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Specialité: Géosciences, Ecologie, Paléontologie et Océanographie

par
Hendrik NOWAK

L'avènement du règne animal de l'intervalle cambro-ordovicien : apports de la palynologie

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Thèse dirigée par Thomas SERVAIS

Date de soutenance prevue le 11 Decembre 2015

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Doctoral School Sciences of Matter, Radiation and the Environment

Thesis for obtaining the title of Doctor of the University of Lille 1

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The rise of animal life of the Cambro-Ordovician interval: contributions from palynology

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Thesis directed by Thomas SERVAIS

Public defense scheduled for the 11th December 2015

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Résumé

Le Cambrien et l'Ordovicien étaient une période de changements importants dans l'histoire de la vie, lorsque les embranchements animaux actuels ont émergé et des écosystèmes de style moderne se sont développés au cours de l'explosion cambrienne et la radiation ordovicienne. Ces deux événements sont au centre du projet RALI (Rise of Animal Life). Dans le cadre de ce projet, ce travail de thèse se focalise sur trois sujets clés concernant des palynomorphes par rapport aux biodiversifications cambro-ordoviciennes : 1) La biodiversité des acritarches du Cambrien, 2) les palynomorphes de la formation de Fezouata (Ordovicien Inférieur, Maroc), et 3) les palynomorphes inhabituels (« Small Carbonaceous Fossils », SCF) du Lagerstätte de Winneshiek (Ordovicien Moyen, Iowa, Etats-Unis). Pour l'analyse de la biodiversité des acritarches, les données d'apparition des espèces et des genres des acritarches au cours du Cambrien sont assemblées à partir de la littérature et divers indices de diversité sont calculés. Les résultats montrent un lien possible entre les biodiversités des acritarches et des invertébrés marins pendant l'explosion cambrienne, mais aussi un biais sérieux dans les données des acritarches. La formation de Fezouata contient des faunes exceptionnellement bien préservées, qui témoignent des premiers stades de la radiation ordovicienne. Des échantillons provenant de cette Konservat-Lagerstätte (un site avec des fossiles à conservation exceptionnelle) et de la formation de Fezouata dans le sous-sol ont délivré des acritarches et chitinozoaires abondants et diversifiés. Leurs implications biostratigraphiques, paléogéographiques, taphonomiques, et paléoenvironnementales sont discutées. Les schistes de Winneshiek, qui contiennent également un Konservat-Lagerstätte, sont riches en vestiges organiques, y compris d'éventuelles mandibules et plaques filtrantes des crustacés, ainsi que des « algues » filamenteuses avec des cellules géantes, qui sont présentés ici.

Mots clés : paléopalynologie, micropaléontologie, acritarches, chitinozoaires, algues, crustacées, Cambrien, explosion cambrienne, Ordovicien, radiation ordovicienne, biodiversité, évolution, biostratigraphie, paléobiogéographie, Gondwana, Baltica, Lagerstätten

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Abstract

The Cambrian and Ordovician were times of important changes in the history of life, as the present animal phyla emerged and modern-style ecosystems developed during the so-called Cambrian explosion and the Great Ordovician Biodiversification Event. These two events are the focus of the project RALI “The Rise of Animal Life”. As a part of this project, the present thesis concentrates on three key topics regarding palynomorphs in relation to the Cambro-Ordovician biodiversifications: 1) The biodiversity of Cambrian acritarchs, 2) palynomorphs from the Fezouata Formation (Lower Ordovician, Morocco), and 3) unusual palynomorphs (Small Carbonaceous Fossils, SCFs) from the Winneshiek Lagerstätte (Middle Ordovician, Iowa, USA). For the analysis of acritarch biodiversity, occurrence data of acritarch species and genera during the Cambrian are assembled from the literature and various diversity indices are calculated. The results indicate a possible link between the biodiversities of acritarchs and marine invertebrates during the Cambrian explosion, but also a heavy bias in the acritarch data. The Fezouata Formation bears exceptionally preserved biotas, which document the early stages of the GOBE. Samples from this Konservat-Lagerstätte (site yielding exceptionally preserved fossils) and from the sub-surface of the Fezouata Formation yielded abundant and diverse acritarchs and chitinozoans. Their biostratigraphic, palaeogeographic, taphonomic, and palaeoenvironmental implications are discussed. The Lagerstätten-bearing Winneshiek Shale is rich in organic remains, including possible crustacean mandibles and filter plates, as well as giant-celled filamentous algae, which are here presented.

Keywords: palaeopalynology, micropalaeontology, acritarchs, chitinozoans, algae, crustaceans, Cambrian, Cambrian explosion, Ordovician, Great Ordovician Biodiversification Event, biodiversity, palaeobiogeography, Gondwana, Baltica, Lagerstätten

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1.1 Introduction

1.1.1 Biodiversification de l'intervalle cambro-ordovicien

Ensemble, le Cambrien (541,1 ± 1,0 Ma à 485,4 ± 1,9 Ma) et l'Ordovicien (485,4 ± 1,9 Ma à 443,8 ± 1,5 Ma), constituent les premiers 100 Ma environ du Phanérozoïque (Cohen *et al.*, 2013, mise à jour) (Fig. 3). L'intervalle cambro-ordovicien est reconnu comme une période de grande importance dans l'histoire de la vie, au cours de laquelle la diversité des invertébrés marins a augmenté considérablement dans tous les rangs taxinomiques (Sepkoski, 1981 ; 1995 ; 1997 ; Sepkoski *et al.*, 1981) (Fig. 4). Généralement, deux épisodes de diversification sont distingués, l'*explosion cambrienne* et la *grande biodiversification ordovicienne* (ou *radiation ordovicienne*, en Anglais : *Great Ordovician Biodiversification Event* ; GOBE), qui sont séparées par un épisode de faible diversité au cours du Cambrien moyen et supérieur. En revanche, Droser et Finnegan (2003) se sont demandés si les deux étaient des événements indépendants ou si la radiation ordovicienne était une extension de l'explosion cambrienne. Des courbes de biodiversité standardisés publiées récemment indiquent également une biodiversification de longue durée entre le Cambrien et la fin du Dévonien (Alroy *et al.*, 2008), mais Na et Kiesling (2015) montrent une diversité en baisse entre le Cambrien inférieur et supérieur. Sepkoski (1981 ; 1984) a constaté que l’essentiel de la variation de la diversité des invertébrés marins pendant le Phanérozoïque peut être expliqué par un regroupement des classes d'animaux en trois *evolutionary faunas* (= faunes évolutives), à savoir : la faune évolutive cambrienne, qui est dominante dans le Cambrien ; la faune évolutive paléozoïque, qui est devenue dominante au cours de la radiation ordovicienne ; et la faune évolutive moderne, qui est la plus importante dès l'extinction du Permien-Trias. Ce modèle a beaucoup attiré l’attention, mais il a été mis en cause par Alroy (2004).

L'explosion (ou radiation) cambrienne est marquée par l'apparition de presque tous les embranchements animaux actuels dans un laps de temps relativement court, au cours du Cambrien « inférieur », c'est-à-dire entre le Fortunien et l'Étage 3 (par exemple Na et Kiessling, 2015 ; Conway Morris, 2000). Le déroulement exact, les déclencheurs et les mécanismes en effet sont discutables (par exemple Budd, 2008). Des études fondées sur le principe de l'horloge moléculaire (Erwin *et al.*, 2011) et la découverte de possibles embryons de métazoaires dans le Néoprotérozoïque (par exemple Xiao et Knoll, 2000) suggèrent une divergence de quelques groupes avant le Cambrien.

