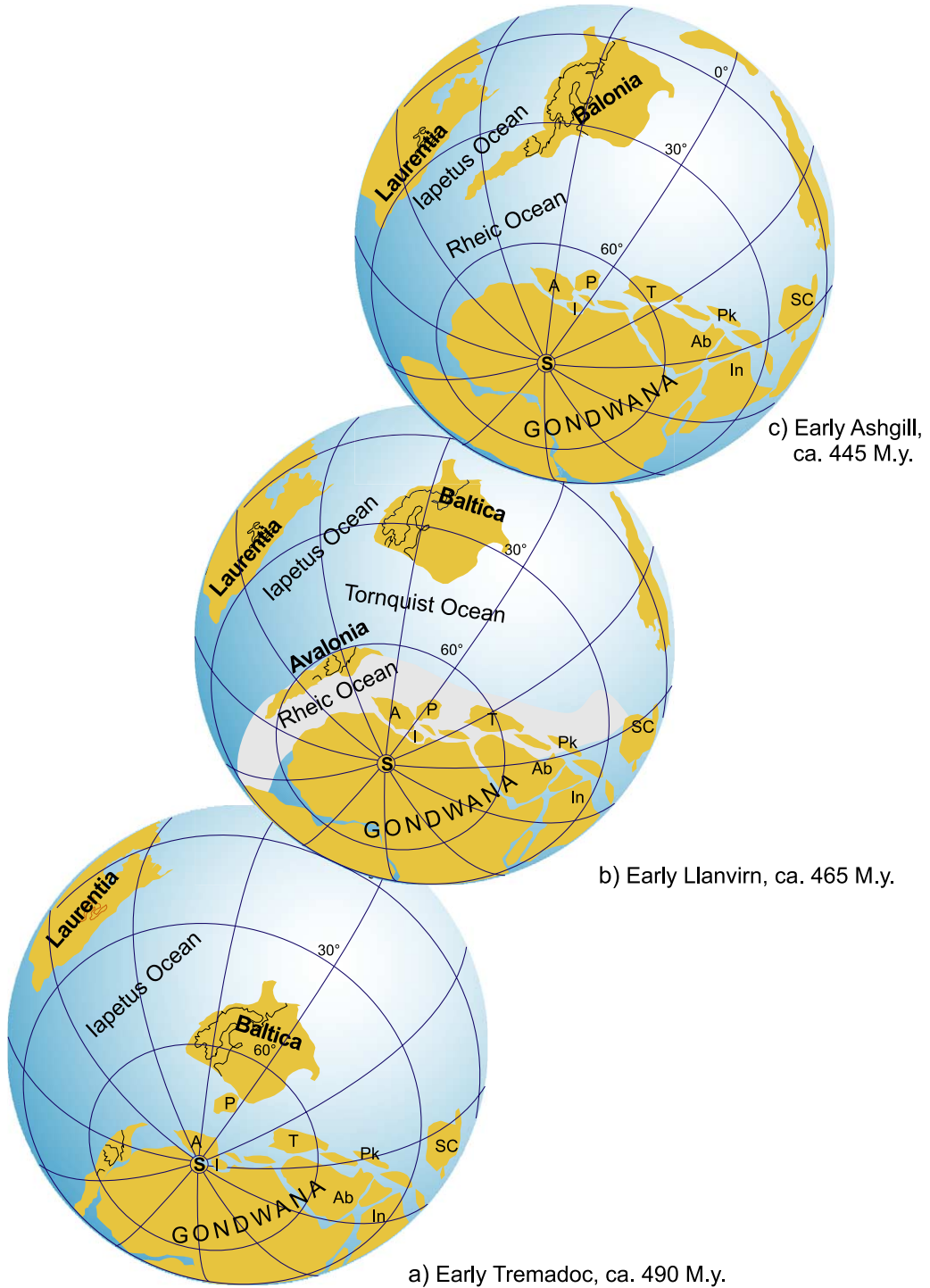
ancies, all the widely accepted palaeogeographic reconstructions, based on palaeomagnetic (Torsvik and Trench, 1991; Torsvik et al., 1992), palaeontological (Erdtmann, 1998; Paris, 1998), lithological (Scotese and Barret, 1990; Scotese et al., 1999); and geodynamical (Williams, 1997) data, as well as maps developed on the basis of the integration of multidisciplinary data (e.g., Scotese and McKerrow, 1990, 1991), place present-day North Africa within circumpolar regions during Cambro-Ordovician times. Uncertainties exist on the exact position and movement of the South Pole, but the prevailing opinion is that the North African part of Gondwana remained within the antarctic Polar Circle (60° Lat S) during the entire Ordovician, while moving northwards at a high drifting speed (10 cm year^{-1}; Pharaoh, 1999).

Avalonia (Figs. 1 and 2) was first defined by Cocks and Fortey (1982) on the basis of its sequence of Cambrian to Silurian faunas. Existing European terranes with Avalonian faunal assemblages include part of northern Germany, all of Belgium, England and Wales, and southern Ireland (East Avalonia). The Avalonian faunal assemblages have a high-latitude (Gondwanan) affinity prior to the Llanvirn, and a warm temperate character in the Late Ordovician (Cocks and Fortey, 1982; Cocks et al., 1997). The crystalline basement of Avalonian terranes has definite Cadomian consolidation ages, confirming the Gondwanan origin of Avalonia (Pharaoh, 1999). Changes from dominantly Gondwanan faunas to more Baltic-like assemblages start from Caradoc times (Cocks et al., 1997; Samuelsson et al., 2001; Vecoli and Samuelsson, 2001). Palaeomagnetic reconstructions substantiate the latitudinal changes suggested by the faunas, showing a northward drift of Avalonia from 60° S in Early Ordovician to ca. 30°S by Early Silurian (Trench and Torsvik, 1992; Pharaoh, 1999). The northwards drift of Avalonia during the Ordovician was driven by subduction of the Tornquist Ocean (a part of the Iapetus Ocean), and the opening of the Rheic Ocean behind the Avalonian trailing edge

(Cocks and Fortey, 1982; Pharaoh, 1999). Due to the closure of the Tornquist Ocean, Avalonia collided with Baltica in latest Ordovician times (Ashgill; Cocks et al., 1997; Vecoli and Samuelsson, 2001).

The Palaeozoic Massifs of central and southern Europe (e.g., Armorican Massif, Bohemian Massif, the Iberian Peninsula; Figs. 1 and 2), comprising the Variscan orogen are considered as tectonostratigraphic entities (crustal blocks plus their sedimentary cover) originated from the fragmentation of the northern margin of Gondwana. The areal extension, tectonic history and significance, and even the terminology applied to these terranes, are objects of much controversy (e.g., Paris and Robardet, 1990; Havlíček et al., 1994; Erdtmann, 1998; Paris, 1998; Pharaoh, 1999), but there is general agreement in considering these microplates located at high-latitude palaeopositions adjacent to the North African margin of Gondwana during the entire Ordovician (Figs. 1 and 2). A possible exception is constituted by the microplate Perunica, defined by Havlíček et al. (1994) as corresponding to the Bohemian Massif, which according to macrofaunal evidence, was located in intermediate to lower latitudes, closer to Baltica than to Gondwana during Tremadoc times. In post-Tremadoc times, however, Perunican macro-, microfaunal and microphytoplankton assemblages show clear northern Gondwanan affinities (Vavrdová, 1974; Havlíček et al., 1994). Turkey and Arabia are also considered as separate tectonostratigraphic units, parts of a larger composite terrane named Cimmeria, positioned along the northern margin of Gondwana from Cambrian through Carboniferous times, in a more easterly position with respect to the North African margin (Scotese and McKerrow, 1990 and references therein).

In summary, according to the above discussion, the localities considered in the present study (North Africa, the Central European terranes, Turkey, and the Arabian peninsula), all have a Gondwanan palaeogeographical affinity and share essentially the same geodynamic setting and evolution; these localities

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Fig. 1. Palaeogeographic evolution of Gondwana, Baltica, and Laurentia and the surrounding ocean basins from earliest to latest Ordovician times. Drifting paths and rotation of Baltica and Laurentia from Berthelsen (1992); position and geography of northern Gondwana terranes from Scotese and McKerrow (1991); drifting path of Perunica from Havlíèek et al. (1994); position and drifting path of Avalonia from Cocks and Fortey (1982), Cocks et al. (1997), Berthelsen (1992), and Vecoli and Samuelsson (2001). Key to symbols: A, Armorica; P, Perunica; I, Iberia; T, Turkey; Ab, Arabia; Pk, Pakistan; In, India; SC, South China; S, South Pole. The shaded area in diagram (b) indicates the extension of the Middle Ordovician Peri-Gondwana Acritarch Province.
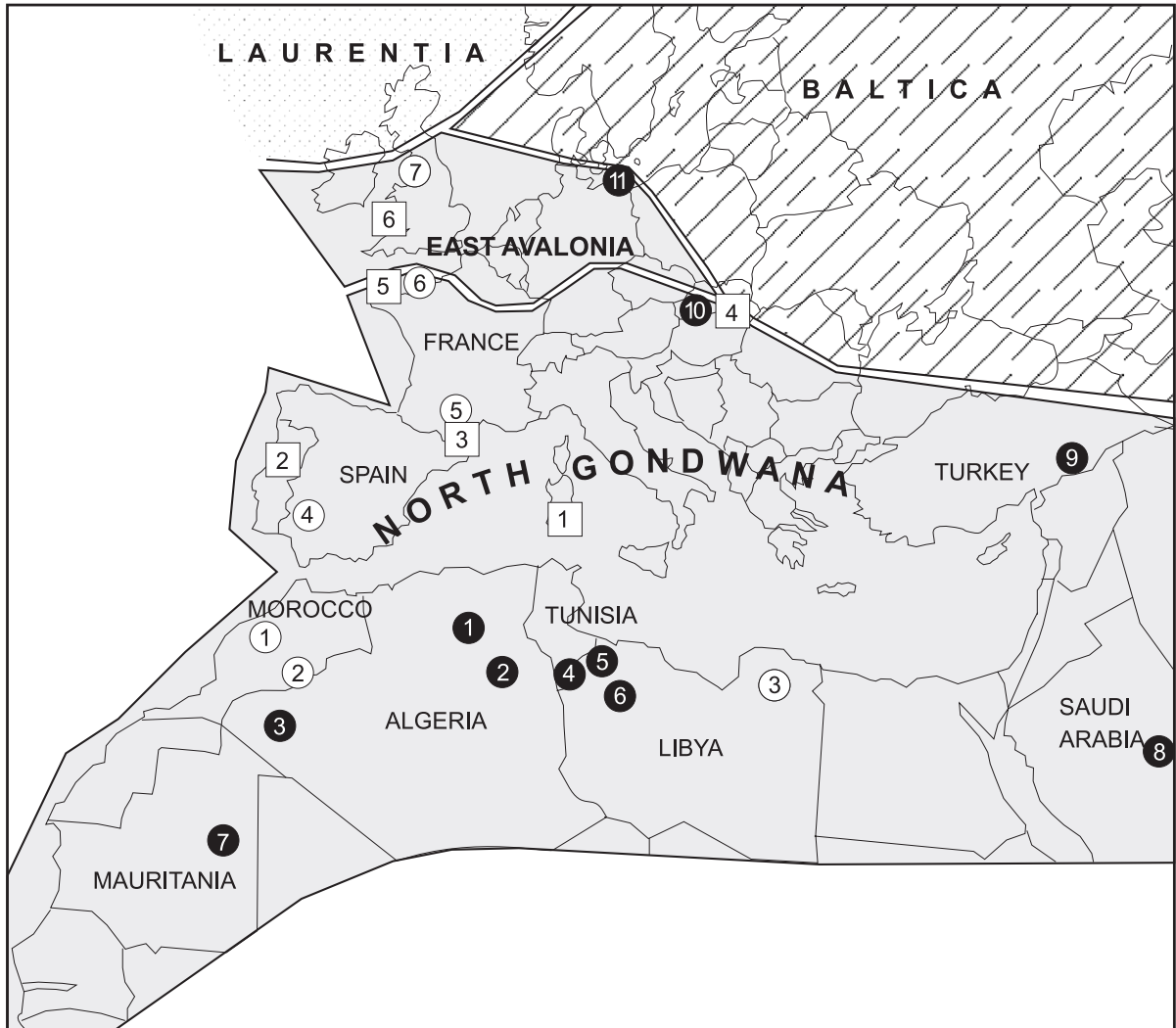
Fig. 2. Location of study sections and other localities discussed in text on present-day geography. Grey areas correspond to palaeogeographic domains of the northern Gondwana margin during Cambro-Ordovician times. Crustal sutures among the palaeocontinents Laurentia, Baltica, Gondwana, and the Avalonia microcontinent are also shown. Black circles: localities directly studied or re-examined by us. 1, boreholes Uc101 and NL2, Algerian Sahara; 2, boreholes GD1bis and GS2, Algerian Sahara; 3, Tindouf Basin, Western Algeria; 4, boreholes Tt1, St1, Sn1, Ghadamis Basin, southern Tunisia; 5; boreholes A1-23 and B1-23, Ghadamis Basin, northwestern Libya; 6, boreholes A1-70, A2-70, A3-70, C1-34, B2-34, Ghadamis Basin, northwestern Libya; 7, Hodh area, southeast Mauritania; 8, central Saudi Arabia (Le Hérissé et al., 2003); 9, Dadas section and other subsurface sections of the Diyarbakir area, southeastern Turkey (Le Hérissé in Steemans et al., 1996); 10, Klabava Formation, Bohemia; 11, subsurface of Rügen, northern Germany (Vecoli and Samuelsson, 2001). White circles: areas from which data were retrieved from published sources. 1, Tadla Basin, Morocco (Cramer et al., 1974a,b; Cramer and del Díez, 1977); 2, Anti-Atlas, Morocco (Elaouad-Debbaj, 1984, 1988a,b); 3, northeastern Libya (Molyneux, 1988; Molyneux and Paris, 1988); 4, Sierra Morena, Spain (Mette, 1989); 5, Montagne Noire, France (Martin, 1973; Rauscher, 1974); 6, May-sur-Orne Syncline, Normandy, France (Rauscher, 1974); 7, Lake District, England (Molyneux and Rushton, 1988; Cooper and Molyneux, 1990). Squares: other localities discussed in text. 1, central and southern Sardinia (Pittau, 1985; Albani, 1989); 2, Synclinal de Buçao, Portugal (Elaouad-Debbaj, 1978); 3, Mouthoumet Massif, Aude, France (Cocchio, 1981, 1982); 4, Bohemia (Vavrdová, 1965, 1966, 1972, 1973, 1993); 5, Crozon Peninsula, Brittany, France (Henry, 1969); 6, South Wales and Shropshire, England (Rasul, 1979; Rasul and Downie, 1974; Molyneux, 1987; Molyneux and Dorning, 1989; Turner, 1984).

stayed at high latitudes (>60° Lat S) during the entire Ordovician, with the exception of Avalonia, which reached intermediate latitudes (± 30° Lat S) during Caradoc–Ashgill times.

2.2. Acritarch bioprovinciality in the Ordovician

The use of acritarchs for inferring palaeocontinental affinity and hence for palaeogeographic reconstructions has been considered unreliable by some authors on the assumption that acritarchs are of fully planktic habit (e.g., Fortey and Mellish, 1992; Cocks et al., 1997; Cocks and Verniers, 1998). Cocks and Verniers (1998; p. 400) considered the acritarchs as a "varied selection of biological groups" of planktic behaviour, and hence not particularly useful for inferring palaeocontinental affinity. However, newly developing concepts about acritarch biological affinities, and comparison with dinoflagellate physiology (Colbath and Grenfell, 1995; Moldowan and Talyzina, 1998; Le Hérissé, 2002a,b) seem to indicate that the planktic stage of the acritarch was quite limited in time (e.g., concept of "Benthic plankton" of Dale, 1983) and that most acritarchs were produced by the parent organisms principally in coastal to neritic palaeoenvironments in response to the local establishment of particular palaeoecological conditions (Le Hérissé, 2002a). As a consequence, most of the acritarchs were not dispersed across large oceanic barriers, and detailed studies are confirming that acritarchs are proving to be at least as useful as certain benthic organisms whose life cycles involved a planktic, larval stage, such as brachiopods and trilobites (Le Hérissé, 2002a). The failure of applications of quantitative methods to acritarch assemblages for palaeogeographic reconstructions (Fortey and Mellish, 1992) probably reflected an incomplete acritarch taxonomy at the time, hence depended solely on the use of strongly biased and inconsistent taxonomic databases. It has been clearly shown by later studies that when applied to taxonomically sound databases, quantitative methods such as cluster analysis and/or similarity indexes on acritarchs (as well as on chitinozoans) give useful results for palaeogeographic reconstruction (e.g., Le Hérissé and Gourvennec, 1995; Le Hérissé et al., 1997; Vecoli and Samuelsson, 2001; Samuelsson et al., 2002). We give here a brief summary of the current state of knowledge on acri-

tarch palaeobiogeographic distribution especially for what concerns our study area. More detailed descriptions of models of palaeobiogeographic differentiation of microphytoplankton during Ordovician times, including historical reviews of such concepts, can be found in Playford et al. (1995), Tongiorgi and Di Milia (1999), Vecoli (1999), and Servais et al. (2003).

Recent studies of Ordovician acritarch assemblages from selected localities of known palaeogeographic setting and reliable chronostratigraphic constraints (Playford et al., 1995; Tongiorgi and Di Milia, 1999; Vavrdová, 1997; Vecoli, 1996, 1999), together with a careful review of published work (Vavrdová, 1974, 1997; Li, 1987), show that acritarch biogeographical differentiation developed at least since late Tremadoc–early Arenig times or, more hypothetically, earlier (in latest Cambrian times: Volkova, 1995), gradually leading to a clear separation between at least two distinct acritarch communities, or microfloras. One acritarch community was distributed in palaeogeographic regions belonging to the Peri-Gondwana margin *sensu lato* (Figs. 1 and 2). It is distinguished by the presence of the genera *Arbusculidium* Deunff (1968), *Arkonia* Burmann (1970), *Coryphidium* Vavrdová (1972), *Dicrodiacrodium* Burmann (1970), *Frankea* Burmann (1970) emend. Servais (1993), and *Striatotheca* Burmann (1970). Such an acritarch microflora is often referred to as "Mediterranean", since it was first described as a palaeobiogeographical entity from circum-mediterranean regions (southern-central Europe and North Africa) by Vavrdová (1974). On the basis of the FADs of typical Peri-Gondwana acritarch index-species such as *Striatotheca*, it is possible to define the lower age limit for the differentiation of the Peri-Gondwana acritarch microflora as equivalent to the base of the *H. copiosus* graptolite Zone (upper Tremadoc; Tongiorgi and Di Milia, 1999). A second microflora (termed "Baltic") was distributed in the regions of the East European Platform; its palaeogeographic distribution corresponds to the areas included in the "Baltic Province" of Vavrdová (1974). The Baltic microflora has been recently re-defined by Tongiorgi and Di Milia (1999) on the basis of the presence of species of *Peteinosphaeridium* Staplin et al. (1965) emend Playford et al. (1995), such as *Peteinosphaeridium bergstroemii* Staplin et al. (1965); *P. hymenoferum* (Eisenack, 1931) Fensome et al. (1990); *P.*

dissimile Górka (1969), and on the occurrence of species of *Pachysphaeridium* Burmann (1970) emend. Tongiorgi and Ribecai (1999). This particular microflora evolved from the base of the Volkhov Stage in Baltoscandia (upper Arenig). The palaeobiogeographical differentiation between the Baltic and Peri-Gondwana acritarch microfloras persisted until the basal Caradoc, when a breakdown in acritarch bioprovincialism seems to occur (Le Hérissé in Molyneux et al., 1996; Vecoli, 1999; Samuelsson et al., 2001). Because of the palaeolatitudinal occurrence of the Baltic and Peri-Gondwana acritarch communities (see Fig. 1), it has been often stated in the literature, perhaps in a over-simplified perspective, that the former represents a warm-water, low latitude microphytoplankton assemblage, while the latter was probably a cool to temperate, high-to intermediate latitude microphytoplankton suite. The concept of a latitudinally controlled palaeobiogeographical distribution of acritarch assemblages, first introduced by Cramer (1968, 1971), is no longer accepted (Colbath, 1990; Tyson, 1995, Tongiorgi et al., 1995; Le Hérissé and Gourvennec, 1995; Vecoli, 1999). Other physical factors, such as oceanic currents (Tongiorgi et al., 1995), continental distribution (Colbath, 1990), and palaeoenvironmental conditions (Le Hérissé and Gourvennec, 1995) are now considered as having an important influence on acritarch distribution.

Considering the distribution of the "*messaoudennsis–trifidum*" assemblage as primarily climatically controlled, Servais and Mette (2000) proposed that the term "palaeoprovince", as used in several spatial models for Ordovician acritarchs, should be dropped in favour of the term "realm" in the meaning envisaged by McKerrow and Cocks (1986) and Scotese and McKerrow (1990). These authors favoured the term "realm" for climatically controlled distribution patterns which are common for planktonic organisms as opposed to the term palaeoprovince, which was to be used only for palaeobiogeographical units separated by "barriers". However, the interfaces between physically distinct water masses (e.g., for different salinity, density, temperature), certainly constituted barriers to the oceanic migration of acritarchs as well as of other organisms (see also Havlíèek et al., 1994, p. 27). Thus, in the present paper, we consider that the term palaeoprovince can be applied to palaeogeographically restricted acritarch assemblages.

The acritarch assemblages discussed herein represent cool- to cold-water (latitudinally restricted to >60°S) microphytoplankton communities of the Peri-Gondwana acritarch palaeoprovince (Fig. 1). Because of the broad palaeogeographical extension of this palaeoprovince, the evolving patterns described herein might not be totally representative for the entire Peri-Gondwana margin (e.g., from Argentina to South China), and should not be considered as such until detailed studies are avaliable also from other Peri-Gondwana localities.

3. Material and methods

A fully literature-based analysis of Ordovician acritarch diversity is very likely to produce highly biased results, of little palaeobiological value. A survey of published studies on Ordovician north Gondwanan acritarch assemblages clearly shows the following difficulties: (1) many acritarch species are loosely defined and/or badly illustrated in the literature, so that the replicability of data is limited, and the assignement of a specimen or group of specimens to a species very difficult without the examination of the type material: this has resulted in the inconsistent use of species names in the literature by different authors; (2) in many cases, only the morphologically more distinct forms, with an "a priori" assumed potential for biostratigraphy, have been recorded and described out of a given acritarch assemblage, so that diversity data derived from biostratigraphy-oriented works are necessarily incomplete; (3) acritarchs have often been used to attempt dating of unfossiliferous sequences, and the exact stratigraphic ranges of many published species are imprecisely known; (4) in many instances, relevant locality and stratigraphic information was not released because of confidentiality reasons (e.g., Deunff, 1960, 1961, 1964; Jardiné et al., 1974), limiting the correlation potential of published range-charts. We attempted to circumscribe such biases as much as possible by avoiding to construct an uncritical, fully literature-based taxonomic database, and to use as much as possible data from our own investigations for which extensive taxonomic treatment of acritarch microfloras have been published. The use of literature data was limited to a few, selected publications. We have accessed the type material from many

of our study areas (e.g., the Algerian Sahara, Morocco, Bohemia) to better constrain taxonomic data, and we have incorporated recent and accurate data from our unpublished investigations of coupled acritarch and chitinozoan biostratigraphy, in order to independently constrain the stratigraphic ranges of many acritarch species, as we specify below. Our analysis, covering the latest Cambrian through latest Ordovician times is thus based on the following materials (Figs. 2 and 3).

(1) Acritarch data from the palynological investigation of subsurface stratigraphic sections in Algeria (boreholes UC101, NL2, GD1bis, GS2), northwestern Libya (boreholes A1-70, A1-23, B1-23, B2-34, C1-34, A1-70, A2-70, and A3-70), and southern Tunisia (boreholes Tt1, St1, Sn1). Detailed information regarding acritarch taxonomy and biostratigraphy of these sections has been published by Vecoli (1996, 1999), Vecoli and Playford (1997), and Vecoli et al.

(1995, 1999a, in press). These data have been complemented and chronostratigraphical correlation improved by recent studies on integrated acritarch and chitinozoan biostratigraphic investigation on the boreholes Tt1 and A1-70 (Vecoli, unpublished) and by detailed high-resolution acritarch-based biostratigraphy and ecostratigraphy of uppermost Ordovician sediments from borehole NL2 (Le Hérissé in Paris et al., 2000; Le Hérissé et al., 2003; Le Hérissé and Vecoli, 2003), and by cross-correlation with published chitinozoan-based biostratigraphic datings of Ordovician Algerian sedimentary successions (Oulebsir, 1992; Oulebsir and Paris, 1993, 1995). Data from old investigations by Deunff (1960, 1961, 1964) were also re-evaluated by re-examination of original topotypic material from the Algerian Sahara. This permits derivation of information on acritarch diversity from the following continuous stratigraphic intervals (Fig. 3): from uppermost Cambrian (levels equivalent
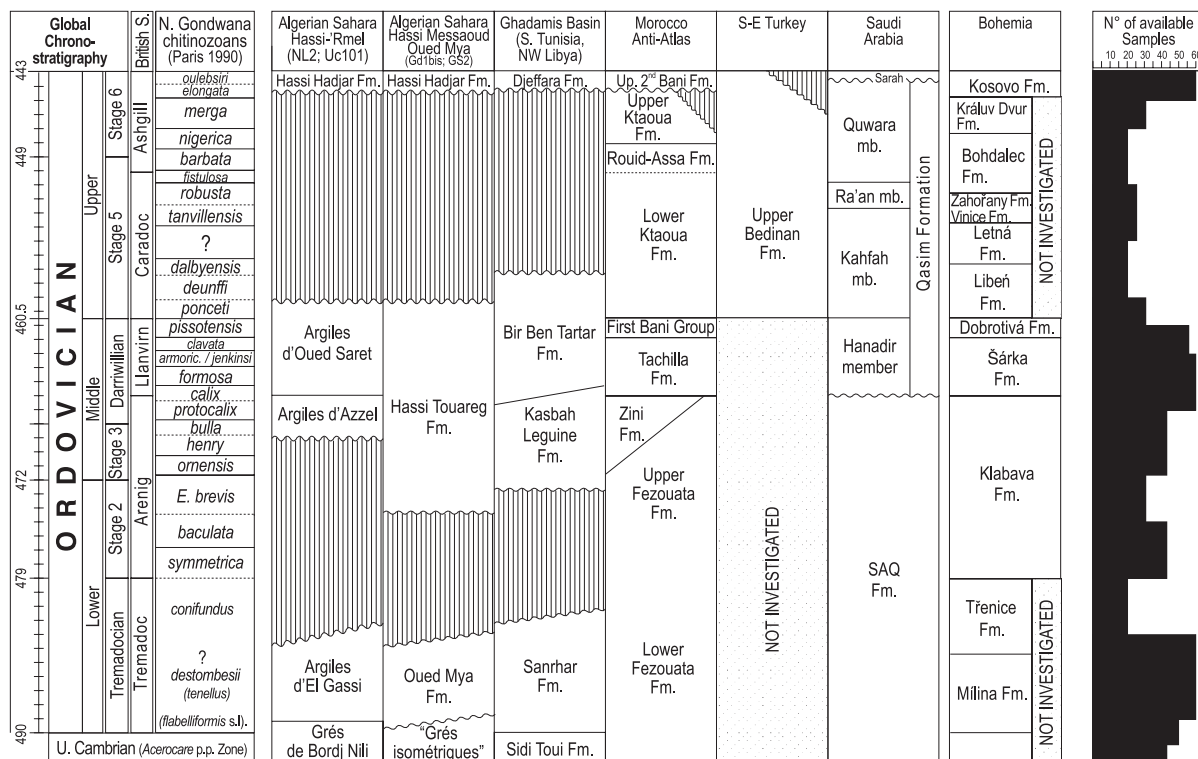

Fig. 3. Ordovician key-successions from northern Africa and Europe used to document the acritarch biostratigraphy of the northern Gondwana margin, and to derive diversity data presented herein. Hatching indicates stratigraphic hiatuses (gap or erosion). The last column to the left illustrates the cumulated quantity of samples that were available for study per stratigraphic interval (i.e., the time slices as defined in Fig. 4).

to the *Acerocare* trilobite Zone; based on indirect correlation, Vecoli, 1996, and confirmed by a later study by Parsons and Anderson, 2000) through lower Tremadoc (*flabelliformis* Zone; co-occurrence of graptolites), from middle Arenig (*brevis* chitinozoan Zone; co-occurrence of chitinozoans index species) to lower Caradoc (*dalbyensis* chitinozoan Zone), and the upper part of the Ashgill (*elongata* and *oulebsiri* chitonozoan Zones).

(2) Acritarch assemblages from Upper Ordovician sedimentary successions of southeastern Turkey, both in outcrop and in subsurface. These are independently dated by means of co-occurring chitinozoans, as middle Caradoc to early Ashgill (*robusta* to top of *barbata* chitinozan Zones), and late Ashgill (*merga* chitinozoan Zone) ages. These data have been published in part by Le Hérissé (in Steemans et al., 1996), and partly come from unpublished studies of exploratory boreholes. A detailed systematic study of these Upper Ordovician Turkish acritarchs is currently being conducted by the present authors.

In total, more than 500 samples and core levels have been examined for this study, permitting to plot the stratigraphic ranges of 245 acritarch taxa.

Selected published studies dealing with independently dated sections, with good taxonomic treatment of the acritarch microfloras, and including good illustrations of the taxa, were also considered herein. The following sources were used:

(a) published acritarch data from independently dated (graptolites and chitinozoans) Moroccan Tremadoc, Arenig–Llanvirn and Caradoc sedimentary successions by Elaouad-Debbaj (1984, 1988a,b; and including re-examination of Deunff's (1977) study); late Arenig–early Llanvirn acritarch data by Cramer et al. (1974a,b), and Cramer and del Díez (1977) from subsurface section of the Tadla Basin in Morocco (independently dated later by means of chitinozoans by Soufiane and Achab, 1993); and Caradoc–Ashgill integrated acritarch and chitinozoan palynostratigraphic data of northeastern Libyan subsurface successions published by Molyneux (1988), Molyneux and Paris (1988), and Hill and Molyneux (1988);

(b) data on independently dated (graptolites) late Tremadoc acritarch suites in England (Lake District: Molyneux and Rushton, 1988; Cooper and Molyneux, 1990), and in Spain (Mette, 1989; Servais and Mette, 2000);

(c) data from Tremadoc, late Arenig, Caradoc, and Ashgill of the Montagne Noire (southern France); from the Llanvirn–Caradoc of the May-sur-Orne Syncline (northern France) by Rauscher (1974);

(d) data from the Arenig–Llanvirn of Bohemia published by Vavrdová (1965, 1966, 1972, 1973, 1977, 1986, 1990a,b, 1993). Four samples (Kl-1, Kl-2, Kl-3, and Kl-4) from early Arenig of Bohemia (Klabava Formation; levels correlated to the *deflexus* and *extensus* graptolite Zones of the British Standard; Tongiorgi, pers. communication and Tongiorgi and Di Milia, 1999) were also re-examined by one of us (M.V.).

Numerous other papers dealing with Ordovician acritarchs of North Africa (Deunff, 1961, 1964; Jardiné et al., 1974; Deunff and Massa, 1975), the Middle East (Iran, Ghavidel-Syooki, 1993, 1996, 2000), and European localities (Downie, 1958; Martin, 1965, 1968, 1973, 1977, 1982, 1993, 1996a,b; Burmann, 1970; Rasul and Downie, 1974; Rasul, 1979; Cocchio, 1981, 1982; Albani et al., 1985; Pittau, 1985; Molyneux, 1987, 1990; Albani, 1989; Molyneux and Dorning, 1989; Molyneux et al., 1996; Servais and Molyneux, 1997), were also taken into account, but these required a careful critical evaluation and were not used directly to compile the range charts (Figs. 4–6) for reasons of database consistency.