La radiation ordovicienne est caractérisée par l’augmentation de la diversité dans la plupart des groupes d'organismes au cours de l'Ordovicien (Webby *et al.*, 2004b). Par rapport à

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l'explosion cambrienne, la radiation ordovicienne a impliqué une augmentation plus forte de diversité, surtout dans les rangs taxinomiques bas, et l'émergence d'écosystèmes plus complexes (Bambach *et al.*, 2007 ; Harper 2006 ; Sepkoski, 1995). Des chaînes trophiques de type moderne se sont développées en ce temps-là (Signor et Vermeij, 1994). Il y a un débat en cours sur les causes intrinsèques (biologiques) et extrinsèques (géologiques) de la radiation ordovicienne. Vecoli *et al.* (2005) ont postulé qu'une augmentation de la production primaire, spécifiquement du microphytoplancton, en était peut-être le déclencheur principal. Une théorie relie l'excursion de $\delta^{13}C_{carb}$ SPICE dans le Cambrien supérieur (Paibien) à une telle augmentation importante du phytoplancton, qui aurait alimenté la radiation ordovicienne qui lui faisait suite (Servais *et al.*, 2008 ; Saltzman *et al.*, 2011).

1.1.2 Palynomorphes du Paléozoïque inférieur

Le terme « palynomorphe » est appliqué à une multitude d'objets organiques étudiés dans le domaine de la palynologie. Il n'a pas de définition universelle. Selon une interprétation pragmatique et commune (par exemple Traverse, 2007), un palynomorphe est tout simplement ce qui survit à un traitement palynologique ou macération (aux acides), ce qui est le cas pour des objets à paroi organique. La paléopalynologie est la sous-discipline de la palynologie qui s'occupe des palynomorphes fossiles. En tant que telle, elle est également une sous-discipline de la (micro)paléontologie.

Les palynomorphes du Paléozoïque inférieur les plus communs sont les acritarches, les chitinozoaires et les spores de plantes terrestres. Il y a en plus une variété de groupes moins fréquents, comme les scolécodontes (Hints *et al.*, 2004 ; Hints et Eriksson, 2007 ; Szaniawski, 1996), des couches internes organiques de foraminifères et des mélanosclérites (Winchester-Seeto et McIlroy, 2006, et références citées). En outre, des fragments de graptolites (Cooper *et al.*, 2001 ; Bulman, 1970) et des cuticules d'euryptérides (scorpions de mer ; Braddy *et al.*, 2004 ; Lamsdell *et al.*, 2015) peuvent figurer dans les échantillons palynologiques en tant que zooclastes. Les palynofaciès peuvent également contenir des phytoclastes (fragments de plantes).

Les acritarches (Fig. 1) ont été nommés et définis par Evitt (1963) comme des microfossiles à paroi organique d'origine incertaine avec une cavité centrale fermée. En général on pense que la plupart des acritarches représente du microphytoplancton (par exemple Downie *et al.*, 1963). Les affinités possibles des acritarches comprennent des dinoflagellés (par exemple Evitt, 1963 ; Talyzina *et al.*, 2000), des algues vertes Prasinophycées (par exemple Tappan, 1980 ; Colbath et Grenfell, 1995 ; Guy-Ohlson, 1996), Colbath, 1983 ; Colbath et Grenfell, 1995 ; Guy-Ohlson, 1996) et Zygnématophycées (par exemple (Tappan, 1980 ; Brenner et Foster, 1994 ; Van Geel et Grenfell, 1996), des cyanobactéries (par exemple Javaux et Marshal, 2006), des kystes d'origine animale, en particulier des oeufs ou embryons (par exemple Van Waveren et Marcus, 1993 ; Xiao et Knoll, 2000), des euglénides (par exemple Colbath et Grenfell, 1995), des champignons (par exemple Butterfield, 2005), et les spores des plantes terrestres (par exemple Chaloner et Orbell, 1971 ; Fensome *et al.*, 1990).

Les chitinozoaires (Fig. 2) sont des microfossiles à paroi organique en forme de cône, de vase, de flacon ou similaire, avec une ouverture à l'une des extrémités (Eisenack, 1931). Leur affinité phylogénétique est inconnue. Selon la théorie la plus acceptée sur leur origine, ce serait des œufs d'un animal marin inconnu à l’état fossile (Paris et Nõlvak, 1999), qui faisait partie du zooplancton épipélagique (Vandenbroucke *et al.*, 2010).

Des micro- ou mésofossiles organiques qui ne sont en général pas pris en considération dans les études palynologiques ou qui sont détruits pendant la macération ont été nommés SCF (*Small Carbonaceous Fossils* = petits fossiles carbonés) par Butterfield et Harvey (2012). Des SCF sont souvent plus grands, plus fragiles et plus rares que les palynomorphes classiques.

1.1.3 Le projet RALI

Le projet RALI (« L'avènement du règne animal (Cambrien-Ordovicien) – organisation et tempo : apports de faunes à préservation exceptionnelle » ; en Anglais : « The Rise of Animal Life (Cambrian-Ordovician) - organisation and tempo: evidence from exceptionally preserved biotas », numéro ANR-11-BS56-0025) est un programme de recherche de quatre ans financé par l’Agence Nationale de la Recherche française (ANR). Il fédère les universités de Lille (Sciences et technologies) et de Lyon 1 en partenariat avec des chercheurs internationaux. Le projet RALI se focalise sur l'intervalle de biodiversification du Cambrien-Ordovicien et sur des sites à conservation exceptionnelle dits Fossil-Lagerstätten (singulier Lagerstätte), ou plus précisément Konservat-Lagerstätten (Seilacher, 1970) datant de cet intervalle. En particulier, la recherche est centrée autour de trois questions principales :

1. Comment est-ce que la biodiversité marine a évolué dans le temps et dans l’espace?
2. Est-ce que les modèles actuels qui identifient l'explosion cambrienne et la radiation ordovicienne comme des événements distincts et un changement des faunes évolutives de Sepkoski (1981, 1984) sont valides ?
3. Comment est-ce que les écosystèmes modernes ont évolué?

Pour répondre à ces questions, le projet a trois objectifs principaux:

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1. L'étude des sites de conservation exceptionnelle, qui ont le potentiel de nous donner une vue plus complète des écosystèmes anciens que les seules faunes coquillières.
2. L'étude des chaînes alimentaires anciennes grâce à l'analyse des contenus d'estomac fossilisés.
3. La création d'une base de données sur les informations morphologiques, écologiques et environnementales concernant les sites de conservation exceptionnelle et l'évaluation de ces données à propos du développement de la biodiversité et des écosystèmes.

1.2 Objectifs

En tant que partie du projet RALI, l'objectif du présent travail de thèse était de fournir des réponses aux questions de RALI avec les méthodes de la palynologie. Parmi les nombreuses questions spécifiques qui se posent dans ce cadre, cette étude se concentre sur trois sujets principaux :

1.2.1 La biodiversité des acritarches du Cambrien

Une question importante pour la compréhension de l'évolution de la vie pendant le Cambrien et l'Ordovicien est la compréhension des chaînes alimentaires. En tant que source de nourriture principale pour des écosystèmes marins d'aujourd'hui, le phytoplancton a probablement aussi eu un rôle important dans les chaînes alimentaires du Paléozoïque inférieur. L'évolution du phytoplancton a peut-être influencé l'explosion cambrienne et elle a probablement déclenché la radiation ordovicienne. En conséquence, une partie de la présente étude a été consacrée à la biodiversité des acritarches du Cambrien, comme une mesure de l'évolution du phytoplancton.

1.2.2 La palynologie du Fossil-Lagerstätte de Fezouata (Maroc)

Le Lagerstätte de Fezouata est situé dans la partie inférieure de la formation de Fezouata (Ordovicien inférieur) dans la région de l'Anti-Atlas au Maroc (Martin *et al.*, 2015) (Fig. 5B). Ce Lagerstätte est remarquable en ce qu’il est probablement le seul Lagerstätte de type « schistes de Burgess » après le Cambrien et parce qu’il contient une faune riche avec des éléments typiques des faunes évolutives cambrienne et paléozoïque (Van Roy *et al.*, 2010, 2015). Le Lagerstätte de Fezouata est un site d'intérêt principal pour le projet RALI, car il offre une vue unique sur une faune marine au début de la radiation ordovicienne. Dans le cadre d'un effort interdisciplinaire pour réévaluer l’ensemble de la formation de Fezouata et le

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Lagerstätte de Fezouata en particulier, cette partie de la thèse délivre des informations bien corrélées sur les assemblages de palynomorphes dans la zone d'affleurement de la formation de Fezouata près de Zagora, qui présente des fossiles à conservation exceptionnelle, et dans le sous-sol de la montagne Adrar Zouggar (Fig. 5B). Des échantillons ont été prélevés sur le terrain entre 2012 et 2014 au cours de plusieurs campagnes. J'ai participé à l'une d'elles fin février - début mars 2013. Le but principal de ce travail était la biostratigraphie des acritarches et des chitinozoaires, qui sont les palynomorphes les plus courants dans la formation de Fezouata. Un objectif secondaire était la recherche des SCF. Leur présence semblait probable, parce que la conservation des fossiles du Lagerstätte de Fezouata comprend des films carbonés ; or des Konservat-Lagerstätten cambriens avec un mode de conservation similaire ont bien délivré des SCF (Butterfield et Harvey, 2012). Malgré tout, aucun SCF n'a encore été récupéré à Fezouata.

1.2.3 Les SCF du Lagerstätte de Winneshiek (Iowa, USA)

Les schistes de Winneshiek (Darriwilien, Ordovicien moyen), qui se trouvent autour de la ville de Decorah, Winneshiek County, Iowa, Etats-Unis (Fig. 5C), contiennent un Konservat-Lagerstätte qui est encore à peine étudié (Lamsdell *et al.*, 2015 ; Liu *et al.*, 2006 ; 2009). Ces schistes fournissent d'excellentes perspectives pour la recherche des SCF, parce que les rapports préliminaires ont fait état de grandes quantités de cuticules d'euryptérides et de la présence d'autres arthropodes. Le Lagerstätte de Winneshiek est l'un des deux Lagerstätten de l'Ordovicien moyen qui soient connus actuellement et qui représentent le pic de la radiation ordovicienne. Il est donc d'un intérêt particulier.

1.3 La biodiversité des acritarches du Cambrien

1.3.1 Article I : Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: A review of Cambrian acritarch diversity

Nowak, H., Servais, T., Monnet, C., Molyneux, S.G. & Vandenbroucke, T.R.A. (2015a) *Earth-Science Reviews* **151**, 117–131, doi:10.1016/j.earscirev.2015.09.005.

Dans cette étude, les données publiées sur les acritarches du Cambrien sont assemblées afin de reconstituer les tendances de leur diversité taxinomique. Nous avons compilé une base de données et calculé différents indices de diversité des espèces et des genres, à l'échelle mondiale et régionale (pour Gondwana et Baltica), et au niveau des dix étages du Cambrien et de quatorze biozones. La diversité globale des espèces d'acritarches commence à un niveau relativement faible à la base du Cambrien, monte à un niveau élevé dans les étages 3 à 5 (ou les zone *Holmia* à *Paradoxides paradoxissimus*), puis chute considérablement à un faible niveau jusqu'à ce qu'elle culmine fortement dans l'Étage 10 (plus précisément dans la zone *Peltura*). Nos résultats montrent que les indices de diversité taxinomique des espèces sont corrélés d'une manière claire avec la distribution du nombre détudes par unité stratigraphique. Les diversités totale et normalisée des genres ne sont pas affectées de la même manière. Les courbes de diversité normalisée des genres montrent une augmentation lente mais irrégulière au cours de l'ensemble du Cambrien. L'analyse de corrélation montre que cet indice est la moins biaisée. Nos courbes de diversité d'acritarches reflètent les courbes de la diversité des invertébrés marins dans une certaine mesure. La corrélation entre les deux est statistiquement significative à condition que le premier et le dernier étage du Cambrien soient exclus de l'analyse. Une croissance de diversité dans l'Étage 3 semble refléter celle des métazoaires (l'explosion cambrienne), mais la diversité des acritarches est surtout affectée par un biais d'échantillonnage. La relation entre les deux groupes reste incertaine. Les courbes régionales sont nettement différentes dans la Série 2 et l'Étage 5. Sur Baltica, la diversité est élevée comme dans la courbe globale, mais elle est faible sur Gondwana. Cette différence peut être attribuée aux données limitées sur Gondwana et peut-être à des différences paléoenvironnementales. Après l'Étage 5, les diversités régionales sont similaires. Un maximum de diversité dans la zone *Peltura* et la chute suivante dans la zone *Acerocare* se reflètent à la fois sur Baltica, sur Gondwana et globalement. La fin du Cambrien est marquée par une extinction importante des espèces, alors que presque tous les genres présents dans l'Étage 10 ont survécu dans l'Ordovicien. Des innovations morphologiques du Cambrien au niveau des genres pourraient bien avoir préparé la diversification rapide des acritarches au cours de l'Ordovicien.

1.3.2 Article II : The onset of the "Ordovician Plankton Revolution" in the late Cambrian

Servais, T., Perrier, V., Danelian, T., Klug, C., Martin, R.E., Munnecke, A., Nowak, H., Nützel, A., Vandenbroucke, T.R.A., Williams, M. & Rasmussen, C.M.Ø. (*soumis à Palaeogeography, Palaeoclimatology, Palaeoecology, publication recommandée après révision mineure*)

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Une diversification importante des différents groupes de plancton est observée entre la fin du Cambrien et l'Ordovicien (Nützel et Fryda, 2003 ; Nützel *et al.*, 2006), conduisant à une *Ordovician plankton revolution* (= « révolution ordovicienne du plancton » ; Servais *et al.*, 2008). Dans ce contexte, l'événement $\delta^{13}C_{carb}$ SPICE vers la fin du Cambrien (Paibien) a été liée à une augmentation importante d' O_2 atmosphérique et à une augmentation de la disponibilité des nutriments dans les océans (Saltzman *et al.*, 2011). Dans le but d'identifier précisément le début de la « révolution ordovicienne du plancton », la littérature et des résultats récents concernant le phytoplancton et tous les groupes du zooplancton sont évalués. En outre, les données sur le développement des stades larvaires planctotrophique d'invertébrés marins sont également examinées. Les changements de la diversité des acritarches lors de l'événement de SPICE sont d'un intérêt particulier. Beaucoup de nouveaux genres présentant des morphologies nouvelles qui progressent dans l'Ordovicien apparaissent dans l'Étage 10 du Cambrien, considérablement éloigné de l'événement SPICE et sans causalité apparente. Aucune des diversifications des différents organismes planctoniques ne peut être liée directement à l'événement de SPICE. Le début de la « révolution ordovicienne du plancton » semble avoir été progressive, et non un événement soudain déclenché par un seul paramètre géologique ou paléoécologique.

1.4 La palynologie de la formation de Fezouata

1.4.1 Article III : Discovery of the *messaoudensis–trifidum* acritarch assemblage (upper Tremadocian–lower Floian, Lower Ordovician) in the subsurface of Morocco

Nowak, H., Akodad, M., Lefebvre, B. & Servais, T. (2015b) *Estonian Journal of Earth Sciences* **64**(1), 80–83, doi:10.3176/earth.2015.14.

La formation de Fezouata dans le forage AZ-1, positionné près de la montagne Adrar Zouggar dans le sud du Maroc, a délivré des acritarches de l'assemblage *messaoudensis-trifidum*. Cet assemblage était connu originalement dans le Groupe de Skiddaw en Angleterre et fut reconnu par la suite dans plusieurs localités de la marge du Gondwana qui étaient situées sous de hautes latitudes australes pendant l'Ordovicien inférieur. Il est rapporté ici pour la première fois en Afrique du Nord. Plusieurs espèces typiques de l'assemblage de *messaoudensis-trifidum* du Groupe de Skiddaw sont présentes, dont quatre sur sept des taxons diagnostiques :

Cymatiogalea deunffii, *C. messaoudensis*, *Caldariola glabra glabra* et *Stelliferidium trifidum*. Les autres taxons enregistrés sont *Cymatiogalea velifera*, *Veryhachium lairdii* s.l., *Impluviculus milonii*, *Vulcanisphaera frequens* et diverses espèces d'*Acanthodiacrodium*, *Actinotodissus*, *Baltisphaeridium*, *Cymatiogalea*, *Leiofusa*, *Goniosphaeridium*, *Impluviculus*?, *Leiosphaeridia*, *Micrhystridium*, *Multiplicisphaeridium*, *Polygonium*, *Priscogalea*, *Solisphaeridium*, *Stellechinatum*? et *Stelliferidium*. L'assemblage du Maroc indique un âge de la fin du Trémadocien.