3.1. Estimates of acritarch diversity and evaluation of biasing effects

Diversity patterns and extinction and origination rates were scaled against the Ordovician Correlation Chart compiled by the IGCP 410 working group (Webby et al., 2004;), which includes accurate correlation among graptolite, conodont, and chitinozoan zonations, and a geochronologic time scale (Figs. 3–9). This chart shows the tripartite subdivision of the Ordovician into three Global Series (the Lower, Middle, and Upper Ordovician) each of which is in turn subdivided into two Global Stages. At the moment, only two of the six Global Stages are formally defined: the Tremadocian, lower stage of the Lower Ordovician, and the Darriwillian, the upper Stage of the Middle Ordovician (corresponding to the Llanvirn of the British subdivision). The Global Stages are numbered 1 to 6 from the lowest (Tremadocian) to the
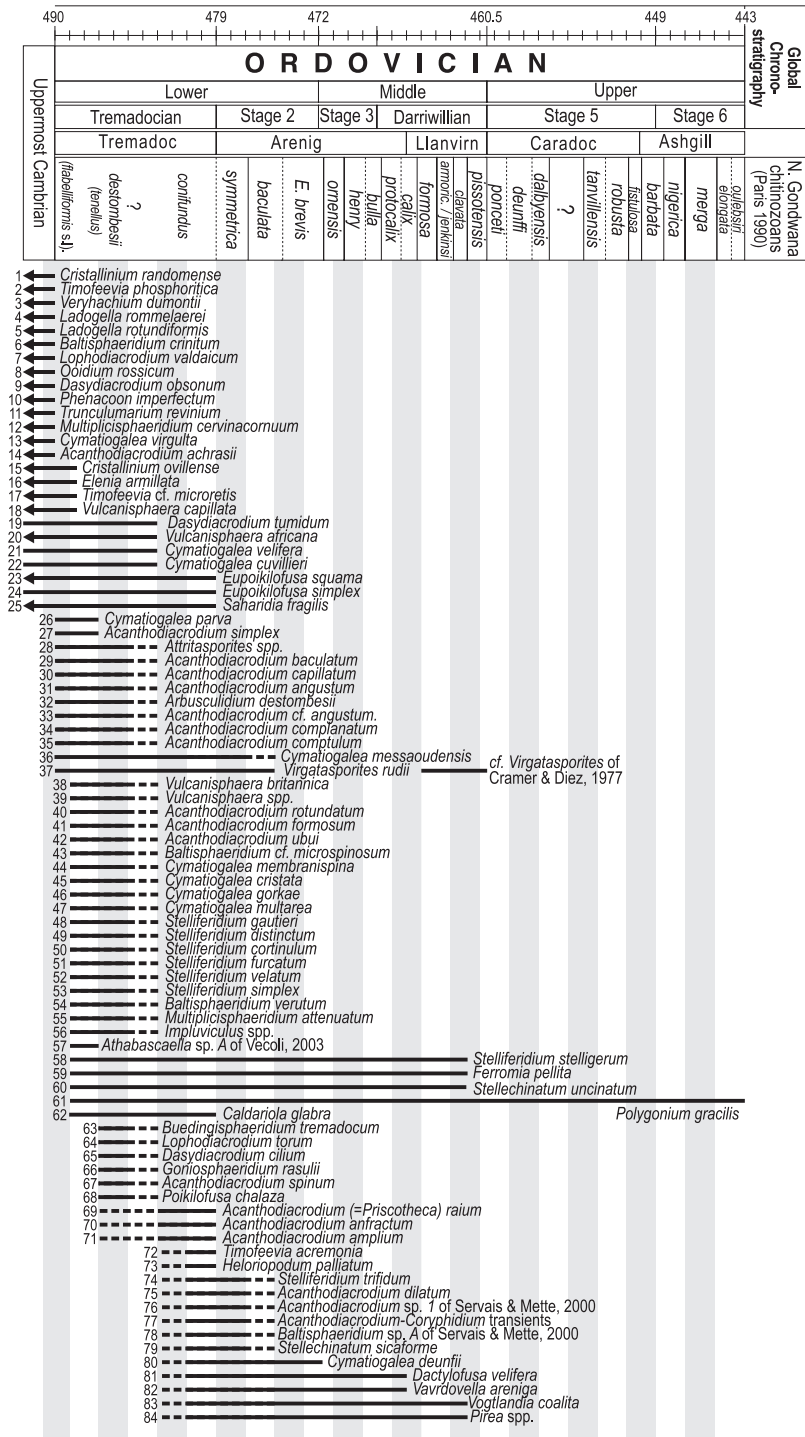
Fig. 4. Stratigraphic ranges of uppermost Cambrian to uppermost Ordovician acritarchs of northern Gondwana (part I). Horizontal banding (white and gray intervals) corresponds to the subdivisions in time-slices of 2-million-year duration used for the diversity counts (see text). Numbers refer to the list of taxa in Appendix A.
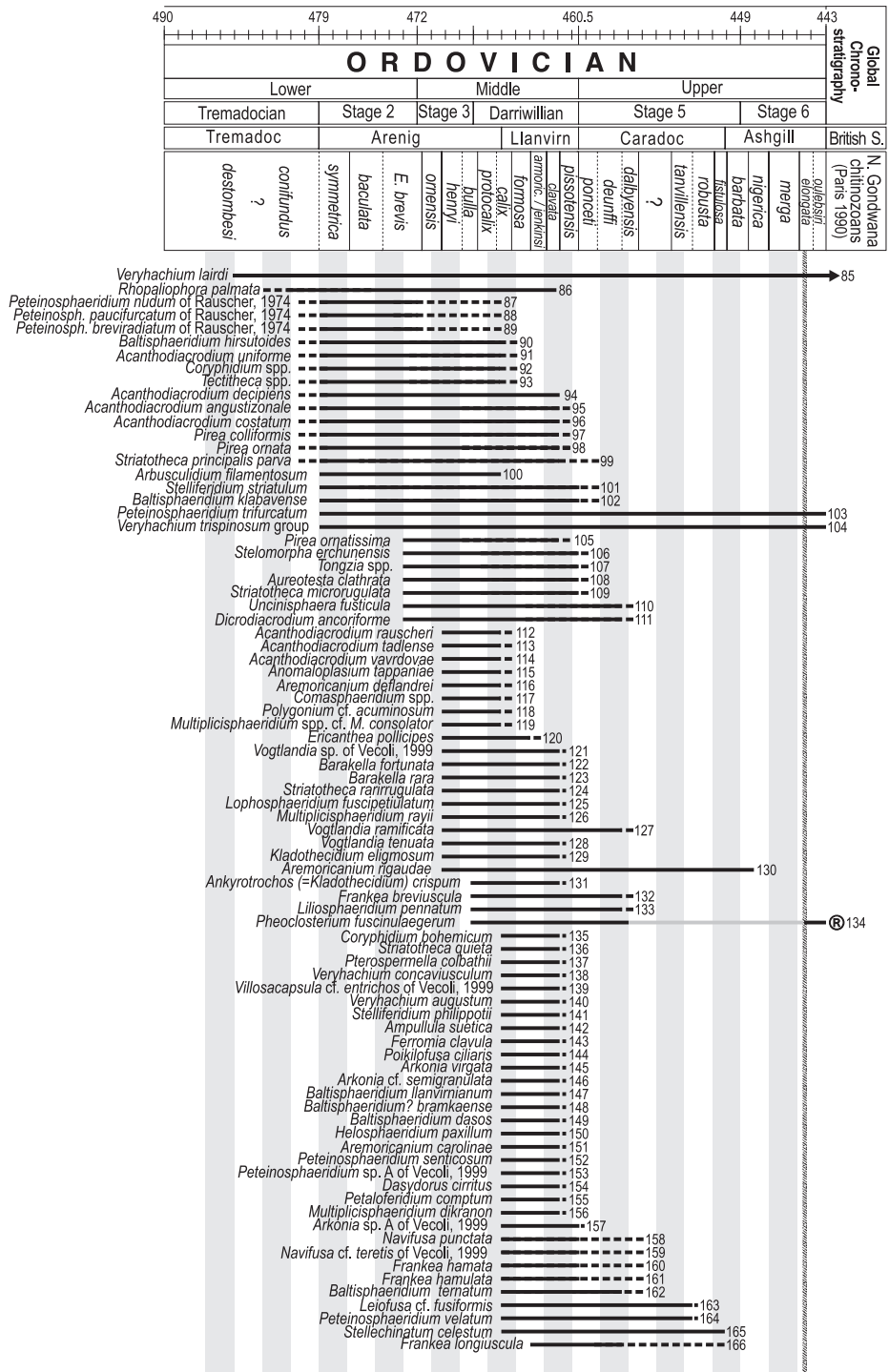
Fig. 5. Stratigraphic ranges of Lower to uppermost Ordovician acritarchs of northern Gondwana (part II). The horizontal band (oblique dashes) in upper Ashgill represents the glacial interval during Hirnantian times. Other symbols as in Fig. 4.
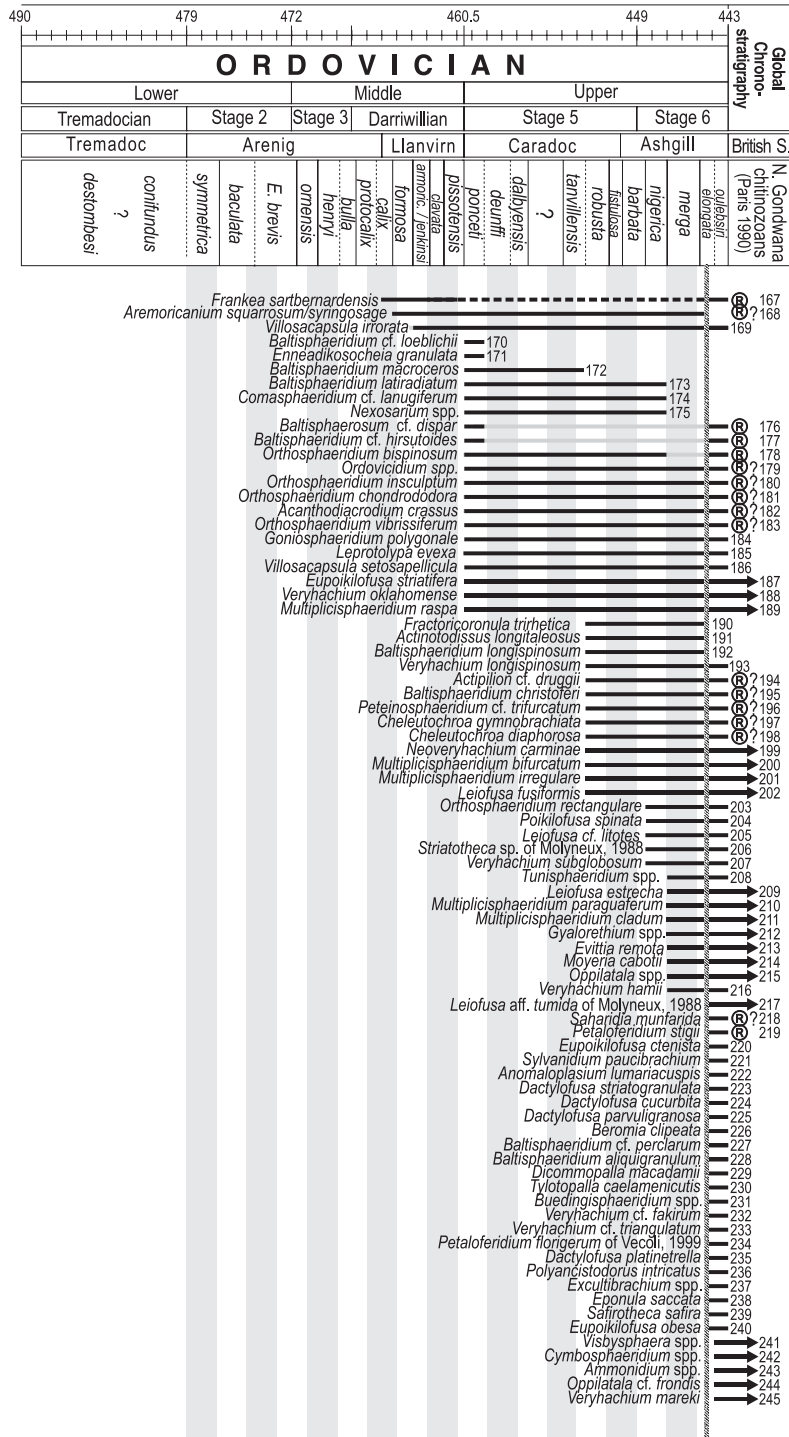
Fig. 6. Stratigraphic ranges of Lower to uppermost Ordovician acritarchs of northern Gondwana (part III). Symbols as in Figs. 4 and 5.

uppermost (still unnamed). Pending the formal definition of all of the Global Stages, in the present article the terms Tremadoc, Arenig, Llanvirn, Caradoc, and Ashgill, are used with reference to the British Standard subdivision sensu Fortey et al. (1995).

Diversity metrics were calculated for a series of 2-million-year-long time-slices into which the entire Ordovician was subdivided; an additional Late Cambrian time slice was considered for a total of 24 time slices (Figs. 4–6); this helps to reduce errors due to unequal duration of stages (for stage-level diversity calculations) or biozones (for biozone-level diversity).

We performed different diversity estimates, as follows (Fig. 7):

(1) *Total diversity*, calculated as the total number of taxa (genera and species) co-occurring during each chronostratigraphic interval. This simple method of evaluating taxonomic richness by raw counts of number of taxa has been criticized as potentially leading to an over-estimation of "true" taxonomic diversity (e.g., Cooper, 1999). According to Bambach (1999), total diversity in an interval would approach the true values of taxonomic standing diversity only if all originations occurred before any extinction took place in the interval. Total diversity has been, however, widely adopted for evaluation and analysis of diversity patterns of various planktonic marine microfossils, hence it has the advantage of permitting easy comparison with previous studies (e.g., Kaljo et al., 1995; Vidal and Moczydlowska-Vidal, 1997; Melchin et al., 1998; Kiessling, 2002; O'Dogherty and Guex, 2002).

(2) *Continuing Diversity*. Continuing diversity considers the number of species crossing one interval to the next, and was considered by Bambach (1999) as the best approximation of true standing diversity. In this case, the change between the number of species entering an interval and leaving that interval can provide a good evaluation of the change in diversity during that time independently from preservational or spatial biasing effects.

(3) *Modified Diversity*. This way to calculate taxonomic diversity was suggested by Cooper (1999) and was adopted by the IGCP 410 "The Great Ordovician Biodiversification Event" clade teams to evaluate the biodiversity of several fossil groups in the Ordovician (Webby et al., 2004;). It involves counting the number of species ranging through the time unit (from the preceding to the following) plus half the number of species ranging beyond the time unit but originating or ending within it, plus half the number of species confined to the time unit. The modified diversity curve appears to smooth out some second-order fluctuations, which are present in the curves obtained with the previous two methods. It is probably a good way to average out some errors and minor irregularities due to uncertainties on the stratigraphic locations of FADs and LADs of the considered taxa (Fig. 7).

We also calculated and plotted origination and extinction rates simply as the number of species originating or going extinct during a time interval, divided by the duration of the interval (2 million years; Fig. 8).

Before analyzing the diversity patterns and their possible palaeobiological meaning, we consider what kind of biasing effects could possibly affect the diversity curves. We discuss the following potential biases: taxonomic, spatial and preservational, and biases due to time averaging.

Taxonomic biases can be significant source of errors especially in literature-based diversity analyses, and depend mostly on the inconsistent adoption, in different studies, of morphological criteria on which fossil taxa are defined and identified. These kinds of biases are particularly relevant for Palaeozoic acritarchs because of the instability and subjectivity of acritarch taxonomy. One major question which is hotly debated and still unresolved is, for example, the allowed range of acritarch intra-specific and intra-generic morphological variability (e.g., Strother, 1996). As stated previously, most of the species and acritarch assemblages which are listed in our range charts (Figs. 4–6), have been fully described, discussed and illustrated in taxonomic monographs (Vecoli and Playford, 1977; Vecoli, 1996, 1999; Vecoli et al., 1999b). Moreover, we directly re-examined type material from a number of Ordovician northern Gondwana localities (e.g., Bohemia, Morocco, Turkey), as described in the previous section. Thus, our database is internally consistent and entirely verifiable. Often, only a minor portion of a given acritarch assemblage is fully identifiable at the specific (and sometimes even at the generic) level. Very small acritarchs, e.g., those included within *Michrystridium* cannot be easily accounted for taxonomically. It is also not possible to evaluate the diversity of
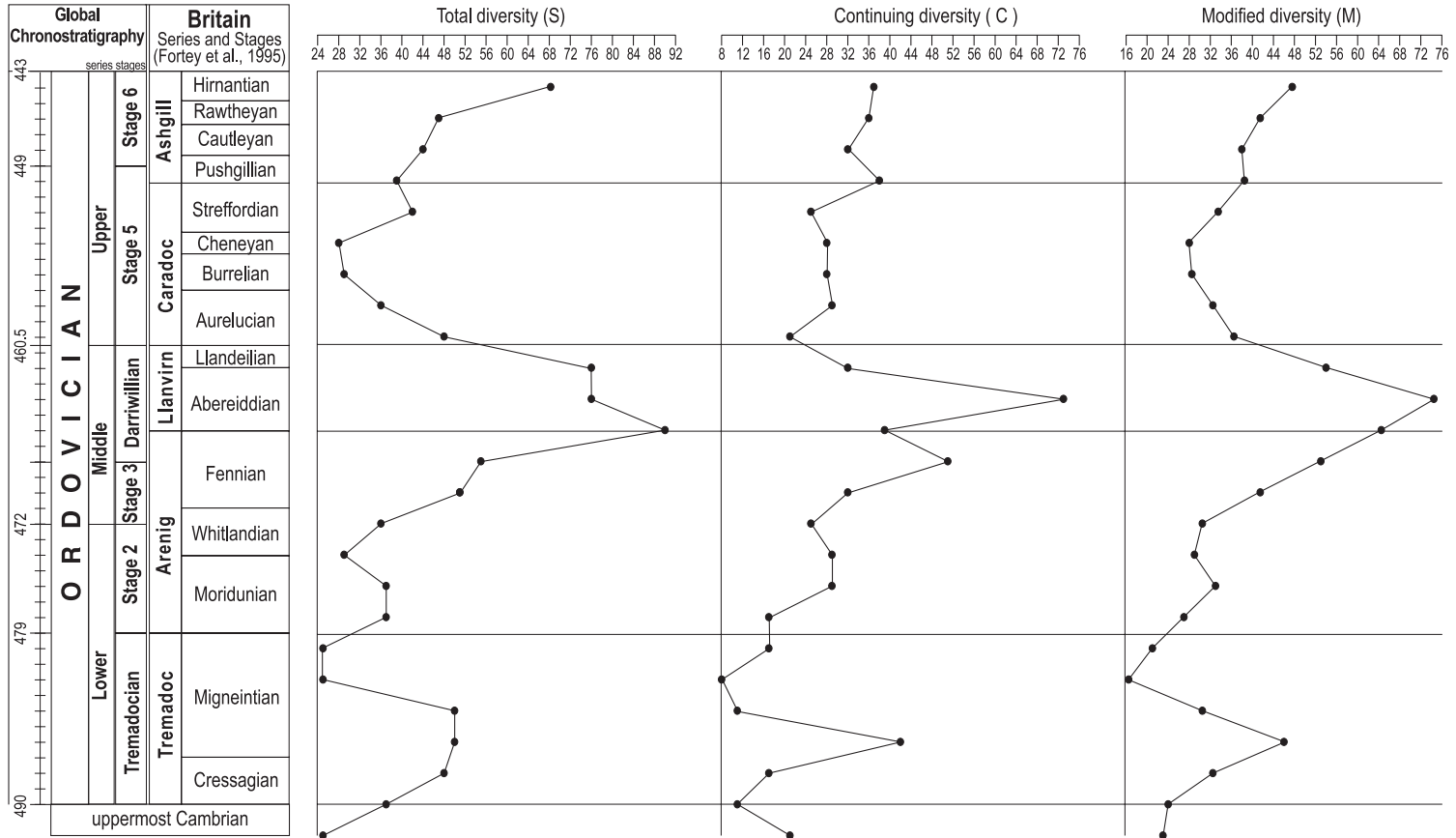
Fig. 7. Curves of Total (T), Continuing (C), and Modified (M) diversities for Cambro-Ordovician acritarchs of northern Gondwana. Resolution is 2 million years.
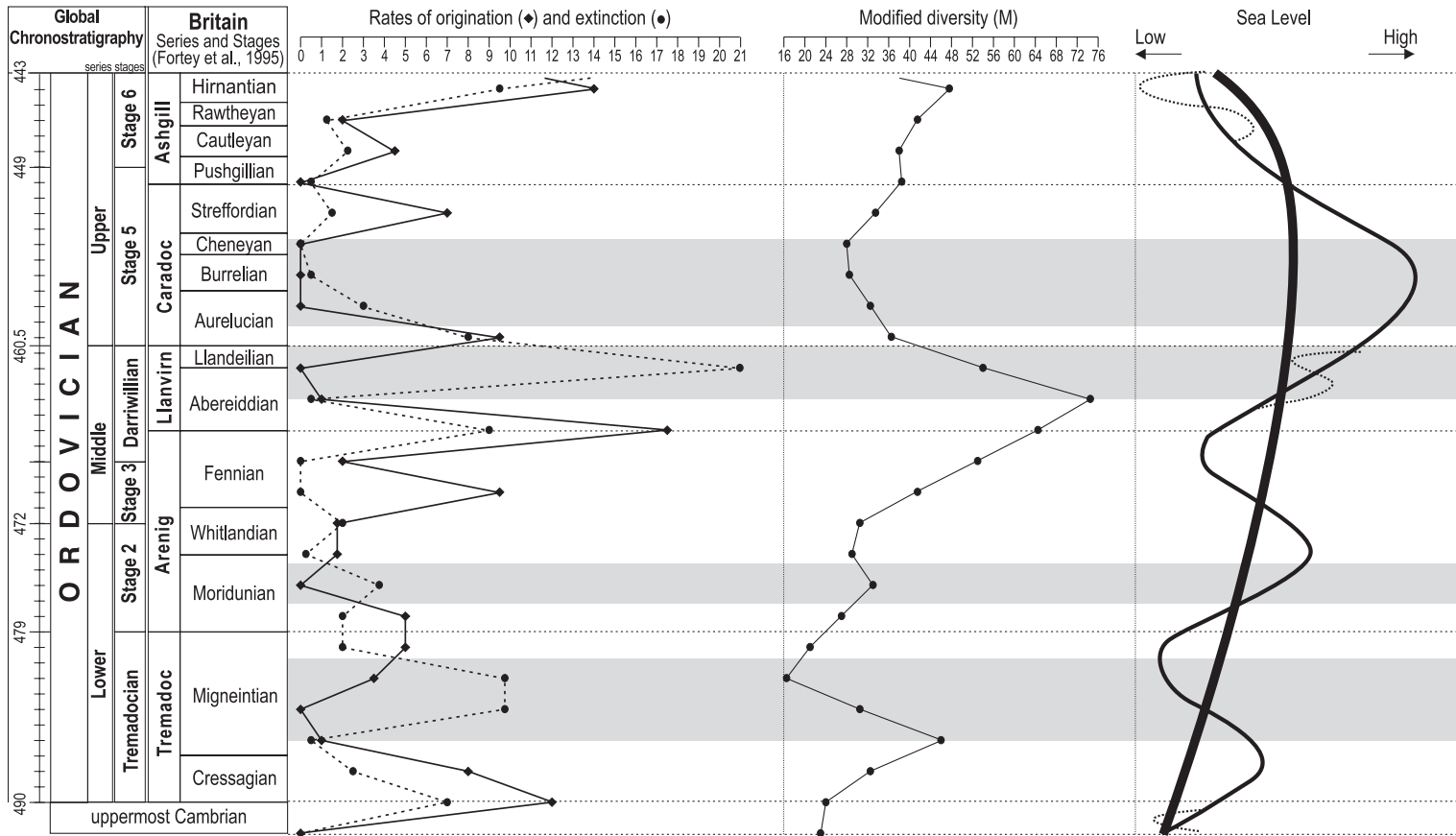
Fig. 8. Biodynamics (origination and extinction rates, modified diversity) of Cambro-Ordovician acritarchs and correlation with sea level oscillations in northern Gondwana. Sea level curve: thick line, first-order cycle; thin line, second order cycles; dotted line, third order cycles.

the featureless, spherical or discoidal acritarchs grouped under the genus *Leiosphaeridia*, for which no viable taxonomy exists. In the present study such acritarchs were not included in the diversity counts on the assumption that on average, their contribution to total assemblage diversity is an essentially constant "bruit de fond" which can be filtered out without affecting significantly the diversity gradients in the temporal dimension.

Other approximations concern "controversial" species, whose morphological variability spectrum is not well established, and/or too narrowly defined morphotypes occurring exclusively in particular stratigraphic levels and in restricted geographical areas ("taxonomic bursts").

In these cases, we opted for a "conservative" approach, by creating "species-groups" (e.g., *Acanthodiacrodium* spp., *Coryphidium* spp., *Multiplicisphaeridium* spp., *Ordovicidium* spp.), which were given a score of one in the diversity counts. On the other hand, we included in our database species left in open nomenclature but which have been well described and figured, and of which the stratigraphic range has been well determined (giving the appropriate reference to the literature source; e.g., *Acanthodiacrodium* sp. of Servais and Mette, 2000).

Spatial and preservational biases are due to areal and/or vertical variability in sampling intensity and in preservation potential of fossils, which in turn influences the taxonomic composition as well as the size of the fossil populations under analysis (Koch, 1991; Sepkoski and Koch, 1996; Westrop and Adrain, 2001). The sampling density of our material (i.e., the number of samples available per stratigraphic unit) is generally regular throughout the investigated interval (Fig. 3). Moreover, the diversity fluctuations do not correlate to the curve which shows the number of samples analyzed in the present study, suggesting the lack of substantial sample-size biases, except perhaps in lowermost Arenig and lower–middle Caradoc (see discussion in the next paragraph).

On average, acritarchs are extremely abundant, well preserved and taxonomically diverse, occurring frequently in the order of several thousands of specimens per gram of rock (unpublished personal data and see also Oulebsir, 1992; Vecoli, in press) in Ordovician sediments of northern Gondwana localities and especially of the North Sahara Platform. In our

material, even those samples which were considered poorly productive yielded acritarchs in the order of hundreds of specimens per gram of rock, and totally barren samples were rare (e.g., Vecoli, 1996, 1999). Calculations based on image analysis showed that the palynological slides from our productive samples contained on average between 15,000 and 30,000 recognizable acritarchs (Vecoli, in press). This very large abundance of specimens and their generally good preservation greatly reduces possible biases due to the uneven species abundance in palaeontological samples (Koch, 1991; Sepkoski and Koch, 1996).

The taxonomic composition of acritarch assemblages, including the relative abundance of species-groups are facies-dependent (Staplin, 1961; Jacobson, 1979; Dorning, 1981; Al-ameri, 1983; Oulebsir, 1992; Vecoli, 2000). Biases on diversity estimates are to be expected if sampling is unevenly distributed among different sedimentary facies, or if the effects of facies shifts along a time coordinate are not taken into account and corrected for. Variations in diversity along an inshore–offshore trend of North African Ordovician acritarch suites were identified and analyzed in a previous study (Vecoli, 2000). On the basis of the results of this latter investigation, we can establish that both inshore and offshore platformal settings are almost equally represented at least in the North African material.

Time averaging. Large variations in sample time-averaging (i.e., the total amount of time which is represented in the analyzed sample) can affect micro-palaeontological samples because of different sedimentation rates, reworking, and bioturbation (e.g., Kiessling, 2002 and references herein). Stable conditions of intracratonic clastic shelf deposition prevailed during Early to early-Late Ordovician over all of the studied area. This uniformity of depositional conditions at the regional scale, and our analysis of silty to shaly samples, collected either from fine-grained succession or from the finer sedimentary intercalations within sandstone bodies, greatly reduce the effect of time-averaging biases in our study. Furthermore, bioturbation is only occasionally present in the studied samples (Massa, 1988; Massa et al., 1977), hence is not likely to introduce errors. Mechanisms of sedimentation linked to glacially driven sedimentary dynamics were more varied and

areally restricted during latest Ordovician (Hirnantian) times, such as slumping and diamictite dikes (e.g., in the Sarah Formation of Saudi Arabia: Senalp and Al-Laboun, 2000; Vaslet et al., 2001), or subglacial channels, ice-rafted debris related to advances, retreats and melting of ice-sheet (e.g., in the Hassi El Adjar Fm. in Algeria, the Kosov Fm. in Bohemia, see also the depositional model of Sutcliffe et al., 2000). The effects of this particular latest Ordovician sedimentary environment need to be considered as potential source of time-averaging biases, especially in relation to phenomena of sediment reworking. Significant quantities of reworked acritarchs derived from the erosion of Tremadoc, Arenig and Llanvirn sediments are often observed in the glacial-derived sediments of Late Ordovician age. For example, in the Kosov Formation of Bohemia, Vavrdová (1982) reported the presence of up to 70% of reworked acritarch specimens in Late Ordovician palynological assemblages. In the glacial-related sediments of Algeria (the ''argiles microconglomératiques''), the amount of allochtonous elements has been estimated as varying between few percent up to 30% of the total acritarch content, in specific levels (Le Hérissé, in Paris et al., 2000, and present study). In many cases, it is easy to detect these reworked elements on the basis of the known age-difference between the enclosing sediments and the reworked species, and to correct the diversity counts accordingly. However, when the age of the reworked specimens is close to the age of the enclosing sediments, or the exact stratigraphic range of a certain species is not known precisely, detecting reworking is much more difficult because acritarchs can be transported over considerable distances without showing any sign of corrosion or mechanical damage (Martin in Dean and Martin, 1992). This is the case of species of *Baltisphaeridium*, *Ordovicidium*, and *Orthosphaeridium*, whose relative abundance in uppermost Ordovician sediments, where reworking is common, might be overestimated by 1% to 5%.

4. Results: Ordovician acritarch diversity and patterns of morphological evolution

The curves of total, continuing, and modified diversity (Fig. 7), show a consistent pattern, with three main positive peaks, respectively, in the lower Tremadoc, middle Llanvirn (absolute maximum), and uppermost Ashgill, separated by two main intervals of low standing diversity in upper Tremadoc and lower–middle Caradoc (Figs. 7 and 8). Important assemblage turnovers occur at the Cambrian/Ordovician boundary and at the Llanvirn/Caradoc transition (Darriwillian/Stage 5 boundary). The Caradoc/Ashgill boundary is characterized by co-occurring minima in both origination and extinction curves. Origination rates prevailed on extinction rates during early Tremadoc, latest Tremadoc to earliest Arenig, middle and late Arenig, at the Arenig–Llanvirn transition (maximum in origination rates), and during middle Caradoc through late Ashgill times (Fig. 8).

Below we give a detailed description of the main changes occurring among Cambro-Ordovician acritarch communities of the northern Gondwana margin, with emphasis on the morphological evolutive trends. The described bio-events also have important biostratigraphic applications and can be used for dating and correlation purposes (Figs. 4–6 and 9). For the sake of clarity, the taxa cited in the next sections are not author-named; the complete nomenclatural citations are reported in the list of Appendix A.

4.1. The Cambro-Ordovician boundary turnover

The latest Cambrian–early Tremadoc was a period of increasing diversity and intense morphological innovation within the acritarch communities, marked by the progressive introduction of new morphologies of Ordovician ''affinity'', associated with stepwise extinctions of the characteristic Cambrian taxa. The Cambrian–Ordovician boundary is palynologically detectable in northern Gondwana by the appearance of particular species of diacrodian acritarchs such as *Acanthodiacrodium angustum* and *A. baculatum*, preceded by the extinction of Late Cambrian forms such as, *Ladogella*, *Ooidium*, *Phenacoon*, *Trunculumarium*. Thorough discussions on the applicability of Gondwanan acritarchs for the Cambrian–Ordovician boundary recognition, were published in Vecoli (1996) and Vecoli and Playford (1997), and need not to be repeated here. However, it is worth mentioning that the level of chronostratigraphic resolution of latest Cambrian–earliest Ordo-

vician northern Gondwana acritarch biostratigraphy is comparable to that of biostratigraphic schemes based on invertebrate faunas (e.g., graptolites and trilobites; Vecoli, 1996).

Typically, Late Cambrian assemblages include ± spherical or polyhedrical, unilayered, radially symmetrical, "tabulated" acritarchs without specialized excystment structures and with or without processes (e.g., *Cristallinium*, *Timofeevia*), and morphotypes characterized by unilayered vesicles showing hemimorphic bipolar symmetry (e.g., *Dasydiacrodium*, *Ladogella*, *Ooidium*, *Trunculumarium*, and *Veryhachium dumontii*). All these taxa disappeared in latest Cambrian times, in proximity of the Cambrian−Ordovician boundary, with the exception of *Dasydiacrodium*. This is reflected by the extinction peak at the C−O boundary (Fig. 8). Because reworking of Late Cambrian acritarchs into younger sediments is very uncommon, LADs of the above taxa can be considered of chronostratigraphic significance, useful for the Systemic boundary recognition within continuous successions (Fig. 9).

Overall, origination rates surpass extinction rates at the Cambrian−Ordovician transition: this is due to the origination of the first representatives of *Acanthodiacrodium*, *Cymatiogalea, Stelliferidium* and *Vulcanisphaera* (also noted by Martin, 1993). The two latter genera are the most common representatives of the Herkomorphitae acritarch group (Martin, 1993), also referred to as "galeate" acritarchs (Servais and Heiserhardt, 1995), and show important morphological innovations such as specialized excystment structures (large circular to polygonal openings with an operculum) and a double-layered wall. Moreover, herkomorph acritarchs (especially *Cymatiogalea*) often display a geometrical partitioning of the surface of the vesicle by the linear arrangement of processes or membraneous structures along the sides of polygonal fields.

In the more proximal settings, the Cambrian−Ordovician transition is often marked by a reduction in diversity and by a net increase in abundance of leiospheres, which can be the dominant or even the exclusive component of the microfloras (Vecoli, 2000). The presence of levels rich in radioactive organic material, dominated by leiospheres and by the acritarch *Saharidia* (whose distribution in limited to proximal facies; Vecoli,

2000), in Cambro-Ordovician successions of the Algerian Sahara was previously noted by Combaz (1967), and was considered by him as marking the start of a marine transgression at the base of the Tremadoc. In the basal Tremadoc sediments of more proximal settings, peculiar morphotypes are present, such as *Attritasporites* and *Virgatasporites*, whose origin as cryptospore-like, possibly terrestrially derived palynomorphs is still questioned (Richardson, 1996; Vecoli, in press). Above this basal Tremadoc widespread low-diversity horizon, a clear increase in specific diversity is observed, which is principally due to the differentiation of the genera *Acanthodiacrodium, Cymatiogalea, Stelliferidium*, and *Vulcanisphaera*.

To sum up, the Cambrian−Ordovician transition is characterized by a marked turnover which caused an overall increase in acritarch diversity. Extinctions of the typically Cambrian acritarchs occurred gradually, step-wise throughout the Late Cambrian, without a mass extinction event. The introduction of innovative morphologies among the acritarch assemblages, such as the first development of specialized excystment structures and a double-walled vesicle started during latest Cambrian times, while the modifications occurring at or near the Cambro-Ordovician boundary involved mainly intrageneric morphological characters (high speciation rates). The main peak in diversity during the early Tremadoc (Figs. 7 and 8) is caused by speciation among herkomorph (*Cymatiogalea*, *Stelliferidium*) and diacromorph (e.g, *Acanthodiacrodium*) acritarchs. This diversity peak may be used as a good chronostratigraphic marker for the lower Tremadoc. The events described here are based on our analysis of northern Gondwanan assemblages, but they appear to have a global character since broadly similar patterns have been described from other areas belonging to widely separated palaeocontinents such as the Sino−Korean Platform (North China), and the northern margin of Laurentia (low palaeolatitudes; Martin and Yin, 1988; Martin, 1992) and the East European Platform (intermediate palaeolatitudes, Volkova, 1990).

4.2. Middle to upper Tremadoc

The acritarch biozonation and stratigraphic correlation of middle to upper Tremadoc sedimentary
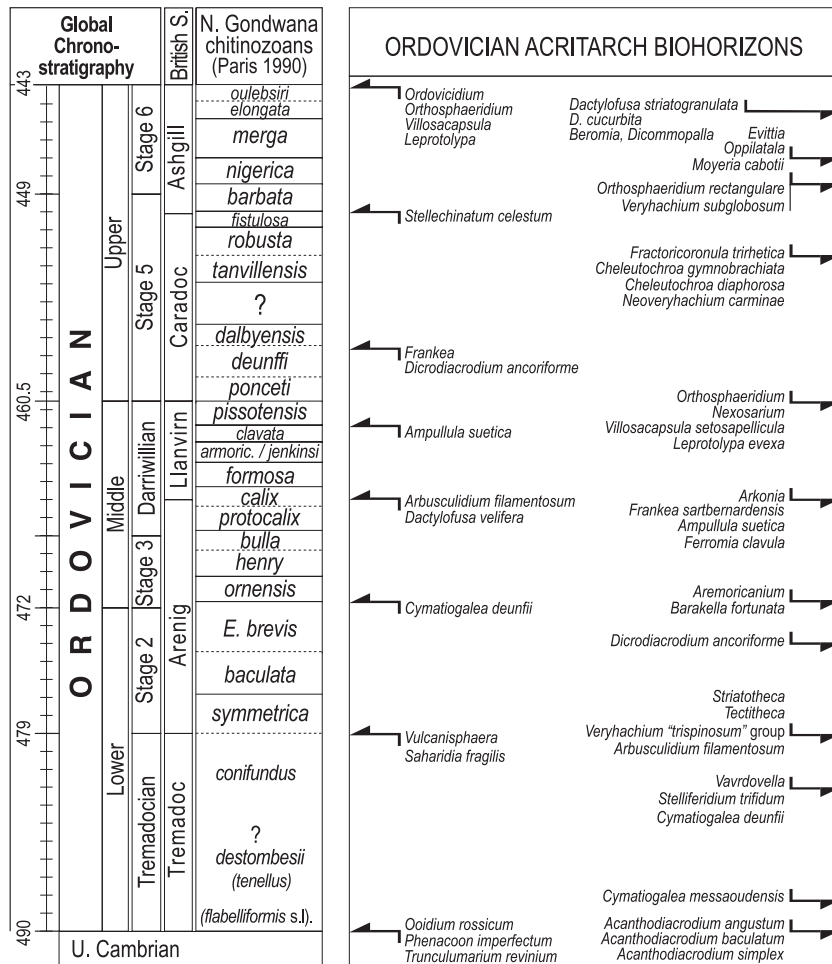
Fig. 9. Selected acritarch biohorizons plotted against the Ordovician chronostratigraphic chart of Webby et al. (2004), and the chitinozoan biozonation of Paris in Webby et al. (2004). In the Acritarch Biohorizons column, the arrows to the left denote LADs, the arrows to the right denote FADs.

successions in northern Gondwana pose some problems. These are due to the relative scarcity of acritarch data from well dated middle and upper Tremadoc stratal sequences but also to the instability of reference zonations based on graptolites (cf. Cooper, 1992, and Cooper in Webby et al., 2004), and the poor resolution of chitinozoan biozonation in the Tremadoc (Paris, 1990, 1996). In addition, upper to uppermost Tremadoc sedimentary successions are often incompletely preserved over large parts of North Africa because of the important late Tremadoc eustatic regression (Fortey, 1984; Ouleb-

sir, 1992; Oulebsir and Paris, 1995; Vecoli et al., 1995). These problems are reflected in our analysis by a larger uncertainty on the determination of middle to upper Tremadoc acritarch stratigraphic ranges (Fig. 4).

Data used here comprise the published studies of Jardiné et al. (1974, Algerian Sahara), Elaouad-Debbaj (1988b, Morocco), Molyneux and Rushton (1988, Lake District), Cooper and Molyneux (1990, Lake District), and our own re-investigation of material from borehole GS-2 (Algerian Sahara) originally studied by Deunff (1960).

After the major morphological innovations occurring near the C–O boundary and in the early Tremadoc, acritarch assemblages of middle Tremadoc age do not show important evolutionary changes. For this reason, the available acritarch zonations of post-*flabelliformis* Tremadoc strata (e.g., Rasul, 1979; Elaouad-Debbaj, 1988b) are not easily applicable outside their type sections. A net tendency towards decreasing acritarch diversity is nonetheless evident, moving from lower to upper Tremadoc, due to the extinction of several species of diacrodian and herkomorph acritarchs (middle Tremadoc peak in extinction rates; Figs. 4 and 8). An evident drop in acritarch diversity is recorded by Elaouad-Debbaj (1988b) in assemblages correlative with the *destombesii* chitinozoan Zone of the Lower Fezouata Formation in Morocco, aged late-early to early-late Tremadoc (Paris, 1990). The acritarch zone C1 of Jardiné et al. (1974; Algerian Sahara), attributed to an undifferentiated middle and upper Tremadoc, based on sparse graptolite fauna is also impoverished compared to the preceding, lower Tremadoc acritarch zones (B0, B1, and B2; Jardiné et al., 1974). However, the inceptions of the morphologically distinctive diacrodian, *Acanthodiacrodium* (= *Priscotheca*) *raium*, as well as of the first quadrangular *Veryhachium* (e.g., *V.* cf. *lairdii*) constitute important events which can be used to identify the middle Tremadoc. We observed an impoverished acritarch assemblage, dominated by *A. raium* in core levels only a few meters below the type stratum of the *conifundus* chitinozoan Zone (Paris, 1990) in well GS2, El Gassi area, Algeria.

Only in the uppermost part of the Tremadoc do origination rates again surpass extinction rates, further increasing diversity. This latter event corresponds to a notable change in acritarch assemblages due to the development of a characteristic acritarch microflora originally described from the English Lake District (Molyneux and Rushton, 1988), named "*trifidum* microflora" by Fortey et al. (1991), and later re-named "*messaoudensis–trifidum*" by Servais and Molyneux (1997). The assemblage is well represented in localities belonging to Peri-Gondwana terranes (Avalonia, Iberia, Turkey, Bohemia), but has never been recorded in North Africa probably because of the absence of late Tremadoc sediments in this latter area. The "*messaoudensis–trifidum*" as-

semblage is characterized by the differentiation of new species of *Acanthodiacrodium*, *Cymatiogalea,* and *Stelliferidium*, but also by the introduction of innovative morphologies at the generic level, as represented by the first inceptions of the quadrangular *Vavrdovella* and *Coryphidium*, and of the bottle-shaped *Pirea*. An interesting feature of inferred latest Tremadoc acritarch suites is the presence of acritarchs showing transient morphologies among the genera *Acanthodiacrodium*, *Vavrdovella*, and *Coryphidium* (Servais and Molyneux, 1997; Servais and Mette, 2000). Considering their stratigraphic occurrence and the morphological relationships among these three genera, it can be proposed that the successive appearances of *Vavrdovella* and *Coryphidium* might have cladogenetic significance. The FAD of *Dactylofusa velifera*, a distinctive form first described from the Tremadoc–Arenig of France (Massif of Mouthoumet) by Cocchio (1981, 1982), seems to be a good marker for the latest Tremadoc. Similarly, *S. trifidum* can be considered a suitable indicator for the latest Tremadoc (and earliest Arenig), but we must note here that the other eponymous species, *C. messaoudensis*, is more problematic in this regard, because its FAD is in the lower Tremadoc "Argiles d'El Gassi" Formation of Algeria (borehole Fld-1, also the type locality of *C. messaoudensis*; Jardiné et al., 1974). The above described latest Tremadoc originations were accompanied by secondary, species-level extinction events within the genera *Acanthodiacrodium*, *Stelliferidium*, and *Vulcanisphaera*. Although the upper limit of the stratigraphic occurrence of the "*messaoudensis–trifidum*" assemblage is not precisely established, most representatives of the microflora range into, and constitute important elements of, typically early to middle Arenig acritarch assemblages.