1.4.2 Article IV : Palynomorphs of the Fezouata Formation (Lower Ordovician, Morocco): age and environmental constraints of the Fezouata Biota

Nowak, H., Servais, T., Pittet, B., Vaucher, R., Akodad, M., Gaines, R. R. & Vandenbroucke, T. R. A. (*soumis à Palaeogeography, Palaeoclimatology, Palaeoecology*)

Cette étude palynologique se concentre sur le Lagerstätte de Fezouata, c'est-à-dire la partie de la formation de Fezouata portant des fossiles de conservation exceptionnelle, et les chitinozoaires du forage AZ-1. Les acritarches du même forage sont présentés dans l'article III (Nowak *et al.*, 2015b). Deux techniques palynologiques ont été utilisées, une technique standard et une technique plus douce pour isoler d’éventuels SCF. Nous avons trouvé des acritarches et chitinozoaires abondants et diversifiés, mais pas de SCF. La présence de l'assemblage d'acritarches *messaoudensis-trifidum* avec toutes ses espèces diagnostiques est confirmée. Les acritarches de l'affleurement et du forage AZ-1 sont globalement comparables. Ils correspondent aux sous-assemblages 1? / 2 de l'assemblage *messaoudensis-trifidum* (voir Cooper *et al.*, 1995), indiquant un âge fin Trémadocien (Molyneux *et al.*, 2007), ce qui est conforme à une précédente datation à l’aide des graptolites (Martin *et al.*, 2015). L'assemblage *messaoudensis-trifidum* est typique pour la marge du (péri-)Gondwana à des latitudes élevées autour de la limite Trémadocien-Floien. Les chitinozoaires de la formation de Fezouata montrent des connections avec d'autres sites du péri-Gondwana, mais aussi avec Baltica, Laurentia et la Chine du Sud. Les chitinozoaires des niveaux attribués à la fin du Trémadocien par acritarches et graptolites comprennent des espèces qui sont jusqu'à présent considérées comme une indication du Floien. *Euconochitina symmetrica*, qui indique le Floien inférieur, est représenté dans une groupe de variation morphologique avec *Eu. paschaensis*. *Eremochitina brevis* indique le Floien supérieur. Ces résultats indiquent que la corrélation entre la chronostratigraphie et la biozonation de chitinozoaires pour la marge du Gondwana nécessite peut-être une révision. En outre, les extensions des deux espèces index se

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chevauchent. En attente d'une redéfinition formelle de ces biozones, nous avons établi ici une biozonation locale en utilisant des zones d'extension partielle pour la groupe *Eu. paschaensis-symmetrica* et *Er. brevis*.

1.4.3 Article V : Conodonts from the Lower Ordovician of Morocco – a contribution to age and faunal diversity of the famous Fezouata Lagerstätte

Lehnert, O., Nowak, H., Sarmiento, G., Servais, T., Gutiérrez-Marco, J.-C. & Akodad, M. (*en préparation pour Palaeogeography, Palaeoclimatology, Palaeoecology*)

Des éléments conodontes fortement recristallisés ont été extraites des échantillons palynologiques du forage AZ-1 et des affleurements de la formation de Fezouata. En particulier, des conodontes ont été extraites de plusieurs échantillons relatifs aux strates avec des macrofossiles exceptionnellement bien préservés. Le matériel est dominé par les taxons de cône simple. L'assemblage permet une datation du Trémadocien? tardif (sous-zone d'*Acodus deltatus* de la zone de *Paroistodus proteus*) au Floien basal (zone de *Prioniodus elegans*). Le manque de taxons charactéristiques d'eaux chaudes / tropicales et tempérées est typique pour les faunes dans les environnements des étagès siliciclastiques subpolaires de l'eau froide pendant l'Ordovicien précoce. Nous proposons donc un « domaine subpolaire ».

1.4.4 Article VI : The Lower Ordovician Fezouata Konservat-Lagerstätte from Morocco: Age, environment and evolutionary perspectives

Martin, E.L.O., Pittet, B., Gutiérrez-Marco, J.-C., Vannier, J., El Hariri, K., Lerosey-Aubril, R., Masrour, M., Nowak, H., Servais, T., Vandenbroucke, T.R.A., Van Roy, P., Vaucher, R. & Lefebvre, B. (2015, *sous presse, en ligne*). *Gondwana Research*, doi:10.1016/j.gr.2015.03.009.

Contrairement aux évaluations précédentes (Van Roy *et al.*, 2010), la distribution des fossiles à conservation exceptionnelle dans les schistes de Fezouata est limitée à deux intervalles stratigraphiques distincts d'environ 25 et 15 mètres d'épaisseur, séparés par un intervalle de 30 mètres d'épaisseur (l'ensemble étant situé entre 260 et 330 m au-dessus du contact basal avec le Groupe Tabanite du Guzhangien). Les graptolites (biozones de *Araneograptus murrayi* et *Hunnegraptus copiosus*) indiquent un âge Trémadocien tardif pour ces intervalles. Des acritarches de l'assemblage *messaoudensis-trifidum* ont été extraits de l'intervalle inférieur.

Cette assemblage est typique de la limite Trémadocien-Floien. Les acritarches aussi indiquent un âge Trémadocien tardif, en corrélation avec le haut de la biozone *A. murrayi* et la base de la biozone *H. copiosus* (Molyneux *et al.*, 2007). Les animaux du biote de Fezouata vivaient dans un environnement marin non restreint, relativement peu profond à proximité de la base des ondes de tempête. Les organismes étaient très probablement ensevelis *in situ* pendant les tempêtes, avec une sédimentation résultant de la décantation de boue suspendue par l'action des vagues.

1.5 SCF du Lagerstätte de Winneshiek

1.5.1 Article VII : Exceptionally preserved arthropodan microfossils of possible crustacean origin from the Middle Ordovician Winneshiek Lagerstätte, Iowa, USA

Nowak, H., Harvey, T.H.P., Liu, H., McKay, R.M. & Servais, T. (*en préparation pour Lethaia*)

Dans les schistes de Winneshiek se trouve une quantité surprenante de possibles mandibules de crustacés minuscules, ainsi que d'éventuelles plaques filtrantes de crustacés. Les mandibules ont une longueur totale de 55 à 130 µm. Elles sont divisées par une constriction en une partie postérieure à forme ovale ou en bâteau et une partie antérieure incluant le bord gnathal. Le bord gnathal s'étend plus ou moins parallèlement à l'axe long de la partie postérieure. Il est à courbure convexe, portant 7 à 11 (normalement 8 à 10) dents cintrées en arrière. L'articulation de base (ou dorsale) sur l'extrémité postérieure est marquée par des rebords notables. Une éventuelle articulation secondaire se trouve sous la constriction, ce qui indiquerait une rotation des mandibules presque autour du grand axe. Ce serait conforme à l'orientation du bord gnathal et sa position excentrique. La présence de dents pointues appropriées pour mordre et le mécanisme de préhension présumé suggèrent un comportement prédateur. Le manque d'une incisive distincte et l'absence apparente d'un palpe mandibulaire sont des caractéristiques indicatives d'une affinité avec les branchiopodes. La courbure du bord gnathal, cependant, est une caractéristique inhabituelle. On trouve de rares setae isolées ou regroupées. Elles sont ramifiées ou non. Dans deux cas, des setae plumeuses forment un filet serré. Cette structure est très similaire à quelques SCF du Cambrien identifiés comme des plaques filtrantes de branchiopodes par Harvey et Butterfield (2008 ; voir aussi Harvey *et al.*, 2012b).