4.3. Arenig radiation and development of palaeobiogeographical differentiation

Data on northern Gondwana early Arenig acritarchs are not abundant. In fact, lower Arenig sediments are not represented over most part of the North Sahara Platform, and the few available data are chronostratigraphically unconstrained (e.g., Jardiné et al., 1974). More information on early Arenig acritarchs comes from Bohemia (Vavrdová, 1993),

and South Wales (Molyneux, 1987). Middle to late Arenig acritarchs are better known, since they have been described from Bohemia (Vavrdová, 1965, 1966, 1972, 1973), South Wales (Molyneux, 1987), France (Rauscher, 1974), Morocco (Cramer et al., 1974a,b; Cramer and del Díez, 1977; Deunff, 1977; Elaouad-Debbaj, 1984), Algeria and Libya (Jardiné et al., 1974; Vecoli, 1999), and Sardinia (Albani, 1989). It follows that the basal Arenig diversity minimum (Fig. 7) might result from, or be enhanced by, a sample-size bias.

Even considering this latter effect, however, the Arenig appears to be a time of overall continuous increase in diversity and of morphological innovation among acritarch assemblages Figs. 5, 7, 8. The FADs of *Aureotesta*, *Tectitheca* and *Tongzia* (Vavrdová, 1993, and personal observation), and of the first representatives of triangular morphotypes of *Veryhachium* (Molyneux, 1987) occur near the base of the Arenig. Other genera, which appeared in latest Tremadoc times such as *Coryphidium*, *Pirea*, *Striatotheca*, and *Vavrdovella*, differentiated further, while herkomorph and diacromorph acritarchs declined both in relative abundance and diversity during the entire Arenig.

A further diversification pulse occurred during middle and late Arenig times, testified by the stepwise occurrences of FADs of morphologically complex and distinctive acritarchs such as *Arbusculidium filamentosum*, *Aureotesta* spp., *Dicrodiacrodium ancoriforme*, *Frankea sartbernardensis*, *Kladothecidium* spp., and *Vogtlandia* spp. The successive levels of appearances of these taxa and their relatively short stratigraphic ranges have important applications in northern Gondwana biostratigraphy (see discussions in Brocke et al., 1995, 2000; Vecoli, 1999; and Fig. 9). Moreover, the above species have a palaeobiogeographic distribution restricted to Peri-Gondwana localities, including South China, Argentina, Iran and Pakistan (Ghavidel-Syooki, 1993, 1995, 1996, 2000; Tongiorgi et al., 1994, in press; Yin, 1995; Brocke, 1998; Quintavalle et al., 2000; Rubinstein and Toro, 2001). During Arenig times, a distinction between two main groups of acritarchs becomes clear: on one hand those forms presenting extreme morphological specialization, short-ranges, and limited biogeographical distribution (e.g., *Arkonia*, *Aureotesta*, *Dicrodiacrodium*, *Vogtlandia*, etc.),

and on the other hand the long-ranging, morphologically conservative forms such as the Veryhachiids, but also some large forms of *Baltisphaeridium* (e.g., *B. klabavense*), which have a wide or even cosmopolitan biogeographical dispersal, hence appear more able to adapt to changing palaeoecological conditions (tolerant forms).

4.4. Llanvirn radiation and maximum palaeogeographical differentiation

Strata of Llanvirn age are well represented in the northern Gondwana region, and are generally very rich in well preserved acritarch microfloras; additionally, the frequent co-occurrence of chitinozoans and/or graptolites in acritarch-yielding samples, permits precise time-correlation. The data discussed herein come principally from our study of subsurface sections of the North Sahara Platform (Vecoli, 1999; Vecoli et al., 1999b, and unpublished results), complemented by the data on Moroccan acritarchs by Elaouad-Debbaj (1984: Tachilla Formation), and on Bohemian acritarchs by Vavrdová (1977, 1986: Šàrka Formation).

At or near the Arenig–Llanvirn boundary, a marked increase in acritarch diversity occurs, and a maximum in origination rates is recorded. The absolute maximum in the Ordovician acritarch diversity is reached in middle Llanvirn times. This first-order radiation is due to: (a) a new differentiation phase among galeate acritarchs (e.g., *Stelliferidium striatulum*); (b) the first occurrence of relatively short-ranging genera characterized by innovative and complex morphologies such as *Ampullula*, *Aremoricanium*, *Barakella*, *Dasydorus*, and *Ordovicidium*; (c) the appearance of new species of *Arkonia*, *Frankea*, *Coryphidium*, and the differentiation of Petenoid genera (*sensu* Playford et al., 1995: *Peteinosphaeridium*, *Liliosphaeridium*), in continuity with morphological trends established in the Arenig. During the Llanvirn, acritarch bioprovincialism was still very pronounced between the Baltica and the Peri-Gondwana provinces. However, starting from the upper part of the Series (Llandeilian Stage) we observe a progressive introduction of taxa showing a Baltic affinity, e.g., *Ampullula*, *Peteinosphaeridium*, *Sacculidium*, and large species of *Baltisphaeridium* (e.g., *B. ternatum*; Vecoli, 1999; Tongiorgi and Di Milia, 1999). Approximately at the same level, a sudden drop in origination rates is

recorded, followed by a steady increase in extinction rates, which caused a progressive and pronounced decline in acritarch diversity and a major turnover in acritarch assemblages. This turnover is responsible for the replacement of typical Middle Ordovician acritarch assemblages by the characteristic Upper Ordovician (Caradoc–Ashgill) suites.

4.5. Caradoc diversity low

The Caradoc Series is incompletely represented in many areas of the North Sahara Platform because of erosional and/or non-depositional events connected with the Late Ordovician glaciation (Figs. 2 and 3). In Algeria, southern Tunisia, and northwestern Libya, only lowermost to lower Caradoc sediments have been penetrated by deep boreholes (Paris et al., 1995, 2000; Vecoli, 1999; Vecoli et al., in press). The records of other North African Caradoc acritarchs documented by Jardiné et al. (1974) and Deunff and Massa (1975) lack sufficient detail (taxonomical and stratigraphical) and hence have little relevance for the present study. In other regions of the North Sahara Platform (e.g., in Cyrenaica, NE Libya), Caradoc sequences have yielded abundant and well preserved acritarchs, but independent age evidence is absent or not sufficient to establish precise chronostratigraphical correlation, and sampling is sparse (e.g., Hill and Molyneux, 1988; Paris, 1988). Acritarch assemblages from the Lower Ktaoua Formation in Morocco were described by Elaouad-Debbaj (1988a). These Moroccan assemblages appear poorly preserved and rather undiversified, but nonetheless are well constrained biostratigraphically by means of independent evidence (chitinozoans and graptolites) and give some useful information. Outside North Africa, Caradoc acritarch assemblages from well dated outcrop sections have been described by Henry (1969: Crozon peninsula, Brittany, France); by Rauscher (1974: Montagne Noire, Massif Central and May-sur-Orne Syncline, Normandy, France); by Elaouad-Debbaj (1978: Synclinal de Buçao, Portugal); and by Turner (1984: Shropshire, England). This latter work remains the most comprehensive among those dedicated to European localities, with almost 60 species of well preserved Caradoc acritarchs described. We note here that during Caradoc times, England, as part of Avalonian plate, was located much closer to Baltica,

hence in intermediate to low latitudes (southern hemisphere), than to northern Gondwana (Vecoli and Samuelsson, 2001). Nonetheless, we documented in the present study the occurrence of 60% of the species occurring in the English Caradoc assemblage described by Turner (1984).

In addition to the above data, recent palynological investigations from the subsurface of Turkey (Le Hérissé and Paris, unpublished) permit a better characterization of northern Gondwana Caradoc acritarch assemblages, because of high palynomorph yields, favourable preservation, and cross correlation with chitinozoan zonation.

The Caradoc is characterized by relatively low standing diversity (Figs. 7 and 8), which results from the major late Llanvirn extinction, which caused the almost complete disappearance of herkomorph (galeate) acritarchs, a marked reduction among diacromorphs (especially *Acanthodiacrodium* and *Arbusculidium*), and the total extinction of many characteristic Middle Ordovician taxa such as *Arkonia*, *Coryphidium*, *Kladothecidium*, *Pirea*, and *Vogtlandia*. A basal Caradoc peak in origination rates is nonetheless distinct, and several new morphotypes of acritarch of definite Late Ordovician morphological affinities first occur, such as *Enneadikosocheia granulata*, *Leprotolypa evexa*, *Nexosarium* spp., *Orthosphaeridium bispinosum*, and *Villosacapsula setosapellicula* (Figs. 6 and 9). Coupled to regularly declining extinction rates throughout the Series, this diversification pulse caused an increasing diversity trend throughout the second half of the Caradoc. Extinction rates show an almost regular decline, from relatively high values in the basal Caradoc, to very low values in the upper Caradoc.

Caradocian assemblages are also characterized by the introduction of large-sized species of *Baltisphaeridium* (e.g., the large and polymorphic *Baltispaeridium macroceros*), *Ordovicidium*, and *Orthosphaeridium*, similarly to what is observed also in Avalonian and Baltican localities (Górka, 1969, 1987; Kjellström, 1971a,b, 1976; Turner, 1984), and by abundance of triangular forms of *Veryhachium* spp. In the uppermost Caradoc, close to the base of the Ashgill (levels equivalent of the *robusta–fistulosa* chitinozoan Zones, observed in Turkey and Saudi Arabia), a number of morphologically distinctive taxa first occur: *Actinotodissus*, *Cheleutochroa*, *Multiplici-*

sphaeridium bifurcatum, *M. irregulare*, and *Neoveryhachium carminae*. Netromorph acritarchs (e.g., *Eupoikilofusa striatifera*, *Leiofusa* sp. cf. *L. fusiformis*) increase in abundance during this interval. This upper Caradoc speciation event is reflected by a peak in the curve of origination rates during Streffordian times (Fig. 8).

The above taxa have long stratigraphic distributions, ranging through to the Ashgill (some even through the Silurian), and show a wide if not global palaeobiogeographical dispersal, occurring in coeval assemblages of Avalonian and North American localities (Turner, 1984; Loeblich and Tappan, 1978; Colbath, 1979). This demonstrates the breakdown of the biogeographical barriers which existed during Arenig–Llanvirn times.

Caradoc acritarch assemblages are often characterized by the presence of considerable quantities of reworked acritarchs from older sediments (Tremadoc to Llanvirn; see also Turner, 1982). Numerous species of well established Llanvirn age such as *Arkonia virgata*, *Frankea sartbernardensis*, and species of *Stelliferidium*, are occasionally found in sediments of inferred but not definitely proven Caradoc age (e.g., in eastern Ireland and North Wales; Molyneux, 1990). We observed rare specimens of *Aremoricanium rigaudae*, *Dicrodiacrodium ancoriforme*, and *Stelliferidium* cf. *S. stelligerum* in Algerian strata attributed to the *deunfii* chitinozoan Zone (borehole NL2, Oued Saret Formation, lower Caradoc). This raises the question whether all such occurrences should be attributed to sediment reworking, or whether these "Middle Ordovician" forms actually range into higher levels. At the present state of knowledge, it is not possible to give a definite answer to this question, and this is reflected in Fig. 6 by a less precise determination of vertical ranges of numerous Middle Ordovician species.

4.6. Ashgill: the effects of a short-lived glaciation

Because of the large global drop in sea-level caused by the glaciation event (ca. 100 m; Ross and Ross, 1992), Ashgill deposits of northern Gondwana are characterized by important and extensive discontinuities (Paris et al., 1995; Ghienne, 2003). However, since they contain abundant organic-walled microfossils (acritarchs and chitinozoans), the dating of Ashgill deposits and the recognition of stratigraphic

discontinuities can be attained with a good degree of precision. This also permits the dating of the onset and duration of the various phases of the end-Ordovician glaciation (Paris et al., 1995; Le Hérissé and Vecoli, 2003). In Algeria, southern Tunisia, and northwestern Libya, glacial-related deposits (the "argiles microconglomératiques" of Saharan geologists; Beuf et al., 1971) of Hirnantian age rests directly on lower Caradoc or upper Llanvirn strata (Oued Saret Fm. in Algeria and Tunisia, Bir-Ben Tartar Fm. in Libya and Tunisia; Paris et al., 1995; Paris, 2000; Vecoli, 1999). In the Tindouf Basin, western Algeria, periglacial sandstones and conglomerates of the Djebilet Quartzite Formation lay unconformably on Precambrian rocks of the Reguibat Shield (Legrand, 1985; Paris et al., 1995; our unpublished acritarch data). Ashgill sedimentary sections in Morocco, southeastern Turkey, and Saudi Arabia are more continuous and have been palynologically investigated by us. In Morocco, an almost complete sedimentary record of the transition from pre-glacial to glacial situation is preserved (e.g., Bourahrouh, 2002), but unfortunately, acritarch yields of these sediments, and especially those related to pre-glacial conditions (Upper Katoua and Lower 2nd Bani Formations) are not abundant and palynomorph preservation is generally poor (Elaouad-Debbaj, 1988a; and personal investigation). In Saudi Arabia and Turkey, pre-glacial deposits, represented by the Quwarah Member of the Qasim Formation and the Bedinan Formation, respectively, (Fig. 3) yield abundant and well preserved palynological assemblages. Post-glacial Hirnantian sediments are well represented in northern Gondwana by transgressive, fine grained deposits (e.g., the M'Kratta Formation of Algeria, the sediments of the Hodh area in Mauritania—personal unpublished data; and the upper Kosov Formation in Bohemia—Vavrdová, 1982; Dufka and Fatka, 1993).

The "pre-glacial" Ashgill assemblages, dominated by species of *Baltisphaeridium*, *Multiplicisphaeridium*, *Ordovicidium*, *Orthosphaeridium*, and netromorph acritarchs, are mostly in continuity with the late Caradoc acritarch suites. Significant morphological innovations occur in the early Ashgill (levels correlated to the *nigerica* and *merga* chitinozoan Zones; Cautleyan), with the FADs of *Evittia remota*, *Moyeria cabotii*, *Poikilofusa spinata*, *Veryhachium hamii*, and species of *Tunisphaeridium* and *Gyalor-*

ethium. Many of these long ranging taxa show already a definite "Silurian" affinity.

The onset of the glaciation in Hirnantian times (levels correlated with the *elongata* chitinozoan Zone) is marked by a burst in the representation of triangular and extremely polymorphic morphotypes of *Veryhachium*, which replace almost completely the quadrangular forms of the same genus. Other genera showing an increase in polymorphism (enhanced intraspecific morphological variability) during glacial conditions are *Multiplicisphaeridium* and the netromorph acritarchs (e.g., *Dactylofusa*, *Leiofusa*, *Navifusa*, *Poikilofusa*). Hence, no extinction event is recorded in assemblages associated to glacial deposits, but only a marked change in relative abundance of taxa, with an over-representation of *Multiplicisphaeridium*, *Veryhachium*, and netromorphs acritarchs compared to pre-glacial conditions. Quite surprisingly, standing diversity increased through the glacial interval (Figs. 6–8), and even new speciations are recorded, with the FADs of morphologically distinctive, hence stratigraphically significant species such as *Beromia clipeata*, *Eupoikilofusa ctenista*, and *Saharidia munfarida*.

Acritarch assemblages associated with post-glacial sediments are well characterized by: (a) presence of reworked specimens of various ages from Tremadoc to pre-Hirnantian Ashgill; (b) a drop in relative abundance of the large *Baltisphaeridium*, *Ordovicidium*, *Ortosphaeridium*; and (c) the FADs of new distinct morphotypes of Silurian "affinity" like *Cymbosphaeridium* spp., *Tylotopalla* spp., and *Visbysphaera* spp.

5. Discussion

Acritarchs are considered to represent, in their majority, the resting cyst stage of the life cycle of unicellular organisms of planktic habit (Tappan, 1980). In analogy with the ecological behaviour of modern microphytoplankton (e.g., the dinoflagellates), it is reasonable to suppose that: (1) at any given time, only a portion of the Palaeozoic microphytoplankton produced preservable cysts (i.e., the acritarchs); (2) the proportion of cyst-producing species within a given community was a function of palaeoenvironmental conditions (De Vernal et al., 1998). It is evident that

the acritarch assemblages cannot be deemed as representative of the total microphytoplankton palaeobiocenoses; nonetheless, as a basis for further discussion, we assume that acritarch diversity dynamics provides indirect but valuable information on: (a) the response of cyst-producing microphytoplankton associations to variations in palaeoecological conditions; and (b) the broad evolutionary patterns of the acritarch-producing parent organisms.

Patterns of microphytoplankton diversification and evolution have often been correlated causally with changes in the palaeoceanographic conditions which in turn can be triggered by climatic and palaeogeographic modifications. For example, Fensome et al. (1996), maintained, on the basis of morphological considerations and molecular evidence, that dinoflagellates underwent a definite major radiation event during Triassic–Early Jurassic times, and considered the breakup of Pangaea as the primary stimulus for such an increased evolutionary activity. The synchronicity of significant global changes in evolutionary rates of dinoflagellate cysts with major palaeoceanographic events during Early Jurassic times was assumed by Bucefalo-Palliani and Riding (2002) as evidence for a primary abiotic control on dinoflagellate evolution. Similar conclusions were reached by the study of evolutionary patterns among Cretaceous radiolarians in relation to global palaeoceanographic events by O'Dogherty and Guex (2002). For the acritarchs, possible relationships between palaeoclimatic changes (especially glacial events in the late Proterozoic and Late Ordovician) and global patterns of radiations and extinctions were briefly discussed in a preliminary investigation by Le Hérissé and Moczydlowska (2000).

In what follows, we review the major modifications in the physical environment (eustasy, geodynamics, palaeoclimate), which are well documented to have occurred during the Ordovician and discuss their possible relevance to the diversification and extinction patterns observed among the acritarchs. A comparative analysis of Ordovician diversity patterns between acritarchs and chitinozoans is also proposed.

5.1. Acritarch biodiversity versus sea-level changes

Based principally on published sources (Beuf et al., 1971; Fortey, 1984; Erdtmann, 1986; Hallam,

1992; Miller, 1992; Ross and Ross, 1992; Sutcliffe et al., 2000) and partly on lithological information derived from core examination and analysis of petrophysical core-logs of North African boreholes, it is possible to reconstruct an Ordovician sea-level curve, relevant for the study area (Fig. 8). Major transgressive trends (second-order, frequency in the order of 10 my) are recognized during early (but not earliest) Tremadoc, early-middle Arenig, and late Llanvirn to early Caradoc times. General regressive trends (second-order) are recognized during late Tremadoc, late Arenig, and late Caradoc–Ashgill times. Third order sequencing (frequency of 1–3 my) organization of sedimentary stacking pattern and its relation with eustatic oscillations in northern Gondwana is largely speculative, and no regional stratigraphic sequence scheme has been developed for the area (Carr, 2002). However, there is evidence for third-order eustatic events (regressive–transgressive couplets) at the base of the Tremadoc, the uppermost Llanvirn (Llandeilo), at or near the Caradoc–Ashgill boundary. The amplitude of the eustatic oscillations (Fig. 8) is expressed qualitatively in arbitrary units, mainly based on lithological indicators of shifts in sedimentary facies (e.g., Loi, 1993, and personal communications). The large and widespread Hirnantian regression, linked to the Late Ordovician glacial event, is also a high-frequency (third order) eustatic feature (Sutcliffe et al., 2000).

Increasing diversity and high origination rates generally correlate to initial phases of second-order transgressive trends during early Tremadoc times, at the Tremadoc–Arenig transition, and during middle Llanvirn times (i.e., the highest peak in origination rates). However, an increase in diversity is also noticeable during the middle Arenig, corresponding to the regressive phase of a second-order eustatic cycle. Relatively high extinction rates and decreasing diversity correlate to a generally regressive phase during the upper-half of the Tremadoc. The highest extinction rates, recorded during late Llanvirn, and the associated decline in diversity seemingly occur during the initial phase of the large, second-order transgressive trend of Llanvirn to Caradoc age. However, it must be noted that a third-order eustatic oscillation, although not well documented in detail (Fig. 8), caused a regression during late Llanvirn to earliest Caradoc times, which could correlate with the large

late Llanvirn extinction event. During Caradoc times, although general conditions of high sea level were predominant, acritarch specific diversity was relatively low. The small peak in origination rates during Steffordian (late Caradoc) times is not linked to any known eustatic event, occurring during the regressive phase of the Late Ordovician second-order cycle. The Hirnantian regression is clearly linked to the onset of glacial conditions, and acritarch dynamics through this interval are therefore discussed in detail the next section. We note here only that acritarch diversity shows a peak corresponding to the maximum of the regression.

The variations in acritarch diversity and origination/extinction rates do not significantly match the eustatic oscillations of the 2nd order. There is insufficient resolution to precisely match acritarch diversity trends to 3rd order cycles. This general lack of correlation between acritarch diversity patterns and sea-level changes can be probably explained by the combined effect of the following factors: (1) the still incomplete knowledge of the regional sea-level curve and sequence stratigraphic framework of the study area (e.g., Carr, 2002); (2) the superposition of different signals in response to contemporaneous, non-eustatic palaeoenvironmental factors (palaeoclimate and palaeogeography, as discussed below); (3) possibly, a non-linear response of acritarch assemblage dynamics to transgressive–regressive trends.

It is now well established that at the scale of a sedimentary basin, acritarch diversity varies along an inshore–offshore transect as a function of varying palaeoecological conditions, including variation in water depth (e.g., Jacobson, 1979; Vecoli, 2000; Tongiorgi et al., 2003). This is due to palaeoenvironmentally controlled proportional changes in species composition of the assemblages (beta diversity of Sepkoski, 1988). At a larger scale, however, the controls of the eustatic factor on evolutionary dynamics of the acritarchs are much more problematical. In fact, standard palaeoecological models such as the species-area effect (e.g., Hallam, 1992) are not directly applicable to the acritarchs, because linear models of resource competition and ecological space occupation do not provide sufficient theoretical background to explain microphytoplankton diversity dynamics (e.g., the plankton paradox of Hutchinson, 1961;

Tappan and Loeblich, 1973; Martin, 1996a,b; Huisman and Weissing, 1999).

5.2. Acritarch biodiversity versus palaeoclimate

The Ordovician is considered by most authors (e.g., Legrand, 1983; Barnes et al., 1996; Scotese et al., 1999, and references herein) as a period of essentially stable hot house climatic conditions interrupted only by the well known, short-lived but severe Hirnantian glaciation (Brenchley et al., 1995). During the Ordovician "hot-house" climatic conditions (prevailing at least from Tremadoc to early-middle Caradoc times) average global temperatures might have been as high as 18–22 °C, no permanent ice cover was present even at the poles (Scotese et al., 1999), and high-latitude sea water temperature did not range below 5 °C (Wilde and Berry, 1986). Several lines of evidence (lithological, isotopical, and palaeontological) are in support of a major oceanic overturn to have occurred in latest Ordovician times in association with the Hirnantian glaciation (but for an alternative scenario see Munnecke et al., 2003). Cold, high latitude waters became denser than the warmer and highly saline, low latitude waters and displaced these latter provoking the advection of oxygen-depleted and metal-enriched deep waters to the surface, with lethal effect on most marine biotas. It is not surprising that such a sudden climatic and oceanographic change severely affected the biosphere at a global scale (Brenchley et al., 1995; Berry et al., 1995; Sheehan, 2003).

Changes in acritarch diversity observed in the late Ashgill (Figs. 6–8) can clearly be related to the effect of the climatic shift from hot-house to ice-house conditions and the associated oceanic overturn on the microphytoplankton communities. Although acritarch extinction rates show an acceleration in the Hirnantian, and overall generic diversity remained relatively low (but not significantly lower than during Caradoc times), a widespread and massive latest Ordovician extinction of the microphytoplankton did not occur, and origination rates surpassed extinction rates (Fig. 8). Even new genera of innovative morphology such as *Evittia* and *Oppilatala* evolved during the Hirnantian. These new genera not only survived during the glaciation, but persisted for long periods of time, constituting important components of

Silurian acritarch assemblages. The development of high morphological intraspecific variability and polymorphism among the netromorphs, the *Micrhystridium* group, and the veryhachiids is also a characteristic signal recorded among acritarch assemblages recovered from glacial-related sediments. All the above-mentioned acritarch forms are extremely long-ranging, and occur ubiquitously (albeit in variable abundances) in Ordovician–Silurian acritarch assemblages independently from palaeoenvironmental conditions. They are regarded here as the more tolerant forms, able to survive and adapt to changing palaeoecological situations. The distinctive "glacial signal" recorded in acritarch assemblages is therefore a strongly selective extinction of only the more stenothermal species, accompanied by increase in origination rates, and high polymorphism among the more ecologically tolerant forms.

Although some authors have suggested the presence of further glacial phases during the Ordovician, little evidence has been put forward in support of such claims. Evidence for a supposed minor glacial phase during earliest Ordovician times, as proposed by Miller (1984) has been deemed as equivocal and unconclusive (Barnes et al., 1996; and also see the review of Tremadoc climate data in Legrand, 1983). More recently, independent investigations have suggested an earlier initiation of the end-Ordovician climatic change, with minor, multiple glaciations developing since the middle-late Caradoc (Nielsen, 2003; Pope and Steffen, 2003). Such putative glacial pulses have been indirectly deduced from patterns of sea level oscillations (Nielsen, 2003), and sedimentological evidence of increased upwelling activity at the southern margin of Laurentia (Pope and Steffen, 2003). However, direct evidence of such glacial phases such as pre-Hirnantian glacial-related sediments are not found anywhere in Gondwana, according to the most up-to-date investigations and biostratigraphic datings (Paris et al., 1995; Bourahrouh, 2002).

Diversity changes of acritarchs (especially in the Silurian) have been incorporated within general models of biotic transitions associated to climatically driven, short-term, cyclic oscillations between oceanic states. These include the P-S model of Jeppsson (1990), Jeppsson et al. (1995), Jeppsson and Aldridge (2000), and the more recent H-A periods model of

Bickert et al. (1997) and Munnecke et al. (2003). Unfortunately, detailed studies on acritarch dynamics across such climatic and oceanic changes have not been documented and the (often assumed "a priori") variation in acritarch diversity is accounted for mainly in qualitative terms, and with insufficient detail (e.g., Jeppsson et al., 1995, pp. 489, 491; Munnecke et al., 2003, p. 119). Accordingly, it is not possible, at the present state of knowledge, to relate pre-Hirnantian acritarch diversity dynamics to minor climatic fluctuations which could have occurred during the course of large part of the Ordovician.

5.3. Acritarch biodiversity versus palaeogeographical evolution and palaeoceanographic changes

The steady increase in acritarch diversity occurring during earliest Arenig to middle Llanvirn times correlates with an increase in palaeogeographical dispersal of the principal Ordovician continental masses (Gondwana, Laurentia, and Baltica; Scotese and McKerrow, 1990, 1991; Schätz et al., 2002; Winchester et al., 2002). The correlation is even more interesting if one notes that the increase in diversity was paralleled by the development of a strong palaeobiogeographical differentiation of acritarch assemblages in the distinctive Baltic and Peri-Gondwana Provinces since the middle Arenig (Vavrdová, 1974, 1997; Tongiorgi and Di Milia, 1999). Such a palaeobiogeographical differentiation persisted until middle Llanvirn times. From early Caradoc onwards, after the important extinction event in the Llandeilian (late Llanvirn), acritarch assemblages appear to have a broadly cosmopolitan character but are less diverse than pre-Caradoc assemblages.

These correlations suggest that acritarch diversification patterns during the Ordovician might have been influenced by palaeogeographical changes, that is, ultimately by plate tectonics. In support of this view, we note that significantly similar patterns of increasing bioprovinciality during Arenig–Llanvirn times are observed globally within most marine faunal groups: conodonts (Bergström, 1990), trilobites, brachiopods, graptolites (Cocks and Fortey, 1990; Neumann and Harper, 1992), and cephalopods (Crick, 1990). Fossil groups of planktonic habit, such as graptolites (Finney and Xu, 1990), and chitinozoans (Vecoli and Samuelsson, 2001; Paris et al., 2004), even show the same strong signal of an "early Caradoc crisis" as seen among the acritarchs, with a marked reduction in diversity paralleling the pronounced bioprovincialism breakdown, even if at larger time scales the diversity trajectories of most marine invertebrates are totally decoupled from those shown by the acritarchs (see discussion below). The Arenig–Llanvirn palaeobiogeographical differentiation and the successive "Caradoc crisis" have been explained in a variety of ways by different authors. Tongiorgi and Di Milia (1999), and Tongiorgi et al. (in press) proposed that climatically and eustatically driven fluctuations in trophic resources were the responsible mechanisms of palaeobiogeographical differentiation. In order to explain the observed changes in palaeogeographical distribution of acritarch assemblages from Baltica and South China during Ordovician times, Tongiorgi et al. (1995) and more recently Raevskaya et al. (in press) emphasized the role of oceanic currents. Finney and Xu (1990) considered that graptolite provincialism was promoted by thermal gradients in oceans and differentiation of water-masses, mainly controlled by palaeoclimatic changes. Regarding the chitinozoans, Paris (in Paris et al., 2004) correlated high origination rates with marine transgressions during middle Arenig and early Llanvirn times, and proposed that palaeoceanic factors (namely increased oceanic communication between Baltica and the northern Gondwana margin) might explain the observed high turnover rates during early Caradoc times.

Numerical palaeoclimatic and palaeoceanographical modeling applied to mid-Cretaceous situations (Poulsen et al., 1998) has shown that even small modifications to continental geometry are potentially able to significantly alter global oceanic circulatory patterns with profound, global effects on the marine environment. Thus, it is not surprising to observe that a first-order correlation exists between palaeogeographic evolution and the evolutionary dynamic response of the marine biota, including the acritarchs. While there are no published investigations on numerical palaeoceanic models for the Palaeozoic, two interpretative, or conceptual, models (Wilde, 1991; Christiansen and Stouge, 1999) of oceanic circulation have been proposed for the Early Ordovician (Figs. 10 and 11). The two models differ in the assumed location of the planetary subtropical high- and temperate low-pressure zones, which are respectively
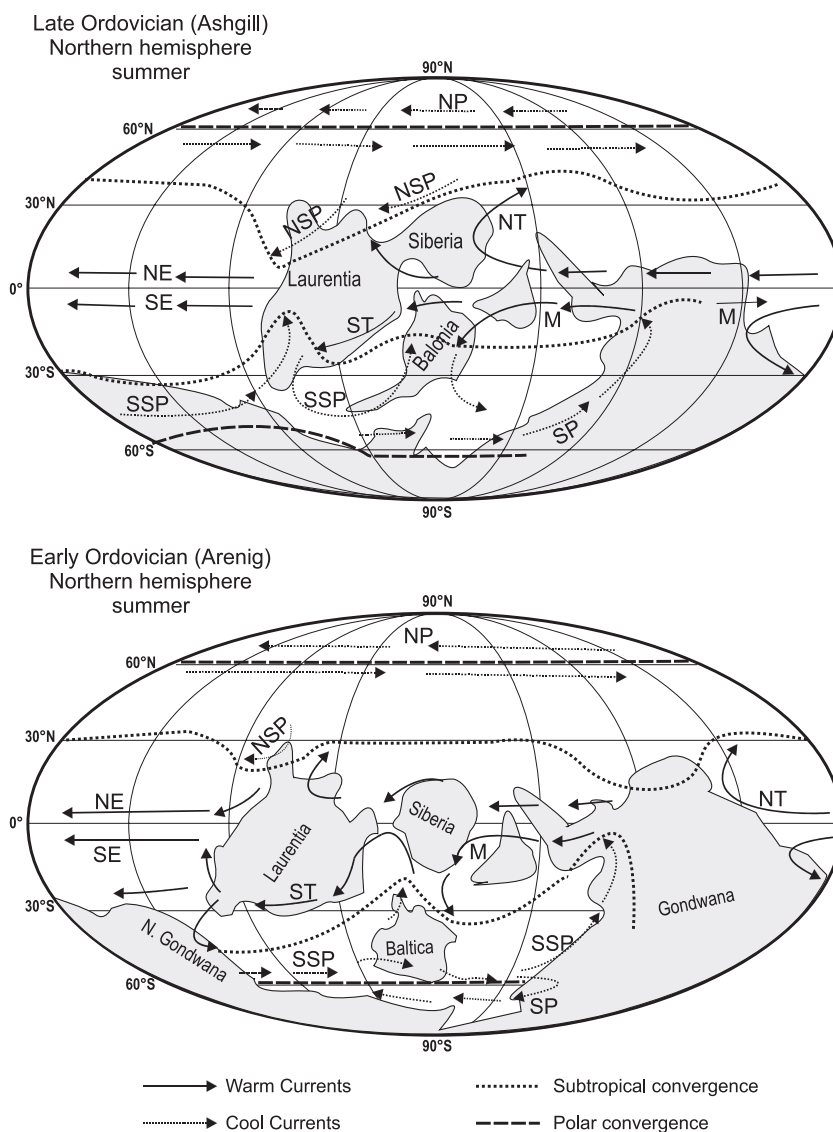
Fig. 10. Reconstruction of global patterns of oceanic palaeocurrents during Arenig and Ashgill times according to Wilde (1991). NP, North Polar current; NSP, North Subpolar current; NT, North tropical current; NE, North Equatorial current; SE, South Equatorial current; M, Monsoonal current; ST, South Tropical current; SSP, South Subpolar current; SP, South Polar current.

placed at 30° and 60° latitudes by Wilde (1991), and 25° and 60° latitudes by Christiansen and Stouge (1999). In terms of patterns of oceanic currents, both models show broadly similar location and geometry of the temperate-cyclone and the subtropical-anticyclone gyres in the region of the northern Gondwana, Baltica, and Laurentia interface (southern hemisphere), but an important difference between the two models consists in the direction of the South Subpolar Current, which flows constantly in a W–E direction in the model of Wilde (1991) and in the opposite direction (E–W) in Christiansen and Stouge (1999) reconstruction (Figs. 10 and 11). Despite this discrepancy in the interpretation of the flow direction of SSC, both models
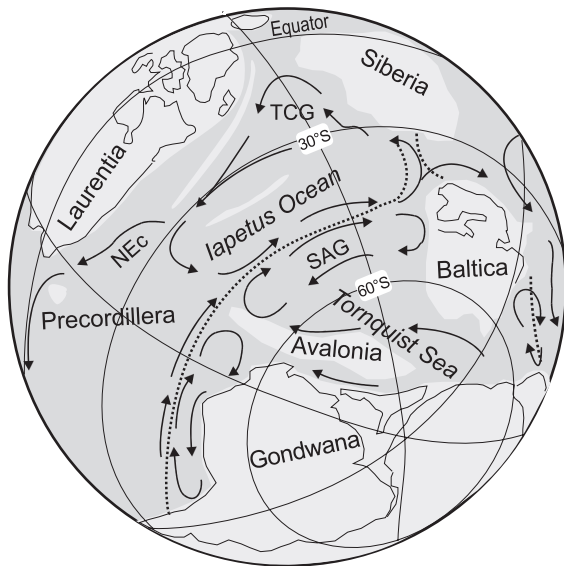
Fig. 11. Reconstruction of oceanic palaeocurrents during Arenig times in the region of interface between Laurentia, Baltica, and northern Gondwana, according to Christiansen and Stouge (1999); slightly modified from the original. Arrows, oceanic currents; TCG, Tropical Cyclonic Gyre; SAG, Subtropical Anticyclonic Gyre; NEc, North Equatorial current; SSP, South Subpolar current; dotted line, boundary between warm and cold surface currents.

explain the Middle Ordovician bioprovincialism in terms of circulation of discrete water masses of different physical properties. It is reasonable to expect that the conspicuous palaeogeographical evolution which occurred from Arenig to Caradoc–Ashgill times, would have strongly modified the global circulatory patterns, and especially in the region of the Gondwana–Baltica–Laurentia oceanic interface. Some clues concerning this latter point are provided by the palaeoceanographic model of Wilde (1991) which shows that from Middle to Late Ordovician the subtropical convergence shifted significantly to the north, causing an expansion of the cool subtropical water masses to include most of the oceanic waters fringing the northern Gondwana margin, southern Laurentia, and the eastern part of Avalonia–Baltica block (Balonia; Fig. 10). This change in water mass configuration might explain the observed increase in cosmopolitanism, following the physical breakdown of palaeobiogeographical barries (including in this term boundary surfaces between water-masses of different chemical–physical properties).