1.5.2 Article VIII : Filamentous eukaryotic algae from the Winneshiek Lagerstätte in Iowa (Middle Ordovician)

Nowak, H., Harvey, T.H.P., Liu, H., McKay, R.M., Campbell, D. & Servais, T. (*en préparation pour Review of Palaeobotany and Palynology*)

Les schistes de Winneshiek contiennent des quantités importantes d'un type distinct d' « algues » filamenteuses eucaryotes avec des cellules géantes. Ces « algues » sont peut-être attribuables aux cladophores. Les cellules sont soit isolées soit connectées en filaments, rarement avec une ramification préservée. Le fragment le plus grand a une longueur totale de 1,25 mm. Les cellules individuelles ont une longueur de 220 à 640 µm et des diamètres de cellules reconstruites d'environ 60 à 240 µm. Les contacts entre les cellules montrent parfois des parois transversales. La plupart des cellules contiennent des objets internes, probablement des restes cytoplasmiques. Quelques spécimens portent des excroissances en forme de bosses ou de tubes, qui peuvent représenter les premiers stades de ramification ou les organes reproducteurs sexuels.

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2 Introduction

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2.1 The Cambrian-Ordovician interval

2.1.1 Geochronology

The Cambrian and Ordovician together make up approximately the first 100 My of the Phanerozoic, with the Cambrian (541.1 ± 1.0 Ma to 485.4 ± 1.9 Ma) spanning about 56 My and the Ordovician (485.4 ± 1.9 Ma to 443.8 ± 1.5 Ma) spanning 42 My (Cohen *et al.*, 2013, updated) (Fig. 1). They represent a part of the lower Palaeozoic. The Cambrian follows the Ediacaran, the Neoproterozoic, the Proterozoic, and the Precambrian. The Ordovician is followed by the Silurian. The Cambrian System/Period is divided into four series/epochs, of which two are still undefined by the International Commission on Stratigraphy (ICS), and ten stages/ages, of which five are still undefined. The Cambrian is currently the only Phanerozoic system with undefined series or stages. Traditionally, the Cambrian was divided into "Lower"/"Early", "Middle", and "Upper"/"Late" series/epochs, but this was abandoned by the International Subcommission on Cambrian Stratigraphy (ISCS) (Babcock & Peng, 2007). The Ordovician is divided into three series/epochs (Lower, Middle and Upper) and seven stages/ages. A set of informal "time slices" has been proposed for the Ordovician by Webby *et al.* (2004a) for the purpose of high-resolution inter-regional correlation. Similarly, Bergström *et al.* (2009) defined 20 "stage slices", aligned with graptolite and conodont biozones.

The base of the Fortunian Stage is also the base of the Terreneuvian Series, the Cambrian System, the Palaeozoic Erathem and the Phanerozoic Eonothem. It is defined by a GSSP (Global Stratotype Section and Point) at the Fortune Head section in eastern Newfoundland and the FAD (First Appearance Datum) of the ichnofossil *Trichophycus* (or *Treptichnus*, *Manykodes*, *Phycodes*) *pedum* (Brasier *et al.*, 1994; Landing, 1994; Landing *et al.*, 2007). This boundary has proven difficult to correlate (Peng & Babcock, 2011) and may be relocated in the future. Most stage boundaries in the Cambrian are defined by the FADs of trilobite index species, while Ordovician stages are defined by the FADs of graptolites or conodonts (Gradstein *et al.*, 2012). The GSSP for the Cambrian/Ordovician boundary is located in the Green Point section of western Newfoundland and coincides with the FAD of the conodont *Iapetognathus fluctivagus* (Cooper *et al.*, 2001; Cooper & Nowlan, 1999). The first planktonic graptolites appear a few metres below in that section.

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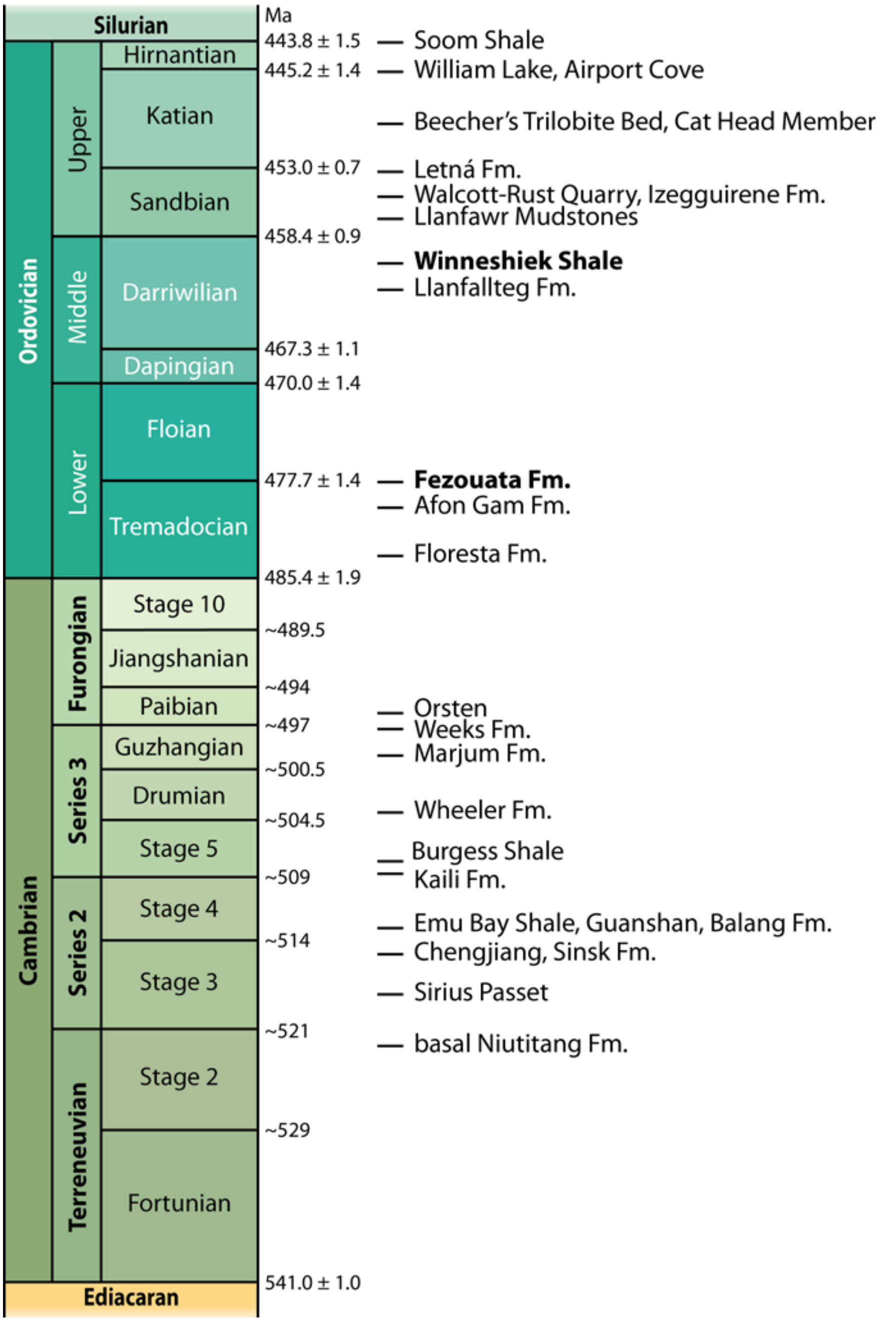

Fig. 1: Chronostratigraphy of the Cambrian and Ordovician and positions of selected Konservat-Lagerstätten. Chronostratigraphy according to the International Chronostratigraphic Chart (state 2015; Cohen *et al.*, 2013, updated). Lagerstätten according to Van Roy *et al.* (2015, their Fig. 5).

2.1.2 Biodiversification

The Cambrian-Ordovician interval is widely recognized as a time of great importance in the history of life, during which the diversity of marine invertebrates drastically increased in all taxonomic ranks (Sepkoski, 1981; 1995; 1997; Sepkoski *et al.*, 1981) (Fig. 2). Commonly, two episodes of radiation are distinguished; the Cambrian Explosion and the Great Ordovician Biodiversification Event (GOBE), which are divided by a time of low diversity during the middle and late Cambrian. In contrast, Droser & Finnegan (2003) questioned whether the two were independent events or the GOBE a mere follow-up of the Cambrian Explosion. Sampling standardized biodiversity curves based on the Paleobiology Database also indicate a rather continuous, long phase of biodiversification between the Cambrian and the late Devonian (Alroy *et al.*, 2008), but a more detailed analysis of the Cambrian using this database again showed declining diversities between the lower and upper Cambrian (Na & Kiessling, 2015). Sepkoski (1981; 1984) found that much of the variation in marine invertebrate diversity throughout the Phanerozoic can be accounted for by grouping animal classes into three "evolutionary faunas"; the Cambrian Evolutionary Fauna, which is dominant in the Cambrian; the Palaeozoic Evolutionary Fauna, which overtook the former during the GOBE; and the Modern Evolutionary Fauna, which rose to prominence after the Permian/Triassic extinction. This model has received much attention, but was put into question by Alroy (2004).

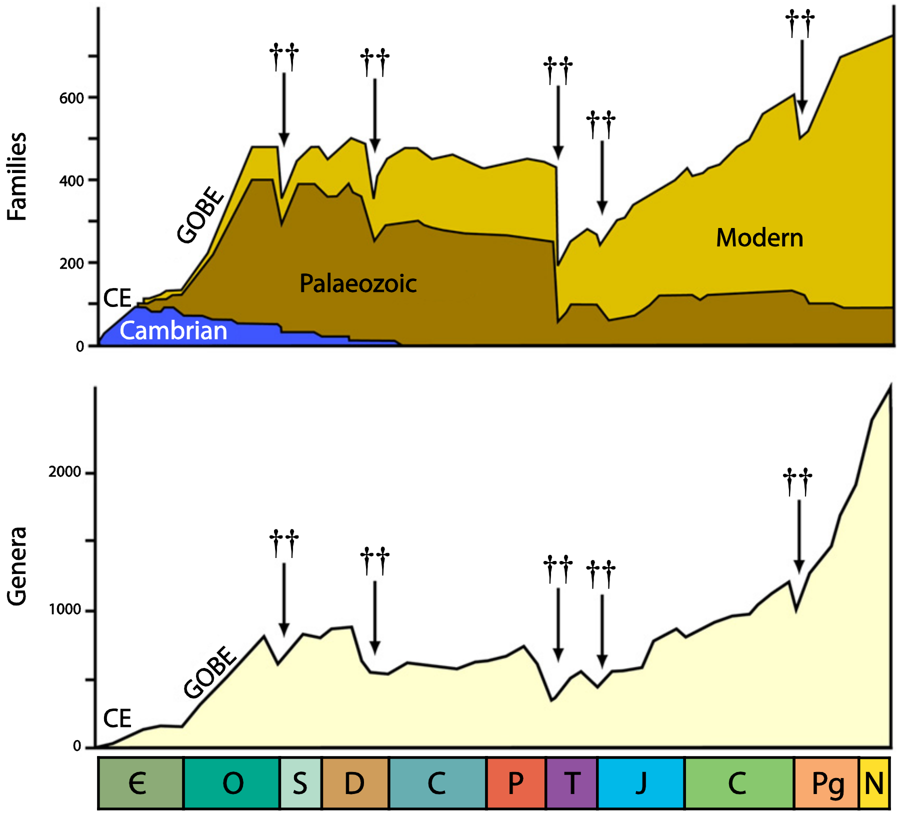

Fig. 2: Biodiversity of marine invertebrates during the Phanerozoic, Evolutionary Faunas, and events. Modified from Servais *et al.* (2010), Family diversity from Sepkoski 1997, Genus diversity from Alroy *et al.* (2008), using the Paleobiology Database. EC = Cambrian Explosion. GOBE = Great Ordovician Biodiversification Event. †† = Mass extinction event.

2.1.2.1 Cambrian Explosion

The Cambrian Explosion (or radiation) is marked by the seemingly sudden appearance of almost all present animal phyla in a relatively short time window, during the "early" Cambrian Fortunian Stage to Stage 3 (e.g. Conway Morris, 2000; Na & Kiessling, 2015). The exact timing, triggers, and mechanisms are debatable (e.g. Budd, 2008; Maruyama *et al.*, 2014; Zhang *et al.*, 2014). Molecular clock evidence (e.g. Erwin *et al.*, 2011) and possible metazoan embryos from the Neoproterozoic (e.g. Xiao & Knoll, 2000; Xiao *et al.*, 2012; comp. Huldtgren *et al.*, 2011) suggests a divergence of several lineages already during the late Neoproterozoic. Assuming an Ediacaran origin of arthropods, Lee *et al.* (2013) found that rates of phenotypic and molecular evolution in this group during the Cambrian Explosion were unusually high, but plausible. The Cambrian Explosion followed the extinction of Ediacaran faunas (Conway Morris, 1998a; 1998b; Harper, 2006; Vannier *et al.*, 2009). It involved the appearance of biomineralized skeletons in different lineages ("biomineralisation event"; Bengtson, 2004; Kouchinsky *et al.*, 2012). It also includes a change in bioturbation, the so-called "agronomic revolution" (Seilacher & Pflüger, 1994) or "Cambrian substrate revolution" (Bottjer *et al.*, 2000), during which the biomats that dominated Ediacaran seafloors all but disappeared and vertical burrowing created a mixed layer in the sediment. Archaeocyaths built the first metazoan reefs during this time (e.g. Debrenne, 2007). Much more of the potential ecospace was utilized in the Cambrian compared to the Neoproterozoic, yet still far less life modes than in later ecosystems were realized (Bambach, 1983; Bambach *et al.*, 2007). Trophic chains gained complexity (Vannier, 2007; Vannier *et al.*, 2009). Predation may have shaped the Cambrian Explosion, if not triggered it (Bengtson, 2002). A rise in oxygen is one debated, but hard to prove, possible trigger, and at least a requirement (Budd, 2008; Nursall, 1959). Different explanations were discussed by Marshall (2006). Dalziel (2014) forwarded the idea that the opening of the Iapetus Ocean between Laurentia and Gondwana during the early Cambrian and its connection with the Palaeo-Pacific Ocean played a role through changes in ocean circulation and chemistry, upwelling, and mixing of previously seperated (cryptic) faunas.

2.1.2.2 The Great Ordovician Biodiversification Event

The GOBE, as currently understood, encompasses increasing diversities in most groups of organisms during the Ordovician (Webby *et al.*, 2004b). The diversification was followed by the end-Ordovician (Hirnantian) extinction that is counted among the "Big Five" mass extinctions of the Phanerozoic (Sepkoski & Sheehan, 2001) (Fig. 2). Compared to the Cambrian Explosion, the GOBE involved a stronger increase in diversity, especially at low taxonomic ranks, and the emergence of more complex ecosystems, with more ecospace occupation (Bambach *et al.*, 2007; Sepkoski, 1995; Harper, 2006). Modern trophic chains developed (Signor & Vermeij, 1994). Vecoli *et al.* (2005) postulated that an increase in primary production, specifically microphytoplankton, was possibly the main trigger. One theory links the late Cambrian (Paibian) SPICE $\delta^{13}C_{carb}$ excursion to a major turnover in phytoplankton, causing a rise in phytoplankton diversity, which could have fuelled the ensuing GOBE (Saltzman *et al.*, 2011; Servais *et al.*, 2008). The appearance of planktotrophic larvae in seperate lineages during the Early Ordovician was also attributed to an increased abundance of phytoplankton, and to predation (Nützel *et al.*, 2006; Nützel & Frýda, 2003; Signor & Vermeij, 1994). Miller & Mao (1995) suggested a link between rising diversity and orogenic activity. Strong volcanic activity during a superplume event may have enhanced nutrient supply in the oceans (Barnes, 2004; Servais *et al.*, 2009). Frequent impacts after an asteroid breakup could have destabilized the ecosystems, promoting competition (Schmitz *et al.*, 2008). Global transgressions and low cratonic relief resulted in extensive epeiric seas, providing additional niche space, assuming a species-area effect (Barnes, 2004; Sepkoski, 1976). There is an ongoing debate on the intrinsic (biological) and extrinsic (geological) triggers of the GOBE (Servais *et al.*, 2010).