5.4. Acritarch versus marine invertebrate biodiversity

Considering that acritarchs represent the fossil record of an important component of the oceanic primary producers especially in Pre-Mesozoic times, an interesting question to be addressed is if it is possible to establish any relationship between fossil microphytoplankton and marine invertebrate diversity (generic or specific) during the Palaeozoic. In a preliminary and global survey of Phanerozoic acritarch diversity, Strother et al. (1996) and Strother (1996) affirmed that phytoplankton and invertebrate diversities were decoupled from each other. If we compare our diversity curve with published, Sepkoski-style curves of specific or generic invertebrate diversity in Cambro-Ordovician times (e.g., Sepkoski, 1996), the decoupling between acritarch and marine invertebrates evolutionary trends is confirmed. In this respect, the biodynamical behaviour of acritarch populations across periods of global ecological perturbations such as the end-Ordovician, the various Silurian, and the end-Devonian biotic crises are particularly interesting. As we have described previously, the acritarch record of the end-Ordovician crisis does not mirror the extinction patterns observed among the marine invertebrates. Extinction events among acritarchs through the Early Silurian Ireviken event at Gotland (Gelsthorpe, 2002a,b) seemingly do not correlate with observed extinction datums among conodont and trilobite fauna (Jeppsson, 1990). According to Le Hérissé (unpublished), changes in diversity of acritarch assemblages consistently occur before the major extinctions of pelagic graptolites and conodonts at the Ireviken and Lundgreni events at Gotland, Sweden. The global Frasnian–Fammenian biotic crisis (McGhee, 1996), which caused the extinction of three-quarters of all animal species and more than half of all the genera (Sepkoski, 1986), did not affected much the acritarchs, which declined in diversity only much later, i.e., at the Devono-Carboniferous boundary (Vanguestaine, 1986; Martin, 1993; Riegel, 1996; Strother, 1996; Streel et al., 2000).

A simple and direct producer–consumer relationship between acritarch and metazoan biotas has been suggested in the past, with high acritarch diversity assumed as index of high primary production and

food availability for consumers (e.g., Tappan, 1968, 1971, 1982, 1986; but also see Jeppsson et al., 1995; Moczydlowska, 2002). Based on this concept, and on biostratigraphic correlation of bioevents, Moczydlowska (2002) even suggested a direct relationship between phytoplankton and metazoan evolutive diversification patterns. However, some recent studies demonstrate that such views are in contrast both with fossil evidence and ecological considerations (Martin, 1995, 1996; Falkowski and Rosenthal, 2001; Katz et al., 2003). For example, Falkowski and Rosenthal (2001) argued that the application of number of genera in marine animals does not correlate with diversity of their ultimate food source (the phytoplankton), nor it does correlate with productivity. This is also a consequence of the problem of equivalence of taxa, which are to be compared in diversity studies. Marine invertebrate diversity is best represented at familial level (Benton, 1995; Falkowski and Rosenthal, 2001), but taxonomic difficulties impede an evaluation of acritarch diversity at taxonomic rank higher than generic level. It is also to note that absence of acritarchs in the oceanic sediments cannot be directly related to absence of primary producers in the water column.

Further complications of the oceanic producers–consumers evolutive relations are the lack of food specificity of marine invertebrates, the high heterogeneity of marine trophic resources (Strother et al., 1996), and the different abilities of the various organismal stock to react to contractions/expansions of the base of the food chain, in particular to survive periods of nutrient starvation. These factors are mainly related to metabolic needs, biomass, and general physical activity, or more simply, the "energetics" of the different marine fauna, as defined by Bambach (1999). The latter author introduced the concept of change in energetics in marine faunas in order to explain the observed lack of correlation between increased nutrient input (hence augmented productivity) in the oceans, and the expected increase in marine diversity, and the offset of in diversification rates of marine faunas, during the two main phases of land plant and terrestrial ecosystem evolution in Ordovician through Carboniferous, and Cretaceous through Cenozoic times. In the more general situations, and according to Bambach (1999), we can expect that differentiation patterns of

"low energy" consumers would be less dependent on fluctuations of trophic resources (including the phytoplanktonic acritarch parent organisms), than "high energy" predators. Such complex and heterogeneous responses of the organismal stocks to oscillations in nutrient levels further complicate the analysis of the correlations between phytoplankton and marine invertebrate faunas biodiversification patterns.

Thus, the relationships between level of oceanic primary production, diversity and abundance of organic-walled microphytoplankton cysts in the oceanic sediments, and evolution of metazoan phyla are much less straightforward than it might appear and require further detailed analyses.

Keeping in mind these difficulties, and the recent findings that Phanerozoic metazoan diversification patterns followed different trends in different geodynamic domains (Miller, 1997; Cope and Babin, 1999), it is evident that any meaningful analysis of the trophic relationships among different groups of organismal stocks should be first of all conducted at the scale of palaeobioprovince, within a geodynamically homogeneous area, and only if reliable biostratigraphic correlation is available (Erwin, 1999).

In the present investigation, we limit the comparison of diversity trends between Ordovician acritarchs and chitinozoans from northern Gondwana (Fig. 12). Comparison with diversity trends of other fossil groups are not feasible because of the scarcity of detailed regional studies (see Erwin, 1999), with the notable exception of the investigations by Babin (1993) and Cope and Babin (1999) on diversification trends of Gondwanan bivalves. These latter accounts, however, are conducted at higher taxonomic level (families) and diversification trends described in narrative form, making quantitative comparison with our diversity curve difficult.

Other reasons for focusing on chitinozoans are the following:

(1) Although the origin and biological affinities of chitinozoans are still debated (Miller, 1996), general consensus is converging on the hypothesis that these microfossils represent eggs of soft-bodied metazoans (Grahn, 1981; Paris et al., 1999). According to Paris and Nõlvak (1999), the diversity of chitinozoan assemblage are fully representative of the corresponding diversity of the "chitinozoan animal".
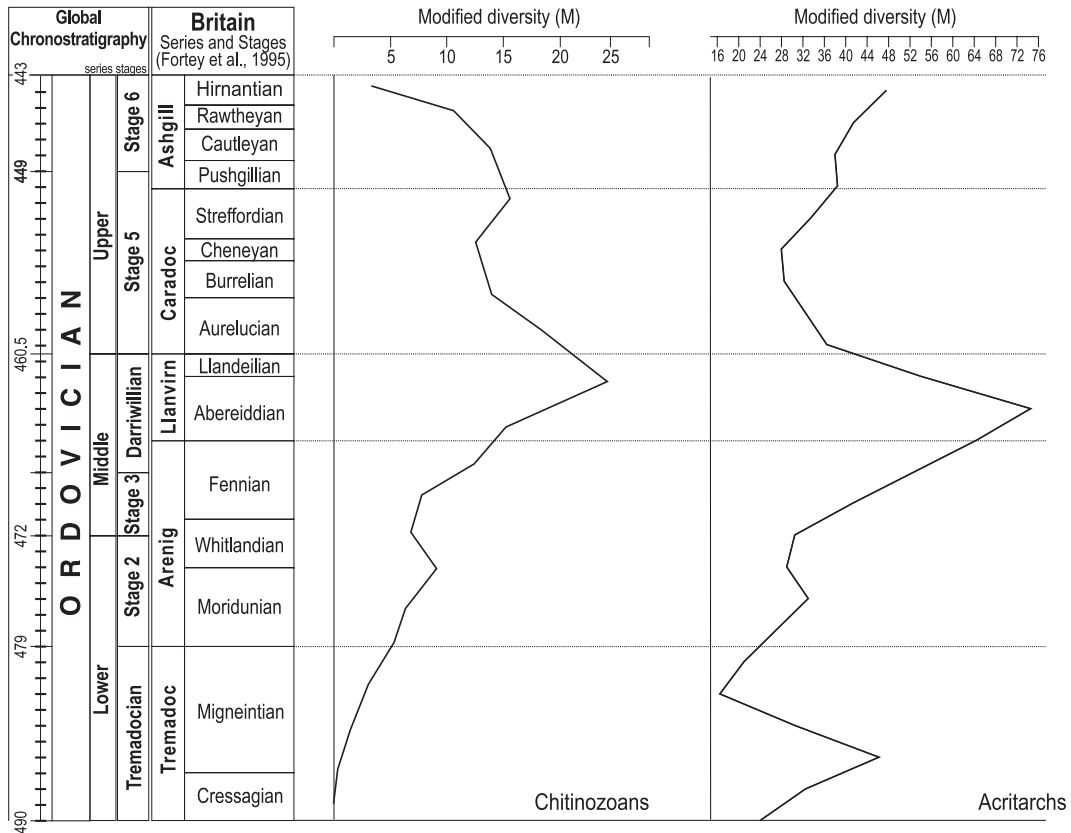
Fig. 12. Comparison between Ordovician diversity of chitinozoans (from Paris in Paris et al., 2004) and acritarchs from northern Gondwana.

(2) Accepting this view, even if their feeding strategies and preferences are unknown, the "chitinozoan animals" can be considered at the lowest trophic level among consumers.

(3) Chitinozoans and acritarchs are often found associated in the same rocks, and are extracted using the same laboratory procedures. A recent analysis of Ordovician chitinozoan diversity from northern Gondwana is available for comparison (Paris et al., 2004), permitting a very good degree of temporal and spatial correlation with acritarch diversity dynamics.

Northern Gondwana chitinozoan assemblages are characterized by overall low diversity (10 to 20 species per time slices of 2–3 million year duration on average) and high specimen abundance in the sediments (order of 100s of specimens per gram of rock), a distribution pattern similar to those of modern marine faunal groups. The Ordovician chitinozoan diversity curve (Modified Diversity; Paris in Paris et al., 2004) shows the following features (Fig. 12): a steady increase from the basal Tremadoc to Llanvirn, a maximum diversity peak in the late Llanvirn, a diversity drop in early Caradoc followed by a further diversity maximum in middle-late Caradoc times, and a progressive decline starting in late Caradoc times, culminating in the latest Ordovician mass-extinction. Origination rates surpassed extinction rates during most of the Early Ordovician, highlighting the Tremadoc radiation, and generally mirroring the diversity curve for the rest of the Ordovician. Distinct peaks in origination rates were recorded during early Arenig, late Llanvirn, and late Caradoc times. Extinctions counterbalanced originations from the middle Arenig to the latest Llanvirn, and peaked during middle Caradoc and Hirnantian times.

Paris (in Paris et al., 2004) considered the Tremadoc through late Llanvirn increase in diversity as due to intrinsic factors such as the high evolutionary potential of the radiating chitinozoa clade, which was favoured by stable climatic conditions and available ecospace. This Early Ordovician chitinozoan radiation is a global feature observed in all palaeoplates. The Hirnantian crisis was also global in character and deemed as to reflect the response to onset of particularly adverse climatic conditions of the end-Ordovician glaciation. This crisis was however not a sudden one because it was clearly preceded by a steady decline in diversity during middle Caradoc to middle Ashgill times. This diversity decline was attributed by Paris (in Paris et al., 2004) to a global change, possibly increased CO_2 partial pressure, and/or volcanic activity.

According to Paris (in Paris et al., 2004), marine transgressions as well as changes in palaeogeography and associated modification of water masses mixing, favoured increase in chitinozoan diversity and origination rates, such as observed during middle Arenig, early Llanvirn, and the high turnover rates during the early Caradoc. The possible role of oscillations in nutrient availability and oceanic primary production on chitinozoan diversity dynamics were not discussed in the investigation of Paris et al. (2004).

Comparing acritarch and chitinozan diversity curves (Fig. 12) highlights the following: similar features are an overall diversity increase from the earliest Tremadoc to the Llanvirn, the maximum diversity peak during late Llanvirn times, the highest turnover rates recorded at about the Llanvirn–Caradoc transition, and the early Caradoc diversity drop. Two maxima in the chitinozoan curve (early Arenig and late Llanvirn) correspond, within the limits of error bars, to maxima in the acritarch curve. On the other hand, the two diversity curve are partly decoupled during Tremadoc and late Ashgill (Hirnantian) times. The overall good correlation between the two diversity curves might be an indication of causal links between evolutionary patterns of the acritarchs and those of the chitinozoans, which represent microzooplankton and hence are directly linked through trophic relations to the oceanic microphytoplankton.

6. Conclusions

Clues on the mechanisms of palaeoenvironmental control on processes of biotic diversifications in the geological past can be obtained through a careful qualitative and quantitative evaluation of evolutionary patterns of the various fossil groups in the background of a changing geosphere. A new study approach is to analyze such patterns within geodynamically and palaeobiogeographically homogeneous areas, instead of globally, because organismal diversification trajectories bear strong geographic overprints (Miller, 1997).

Mostly based on original investigations and on first-hand revision of published works, leading to the compilation of a taxonomically consistent and chronostratigraphically well constrained dataset, in the present paper we have analyzed the diversity and biodynamics patterns of acritarch communities during latest Cambrian through latest Ordovician times in the regions of the northern Gondwana margin.

The following conclusions can be drawn:

(1) The taxonomic composition of acritarch assemblages and their distribution in the sediments reflect the different ecological tolerances and life cycles of the planktonic producers;

(2) It appears that evolutionary patterns of the acritarchs were primarily influenced by changes in palaeogeography and palaeoceanographic conditions;

(3) Acritarchs show a strong survival capability during periods of ecological perturbations such as the end-Ordovician glaciation;

(4) Good correlation exists between the diversity curves of the acritarchs and the chitinozoans during the Ordovician;

(5) The use of acritarchs to infer levels of oceanic production or the relationships between Palaeozoic microphytoplankton and metazoan evolution are more complex than previously suggested, and require further detailed palynological studies coupled to biogeochemical investigations.

Appendix A

List of taxa cited in text and in the range charts with author-names. The numbers refer to the entries in the range charts of

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Genus *Acanthodiacrodium* Timofeev, 1958 emend. Deflandre and Deflandre-Rigaud, 1962
14 *Acanthodiacrodium achrasii* Martin, 1973
71 *Acanthodiacrodium amplium* Rasul, 1979
70 *Acanthodiacrodium anfractum* Rasul, 1979
95 *Acanthodiacrodium angustizonale* Burmann, 1968
31 *Acanthodiacrodium angustum* (Downie) Combaz, 1967
29 *Acanthodiacrodium baculatum* Vecoli, 1996
30 *Acanthodiacrodium capillatum* Vecoli, 1996
34 *Acanthodiacrodium complanatum* (Deunff) Umnova, 1975
35 *Acanthodiacrodium comptulum* Rasul, 1979
96 *Acanthodiacrodium costatum* Burmann, 1968
182 *Acanthodiacrodium crassus* (Loeblich and Tappan) Vecoli, 1999
94 *Acanthodiacrodium decipiens* Timofeev, 1959 *ex* Downie and Sarjeant, 1965
75 *Acanthodiacrodium dilatum* Molyneux in Molyneux and Rushton, 1988
41 *Acanthodiacrodium formosum* Górka, 1967
112 *Acanthodiacrodium rauscheri* Cramer and Díez, 1977
69 *Acanthodiacrodium* (=*Priscotheca*) *raium* (Deunff) Tongiorgi in Bagnoli et al., 1988
40 *Acanthodiacrodium rotundatum* Górka, 1967
27 *Acanthodiacrodium simplex* Combaz, 1967
67 *Acanthodiacrodium spinum* Rasul, 1979
113 *Acanthodiacrodium tadlense* Cramer and Díez, 1977
42 *Acanthodiacrodium ubui* Martin, 1969
91 *Acanthodiacrodium uniforme* Burmann, 1968
114 *Acanthodiacrodium vavrdovae* Cramer and Díez, 1977
76 *Acanthodiacrodium* sp. *1* of Servais and Mette, 2000
33 *Acanthodiacrodium* sp. cf. *A. angustum* (Downie) Combaz, 1967
Genus *Actinotodissus* Loeblich and Tappan, 1978
191 *Actinotodissus longitaleosus* Loeblich and Tappan, 1978
Genus *Actipilion* Loeblich, 1970
194 *Actipilion* sp. cf. *A. druggii* Loeblich, 1970
Genus *Ammonidium* Lister, 1970
243 *Ammonidium* spp.
Genus *Ampullula* Righi, 1999 emend. Brocke, 1998
142 *Ampullula suetica* Righi, 1991

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Genus *Ankyrotrochos* Vecoli, 1999
131 *Ankyrotrochos crispum* (Vavrdová) Vecoli, 1999
Genus *Anomaloplasium* Tappan and Loeblich, 1971
222 *Anomaloplasium lumariacuspis* Tappan and Loeblich, 1971
115 *Anomaloplasium tappaniae* Cramer and Díez, 1977
Genus *Arbusculidium* Deunff, 1968 emend. Welsch, 1986
32 *Arbusculidium destombesii* Deunff, 1968
100 *Arbusculidium filamentosum* (Vavrdová) Vavrdová, 1972
Genus *Aremoricanium* Deunff, 1955
151 *Aremoricanium carolinae* Kjellström, 1976
116 *Aremoricanium deflandrei* Henry, 1969
130 *Aremoricanium rigaudae* Deunff, 1955
168 *Aremoricanium squarrosum* Loeblich and MacAdam, 1971
Genus *Arkonia* Burmann, 1970
145 *Arkonia virgata* Burmann, 1970
146 *Arkonia* sp. cf. *A. semigranulata* Uutela and Tynni, 1991
157 *Arkonia* sp. A of Vecoli, 1999
Genus *Athabascaella* Martin, 1984
57 *Athabascaella* sp. A of Vecoli (in press)
Genus *Attritasporites* Combaz, 1967
28 *Attritasporites* spp.
Genus *Aureotesta* Vavrdová, 1972
108 *Aureotesta clathrata* (Vavrdová) emend. Brocke et al., 1997.
Genus *Baltisphaeridium* Eisenack, 1958 ex Eisenack, 1959 emend. Eiserhardt, 1989
228 *Baltisphaeridium aliquigranulum* Loeblich and Tappan, 1978
195 *Baltisphaeridium christoferi* Kjellström, 1976
6 *Baltisphaeridium crinitum* Martin, 1978
149 *Baltisphaeridium dasos* Colbath, 1979
90 *Baltisphaeridium hirsutoides* (Eisenack) Eisenack, 1959
102 *Baltisphaeridium klabavense* (Vavrdová) Kjellström, 1971a,b
173 *Baltisphaeridium latiradiatum* (Eisenack) Staplin et al., 1965
147 *Baltisphaeridium llanvirnianum* Deunff, 1977
192 *Baltisphaeridium longispinosum* (Eisenack) Eisenack, 1959
172 *Baltisphaeridium macroceros* (Deunff) Elaouad-Debbaj, 1978
162 *Baltisphaeridium ternatum* (Burmann) emend. Rauscher, 1974
54 *Baltisphaeridium verutum* Vecoli, 1996
148 *Baltisphaeridium*? *bramkaense* Górka, 1979
78 *Baltisphaeridium* sp. *A* of Servais and Mette, 2000
177 *Baltisphaeridium* sp. cf. *B. hirsutoides* (Eisenack) Eisenack, 1959
170 *Baltisphaeridium* sp. cf. *B. loeblichii* Colbath, 1979
43 *Baltisphaeridium* sp. cf. *B. microspinosum* (Eisenack) Downie, 1959
227 *Baltisphaeridium* sp. cf. *B. perclarum* Loeblich and Tappan, 1978
Genus *Baltisphaerosum* Turner, 1984
176 *Baltisphaerosum* sp. cf. *B. dispar* Turner, 1984
Genus *Barakella* Cramer and Díez, 1977
122 *Barakella fortunata* Cramer and Díez, 1977
123 *Barakella rara* (Lu Li-chang) emend. Tongiorgi et al., 1995
Genus *Beromia* Vavrdová, 1986
226 *Beromia clipeata* Vavrdová, 1986