2.1.3 Palaeogeography, climate and sea level

Most landmasses in the Cambrian were part of the supercontinent Gondwana, extending from the south pole to beyond the equator (Fig. 3). Other major continents were Laurentia, Baltica and Siberia. Laurentia was still connected to Gondwana at the beginning of the Cambrian, according to Dalziel (2014). Cocks & Torsvik (2005) showed that Baltica turned about 120° counter-clockwise between the middle Cambrian and the Middle Ordovician. Siberia stayed upturned relative to the present orientation throughout the Cambrian (Cocks & Torsvik, 2007). A number of smaller terranes existed, mostly surrounding the Gondwana margin or with uncertain positions, which are grouped under the term “peri-Gondwana” (Torsvik & Cocks, 2013). Terms like “northern”, “western”, etc. are sometimes used to denote parts of (peri-)Gondwana in a way that is inconsistent with the orientation of the continent during the early Palaeozoic (see Servais & Sintubin, 2009 for a discussion). Avalonia separated from Gondwana near the end of the Cambrian, opening the Rheic ocean, drifted northwards during the Ordovician, and merged with Baltica around the Ordovician/Silurian boundary (Cocks & Fortey, 2009).

Most of the northern hemisphere and most of the globe was occupied by the Panthalassic Ocean. The Iapetus Ocean divided Laurentia from Gondwana and Baltica. Baltica was separated from Gondwana by the Ran Ocean, from Avalonia by the Tornquist Ocean, and from Siberia by the Ægir Ocean (Hartz & Torsvik, 2002; Torsvik & Cocks, 2013).

The global sea level is considered to have risen more or less constantly (on a high order) throughout the Cambrian and most of the Ordovician, until it dropped significantly during the late Katian and Hirnatian (Haq & Schutter, 2008). The Ordovician sea level may have been

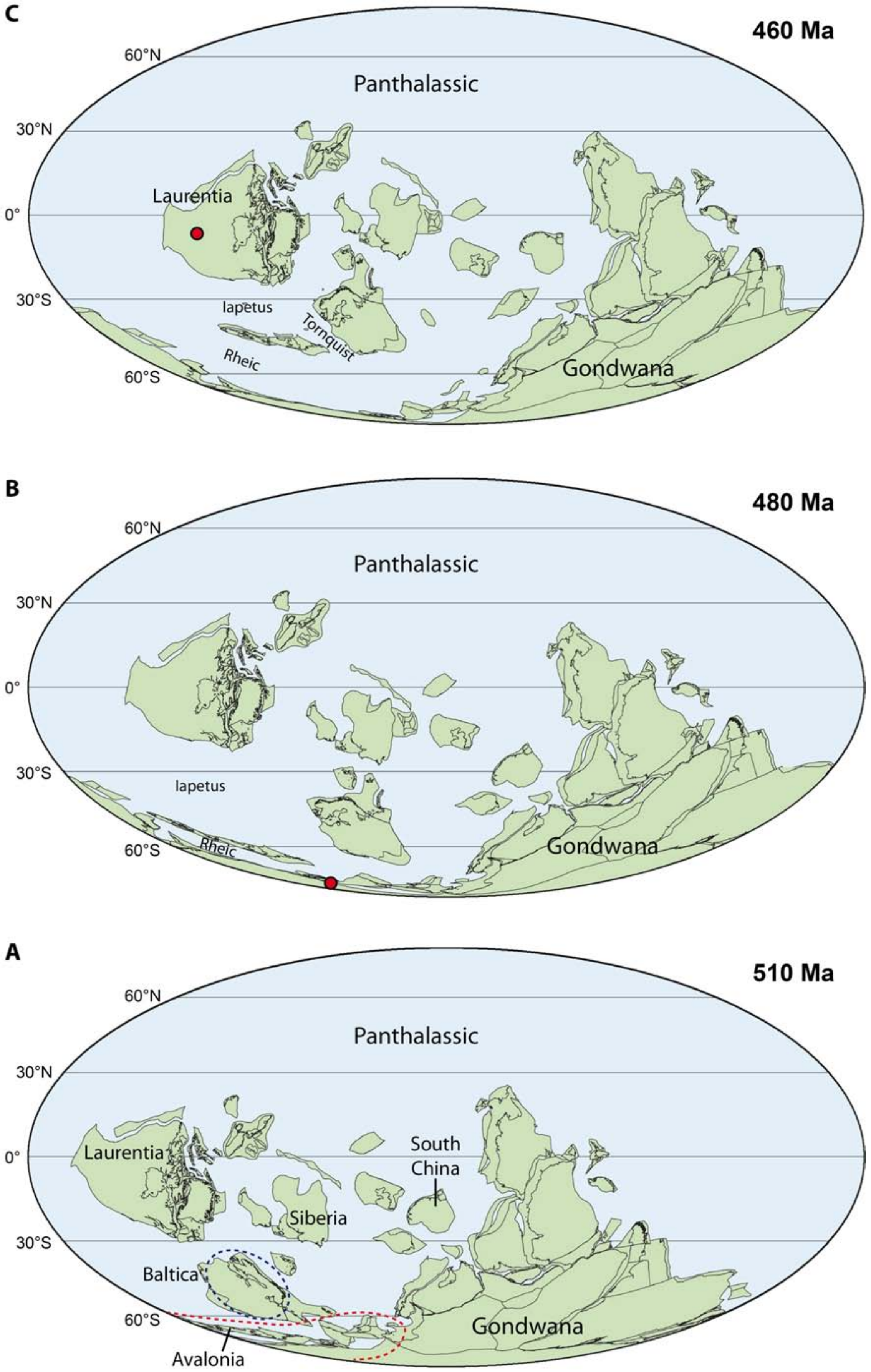

Fig. 3: Palaeogeographical reconstructions from the Cambrian and Ordovician. Modified from Torsvik & Cocks (2013). A: lower Cambrian, 510 Ma, with marked regions selected for regional acritarch biodiversity analysis (see Ch. 3, Art. I). B: Lower Ordovician, 480 Ma, with marked position of the

Zagora area, Morocco (see Ch. 4, Art. III, IV). C: Middle Ordovician, 460 Ma, with marked position of Winneshiek County (see Ch. 5).

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the highest in the Phanerozoic (Hallam, 1992).

According to Babcock et al. (2015), the Cambrian climate was mostly in a greenhouse state, but episodically cold, with rapid changes. The Ordovician experienced a greenhouse climate until glaciation started in the Late Ordovician (e.g. Ghienne et al., 2014). During the Hirnatian, extinction pulses coincided with both cooling and warming events (Brenchley, 2004).

2.2 Lower Palaeozoic palynomorphs

The term “palynomorph” is applied to a multitude of organic objects studied in the realm of palynology. It has no universal definition. According to a common, pragmatic interpretation (e.g. Traverse, 2007), a palynomorph is simply what survives a palynological treatment. A standard palynological treatment involves the application of hydrochloric (HCl) and hydrofluoric acid (HF), which dissolves most inorganic sediments, but leaves organic substances intact. The same resistance makes palynomorphs highly fossilisable, resulting in a rich and extensive fossil record. Palynomorphs are among the oldest known fossils (Javaux *et al.*, 2010). In recent samples and since the Mesozoic, palynomorphs are predominantly spores and pollen. Those were the original targets for palynological studies. As other types of organic objects turned up in the same samples, they were included in the discipline (Traverse, 2007). Palaeopalynology is the sub-discipline of palynology that deals with fossil palynomorphs. As such, it is also a sub-discipline of (micro-)palaeontology.

Palynofacies studies are the investigation of the organic matter in sediments, including palynomorphs. Palynofacies studies are very useful for the understanding of the depositional environment.

The most common lower Palaeozoic palynomorphs are acritarchs (see 2.2.1), chitinozoans (see 2.2.2) and spores of land-plants, besides a variety of less frequent groups (see 2.2.1 and below in this section). The palynofacies can also contain zooclasts (fragments of animal fossils, mostly graptolites and arthropods) and phytoclasts (fragments of plants).