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Genus *Buedingisphaeridium* Schaarschidt, 1963 emend. Lister, 1970
  63 *Buedingisphaeridium tremadocum* Rasul, 1979
  231 *Buedingisphaeridium* spp.
Genus *Caldariola* Molyneux in Molyneux and Rushton, 1988
  62 *Caldariola glabra* (Martin) Molyneux in Molyneux and Rushton, 1988
Genus *Cheleutochroa* Loeblich and Tappan, 1978 emend. Turner, 1984
  198 *Cheleutochroa diaphorosa* Turner, 1984
  197 *Cheleutochroa gymnobrachiata* Loeblich and Tappan, 1978
Genus *Comasphaeridium* Staplin et al., 1965
  174 *Comasphaeridium* sp. cf. *C. lanugiferum* Jacobson and Achab, 1985
  117 *Comasphaeridium* spp.
Genus *Coryphidium* Vavrdová, 1972
  135 *Coryphidium bohemicum* Vavrdová, 1972
  92 *Coryphidium* spp.
Genus *Cristallinium* Vanguestaine, 1978 ex Fensome et al. (1990)
  15 *Cristallinium ovillense* (Cramer and Díez) Fensome et al. (1990)
  1 *Cristallinium randomense* (Martin) Fensome et al. (1990)
Genus *Cymatiogalea* Deunff, 1961 emend. Deunff et al., 1974
  45 *Cymatiogalea cristata* (Downie) Rauscher, 1974
  22 *Cymatiogalea cuvillieri* (Deunff) Deunff, 1974
  80 *Cymatiogalea deunfii* Jardiné et al., 1974
  46 *Cymatiogalea gorkae* Rauscher, 1974
  44 *Cymatiogalea membranispina* Deunff, 1961
  36 *Cymatiogalea messaoudensis* Jardiné et al., 1974
  47 *Cymatiogalea multarea* (Deunff) Eisenack et al., 1973
  26 *Cymatiogalea parva* Vecoli, 1996
  21 *Cymatiogalea velifera* (Downie) Martin, 1969
  13 *Cymatiogalea virgulta* Martin, 1988
Genus *Cymbosphaeridium* Lister, 1970
  242 *Cymbosphaeridium* spp.
Genus *Dactylofusa* Brito and Santos, 1965 emend. Cramer, 1971
  224 *Dactylofusa cucurbita* Jardiné et al., 1974
  225 *Dactylofusa parvuligranosa* (Loeblich and Tappan) Fensome et al. (1990)
  235 *Dactylofusa platinetrella* (Loeblich and Tappan) Fensome et al. (1990)
  223 *Dactylofusa striatogranulata* Jardiné et al., 1974
  81 *Dactylofusa velifera* Cocchio, 1982
Genus *Dasydiacrodium* Timofeev, 1959 ex and emend. Deflandre and Deflandre-Rigaud, 1961
  65 *Dasydiacrodium cilium* Rasul, 1979
  9 *Dasydiacrodium obsonum* Martin, 1988
  19 *Dasydiacrodium tumidum* (Deunff) Tongiorgi, in Bagnoli et al., 1988
Genus *Dasydosrus* Playford and Martin, 1984
  154 *Dasydosrus cirritus* Playford and Martin, 1984
Genus *Dicommopalla* Loeblich, 1980
  229 *Dicommopalla macadamii* Loeblich, 1970
Genus *Dicrodiacrodium* Burmann, 1968
  111 *Dicrodiacrodium ancoriforme* Burmann, 1968 emend. Servais et al., 1996

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Genus *Elenia* Volkova, 1984
  16 *Elenia armillata* (Vandeflit) Volkova, 1984
Genus *Enneadikosocheia* Colbath, 1979
  171 *Enneadikosocheia granulata* Colbath, 1979
Genus *Eponula* Vavrdová, 1986
  238 *Eponula saccata* Vavrdová, 1986
Genus *Ericanthea* Cramer and Díez, 1977
  120 *Ericanthea pollicipes* Cramer and Díez, 1977
Genus Eupoikilofusa Cramer, 1971
  220 *Eupoikilofusa ctenista* Loeblich and Tappan, 1978
  240 *Eupoikilofusa obesa* Vavrdová, 1989
  24 *Eupoikilofusa simplex* Combaz, 1967
  23 *Eupoikilofusa squama* (Deunff) Elaouad-Debbaj, 1988
  187 *Eupoikilofusa striatifera* Cramer, 1964
Genus *Evittia* Brito, 1967 emend. Lister, 1970
  213 *Evittia* (=*Diexallophasis*) *remota* (Deunff) Lister, 1970
Genus *Excultibrachium* Loeblich and Tappan, 1978
  237 *Excultibrachium* spp.
Genus *Ferromia* Vavrdová, 1979 emend. Martin, 1996a,b
  143 *Ferromia clavula* Vecoli, 1999
  59 *Ferromia pellita* (Martin) emend. Martin, 1996a,b
Genus *Fractoricoronula* Colbath, 1979
  190 *Fractoricoronula trirhetica* Colbath, 1979
Genus *Frankea* Burmann, 1970 emend. Servais, 1993
  132 *Frankea breviuscula* Burmann, 1970
  160 *Frankea hamata* Burmann, 1970
  161 *Frankea hamulata* Burmann, 1970
  166 *Frankea longiuscula* Burmann, 1970
  167 *Frankea sartbernardensis* (Martin) Colbath, 1986
Genus *Goniosphaeridium* (Eisenack) emend. Turner, 1984
  184 *Goniosphaeridium polygonale* (Eisenack) Eisenack, 1959
  66 *Goniosphaeridium rasulii* Welsch, 1986
Genus *Gyalorethium* Loeblich and Tappan, 1978
  212 *Gyalorethium* spp.
Genus *Heloriopodum* Servais and Molyneux, 1997
  73 *Heloriopodum palliatum* (Mette) Servais and Molyneux, 1997
Genus *Helosphaeridium* Lister, 1970
  150 *Helosphaeridium paxillum* Vecoli, 1999
Genus *Impluviculus* Loeblich and Tappan, 1969
  56 *Impluviculus* spp.
Genus *Kladothecidium* Vavrdová, 1986
  129 *Kladothecidium eligmosum* (Vavrdová) Vavrdová, 1986
Genus *Ladogella* Golub and Volkova in Volkova and Golub, 1985
  4 *Ladogella rommellaerei* (Martin) Di Milia et al., 1989
  5 *Ladogella rotundiformis* Volkova and Golub, 1985
Genus *Leiofusa* Eisenack, 1938 emend. Combaz et al., 1967
  209 *Leiofusa estrecha* Cramer, 1964
  202 *Leiofusa fusiformis* (Eisenack) Eisenack, 1938
  163 *Leiofusa* sp. cf. *L. fusiformis* (Eisenack) Eisenack, 1938
  205 *Leiofusa* sp. cf. *L. litotes* Loeblich and Tappan, 1978
  217 *Leiofusa* sp. aff. *L. tumida* of Molyneux, 1988
Genus *Leprotolypa* Colbath, 1979
  185 *Leprotolypa evexa* Colbath, 1979
Genus *Liliosphaeridium* Uutela and Tynni, 1991 emend. Playford et al., 1995
  133 *Liliosphaeridium pennatum* (Deunff) Playford et al., 1995

Appendix A (*continued*)

Genus *Lophodiacrodium* Timofeev, 1958 emend. Deflandre and Deflandre-Rigaud, 1962

  64 *Lophodiacrodium torum* Rasul, 1979

  7 *Lophodiacrodium valdaicum* (Timofeev) Downie and Sarjeant, 1965

Genus *Lophosphaeridium* Timofeev, 1959 ex Downie, 1963

  125 *Lophosphaeridium fuscipetiolatum* (Cramer and Díez) Vecoli, 1999

Genus *Moyeria* Thusu, 1973

  214 *Moyeria cabotii* (Cramer) emend. Miller and Eames, 1982

Genus *Multiplicisphaeridium* Staplin, 1961 emend. Turner, 1984

  55 *Multiplicisphaeridium attenuatum* Vecoli and Playford, 1997

  200 *Multiplicisphaeridium bifurcatum* Staplin et al., 1965

  12 *Multiplicisphaeridium cervinacornuum* Welsch, 1986

  211 *Multiplicisphaeridium cladum* (Downie) Eisenack, 1969

  219 *Multiplicisphaeridium consolator* Cramer and Díez, 1977

  156 *Multiplicisphaeridium dikranon* Vecoli, 1999

  201 *Multiplicisphaeridium irregulare* Staplin et al., 1965

  210 *Multiplicisphaeridium paraguaferum* (Cramer) Lister, 1970

  189 *Multiplicisphaeridium raspa* (Cramer) Eisenack et al., 1973

  126 *Multiplicisphaeridium rayii* Cramer et al., 1974a,b

Genus *Navifusa* Combaz et al., 1967 ex Eisenack, 1976

  158 *Navifusa punctata* Loeblich and Tappan, 1978

  159 *Navifusa* sp. cf. *N. teretis* Loeblich, 1970

Genus *Neoveryhachium* Cramer, 1971

  199 *Neoveryhachium carminae* (Cramer) Cramer, 1970

Genus *Nexosarium* Turner, 1984

  175 *Nexosarium* spp.

Genus *Ooidium* Timofeev, 1957 emend. Loeblich, 1970

  8 *Ooidium rossicum* Timofeev, 1957

Genus *Oppilatala* Loeblich and Wicander, 1976

  244 *Oppilatala* sp. cf. *O. frondis* (Cramer and Díez) Dorning, 1981

  215 *Oppilatala* spp.

Genus *Ordovicidium* Tappan and Loeblich, 1971

  179 *Ordovicidium* spp.

Genus *Orthosphaeridium* Eisenack, 1968 emend. Kjellström, 1971

  178 *Orthosphaeridium bispinosum* Turner, 1984

  181 *Orthosphaeridium chondrododora* Loeblich and Tappan, 1971

  180 *Orthosphaeridium insculptum* Loeblich, 1970

  203 *Orthosphaeridium rectangulare* (Eisenack) Eisenack, 1968

  183 *Orthosphaeridium vibrissiferum* Loeblich and Tappan, 1971

Genus *Petaloferidium* Jacobson, 1978

  155 *Petaloferidium comptum* Playford and Martin, 1984

  234 *Petaloferidium florigerum* (Vavrdová) Fensome et al. (1990)

  219 *Petaloferidium stigii* Jacobson, 1978

Genus *Peteinosphaeridium* Staplin et al., 1965 emend. Playford et al., 1995

  89 *Peteinosphaeridium breviradiatum* of Rauscher, 1974

  87 *Peteinosphaeridium nudum* of Rauscher, 1974

  88 *Peteinosphaeridium paucifurcatum* of Rauscher, 1974

  152 *Peteinosphaeridium senticosum* Vecoli, 1999

  103 *Peteinosphaeridium trifurcatum* (Eisenack) Eisenack, 1969

  164 *Peteinosphaeridium velatum* Kjellström, 1971a,b emend. Playford et al., 1995

  153 *Peteinosphaeridium* sp. A of Vecoli, 1999

Appendix A (*continued*)

  196 *Peteinosphaeridium* sp. cf. *P. trifurcatum* (Eisenack) Eisenack, 1969

Genus *Phenacoon* Vecoli and Playford, 1997

  10 *Phenacoon imperfectum* Vecoli and Playford, 1997

Genus *Pheoclosterium* Tappan and Loeblich, 1971

  134 *Pheoclosterium fuscinulaegerum* Tappan and Loeblich, 1971

Genus *Pirea* Vavrdová, 1972

  97 *Pirea colliformis* (Burmann) Eisenack et al., 1976

  98 *Pirea ornata* (Burmann) Eisenack et al., 1976

  105 *Pirea ornatissima* Cramer and Díez, 1977

  84 *Pirea* spp.

Genus *Poikilofusa* Staplin et al., 1965

  68 *Poikilofusa chalaza* Rasul, 1979

  144 *Poikilofusa ciliaris* Vecoli, 1999

  204 *Poikilofusa spinata* Staplin et al., 1965

Genus *Polyancistodorus* Loeblich and Tappan, 1969

  236 *Polyancistodorus intricatus* Colbath, 1979

Genus *Polygonium* Vavrdova, 1966 emend. Le Hérissé, 1989

  61 *Polygonium gracilis* Vavrdová, 1966

  118 *Polygonium* sp. cf. *P. acuminosum* (Cramer and Díez) Sarjeant and Stancliffe, 1994

Genus *Pterospermella* Eisenack, 1972

  137 *Pterospermella colbathii* Vavrdová, 1990

Genus *Rhopaliopora* Tappan and Loeblich, 1971 emend. Playford and Martin, 1984

  86 *Rhopaliopora palmata* (Combaz and Peniguel) emend. Playford and Martin, 1984

Genus *Safirotheca* Vavrdová, 1989

  239 *Safirotheca safira* Vavrdová, 1989

Genus *Saharidia* Combaz, 1967

  25 *Saharidia fragilis* (Downie) Combaz, 1967

  218 *Sharidia munfarida* Vavrdová, 1982

Genus *Stellechinatum* Turner, 1984

  165 *Stellechinatum celestum* (Martin) Turner, 1984

  79 *Stellechinatum sicaforme* Molyneux in Molyneux and Rushton, 1988

  60 *Stellechinatum uncinatum* (Downie) Molyneux, 1987

Genus *Stelliferidium* Deunff et al., 1974

  50 *Stelliferidium cortinulum* (Deunff) emend. Deunff et al., 1974

  49 *Stelliferidium distinctum* (Rasul) Elaouad-Debbaj, 1988

  51 *Stelliferidium furcatum* (Deunff) emend. Deunff et al., 1974

  48 *Stelliferidium gautieri* (Martin) Pittau, 1985

  141 *Stelliferidium philippotii* (Henry) emend. Deunff et al., 1974

  53 *Stelliferidium simplex* (Deunff) emend. Deunff et al., 1974

  58 *Stelliferidium stelligerum* (Górka) emend. Deunff et al., 1974

  101 *Stelliferidium striatulum* (Vavrdová) Deunff et al., 1974

  74 *Stelliferidium trifidum* (Rasul) Fensome et al. (1990)

  52 *Stelliferidium velatum* Vecoli, 1996

Genus *Stelomorpha* Yin, 1994

  106 *Stelomorpha erchunensis* (Fang) emend. Yin, 1994

Genus *Striatotheca* Burmann, 1970

  109 *Striatotheca microrugulata* (Vavrdová) Martin, 1975

  99 *Striatotheca principalis parva* Burmann, 1970

  136 *Striatotheca quieta* (Martin) Rauscher, 1974

  124 *Striatotheca rarirrugulata* (Cramer, Kanes, Díez and Christopher) Eisenack et al., 1976

  206 *Striatotheca* sp. of Molineux, 1988

Appendix A (*continued*)

Genus *Sylvanidium* Loeblich, 1970
  221 *Sylvanidium paucibrachium* Loeblich, 1970
Genus *Tectitheca* Burmann, 1968
  93 *Tectitheca* spp.
Genus *Timofeevia* Vanguestaine, 1978
  72 *Timofeevia acremonia* Rasul, 1979
  2 *Timofeevia phosphoritica* Vanguestaine, 1978
  17 *Timofeevia* sp. aff. *T. microretis* Martin, 1981
Genus *Tongzia* Li, 1987
  107 *Tongzia* spp.
Genus *Trunculumarium* Loeblich and Tappan, 1976
  11 *Trunculumarium revinium* (Vanguestaine) Loeblich and Tappan, 1976
Genus *Tunisphaeridium* Deunff and Evitt, 1968
  208 *Tunisphaeridium* spp.
Genus *Tylotopalla* Loeblich, 1970
  230 *Tylotopalla caelamenicutis* Loeblich, 1970
Genus *Uncinisphaera* Wicander, 1974
  110 *Uncinisphaera fusticula* Vecoli, 1999
Genus *Vavrdovella* Loeblich and Tappan, 1976
  82 *Vavrdovella areniga* (Vavrdová) Loeblich and Tappan, 1976
Genus *Veryhachium* Deunff, 1954 emend. Sarjeant and Stancliffe, 1994
  140 *Veryhachium augustum* Deunff, 1977
  138 *Veryhachium concaviusculum* (Burmann) Vecoli, 1999
  3 *Veryhachium dumontii* Vanguestaine, 1973
  216 *Veryhachium hamii* Loeblich, 1970
  85 *Veryhachium lairdii* (Deflandre) Deunff, 1959 *ex* Downie, 1959
  193 *Veryhachium longispinosum* Jardiné et al., 1974
  245 *Veryhachium mareki* Vavrdová, 1989
  188 *Veryhachium oklahomense* Loeblich, 1970
  207 *Veryhachium subglobosum* Jardiné et al., 1974
  232 *Veryhachium* sp. cf. *V. fakirum* Martin, 1969
  233 *Veryhachium* sp. cf. *V. triangulatum* Konzalová-Mazanková, 1969
  104 "*Veryhachium trispinosum*" group
Genus *Villosacapsula* Loeblich and Tappan, 1976
  169 *Villosacapsula irrorata* (Loeblich and Tappan) Fensome et al. (1990)
  186 *Villosacapsula setosapellicula* (Loeblich) Loeblich and Tappan, 1976
  139 *Villosacapsula* sp. cf. *V. entrichos* of Vecoli, 1999
Genus *Virgatasporites* Combaz, 1967
  37 *Virgatasporites rudii* Combaz, 1967
Genus *Visbysphaera* Lister, 1970 emend. Le Hérissé, 1989
  241 *Visbysphaera* spp.
Genus *Vogtlandia* Burmann, 1970
  83 *Vogtlandia coalita* Martin in Dean and Martin, 1978
  127 *Vogtlandia ramificata* Burmann, 1970
  128 *Vogtlandia tenuata* Burmann, 1970
  121 *Vogtlandia* sp. of Vecoli, 1999
Genus *Vulcanisphaera* Deunff, 1961
  20 *Vulcanisphaera africana* Deunff, 1961
  38 *Vulcanisphaera britannica* Rasul, 1976
  18 *Vulcanisphaera capillata* Jardiné et al., 1974
  39 Vulcanisphaera spp.

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