Cryptospores are the alete spores of early land plants. They are known from the Middle Ordovician to Lower Devonian (Gensel, 2008). Claims of cryptospores from the Cambrian (Strother & Beck, 2000; Strother *et al.*, 2004; Taylor & Strother, 2008) are not unanimously

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accepted (Gensel, 2008; Vecoli *et al.*, 2011). First trilete spores appear in the Upper Ordovician (Steemans *et al.*, 2009). The oldest known fragments of land plant thalli are recorded from the Middle Ordovician (Wellman *et al.*, 2003).

Among the less common groups, foraminifera linings (organic layers inside otherwise biomineralized tests) and melanosclerites (possible hydrozoans) are rare, but known from the early Cambrian onwards, in the case of melanosclerites until the Late Devonian (Winchester-Seeto & McIlroy, 2006, and references therein).

Scolecodonts are the chitinous jaw elements of polychaete worms of the order Eunicida, and from the Triassic onwards also the order Phyllodocida (Szaniawski, 1996). They are present in the fossil record since the latest Cambrian up to the present day (Hints & Eriksson, 2007; Hints *et al.*, 2004; Szaniawski, 1996).

Graptolites were benthic or planktonic colonies of pterobranch hemichordates with an organic colonial skeleton (Maletz, 2014). Planktonic graptolites appeared near the base of the Ordovician and disappeared in the Devonian (Bulman, 1970; Cooper *et al.*, 2001). Fragments of graptolites are common zooclasts in palynofacies from this interval, and are often recorded in palynological slides, next to acritarchs and chitinozoans.

Eurypterid (sea scorpion) cuticles have been long known as components in palynological assemblages (e.g. Miller, 1996b). Eurypterids were chelicerate arthropods that first appeared in the Middle Ordovician (Lamsdell *et al.*, 2015) and went extinct in the Devonian (Braddy *et al.*, 2004).

2.2.1 Acritarchs and phytoplankton

Acritarchs (Fig. 4) were named and first defined as organic-walled microfossils with uncertain affinities by Evitt (1963), after the earlier term "hystrichospheres" (Wetzel, 1933) had implicitely lost this meaning and became obsolete when the eponymous *Hystrichosphaeridium* had been accepted as a dinoflagellate. The original diagnosis (Evitt, 1963, p. 300) was as follows:

> *"Small microfossils of unknown and probably varied biological affinities consisting of a central cavity enclosed by a wall of single or multiple layers and of chiefly organic composition; symmetry, shape, structure, and ornamentation varied; central cavity closed or communicating with the exterior by varied means, for example: pores, a slitlike or irregular rupture, a circular opening (the pylome)."*

Many authors reference the emendation of Downie *et al.* (1963, p. 7):

> *“Unicellular or apparently unicellular microfossils consisting of a test composed of organic substances and enclosing a central cavity. Shape of the test spherical, ellipsoidal, discoidal, elongate or polygonal; test surface smooth, granular, punctate or perforate. Spines or other processes, raised ridges (crests), flanges, wings or other outgrowths present or absent; where present, connected to the test by varied means or lacking such connection. Shell opens by rupture, splitting, or formation of a simple circular pylome. Rarely, a number of tests loosely associated in a chain.”*

Various definitions of the acritarch group were discussed by Servais *et al.* (1996). Following the proposition of Evitt (1963), acritarchs are treated as a form-group *incertae sedis* under the International Code of Botanical Nomenclature. Informal subgroups based on broad morphological similarities were introduced by Downie *et al.* (1963). Other authors adopted this classification or a modification thereof (Strother, 1996). It is commonly assumed that most acritarchs represent microphytoplankton (e.g. Downie *et al.*, 1963). Possible origins of acritarch-like objects include dinoflagellates (e.g. Evitt, 1963; Talyzina *et al.*, 2000), prasinophycean (e.g. Colbath & Grenfell, 1995; Guy-Ohlson, 1996; Tappan, 1980) and zygnematacean green algae (e.g. (Brenner & Foster, 1994; Tappan, 1980; Van Geel & Grenfell, 1996), cyanobacteria (e.g. Javaux & Marshal, 2006), animal cysts, egg cases, or embryos (e.g. Van Waveren & Marcus, 1993; Xiao & Knoll, 2000), euglenids (e.g. Colbath & Grenfell, 1995), fungi (e.g. Butterfield, 2005), and spores of land plants (e.g. Chaloner & Orbell, 1971; Fensome *et al.*, 1990). Acritarchs are known from the Archean onwards (Javaux *et al.*, 2010). They are highly diverse and abundant in the upper Neoproterozoic and lower Palaeozoic and decline drastically around the Devonian/Carboniferous boundary (e.g. Strother, 1996; Tappan, 1980). Several acritarch biozonations have been published for the Palaeozoic (e.g. Molyneux *et al.*, 1996).

Prasinophycean green algae and cyanobacteria were present during the Cambrian and Ordovician and are often studied together with acritarchs.

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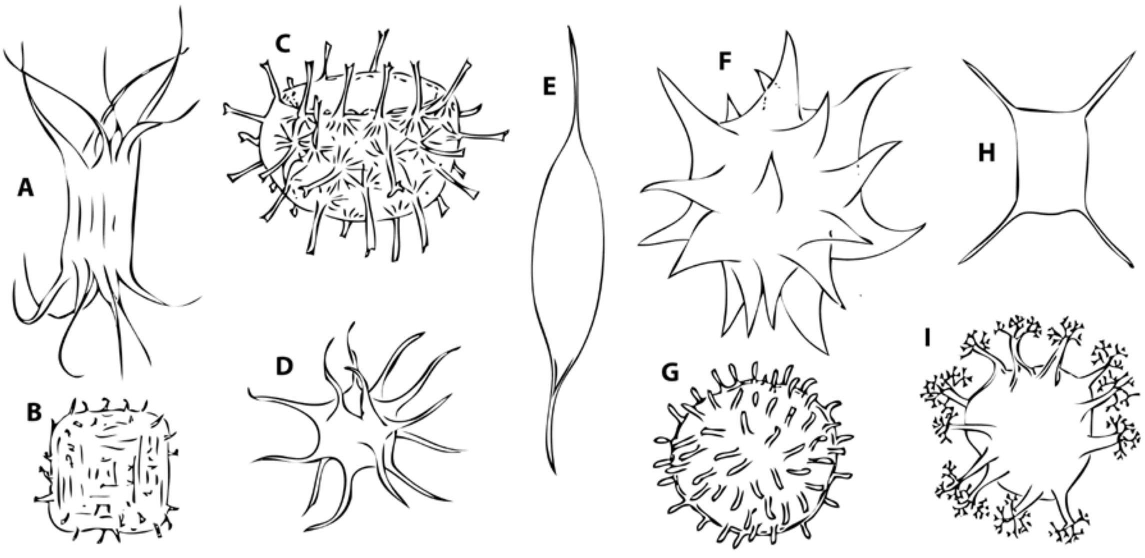

Fig. 4: Examples of acritarch genera present in the Cambrian-Ordovician. Modified from Eisenack *et al.* (1979). A: *Acanthodiacrodium*. B: *Coryphidium*. C: *Stelliferidium*. D: *Micrhystridium*. E: *Leiofusa*. F: *Goniosphaeridium*. G: *Gorgonisphaeridium*. H: *Veryhachium*. I: *Multipliciphaeridium*.

2.2.2 Chitinozoans

Chitinozoans are conical, rod-, flask-, vase-, or similarly shaped organic-walled microfossils with an opening at one end (Eisenack, 1931). The wall consists of three layers; the outer layer, the periderm, can be smooth or ornamented in various fashions; the ectoderm underlies the periderm; the endoderm constitutes the prosome or operculum that closes the opening (Paris, 1981). Sizes range between 70 and 1500 µm, typically 200-300 µm (Eisenack, 1931). They occur as single individuals, in chains, clusters, or in cocoons (Eisenack, 1931; Paris & Nõlvak, 1999). Their phylogenetic affinity is unknown. Various theories on their origin have been forwarded (e.g. Miller, 1996a and references therein), the most accepted one interpreting them as eggs of an otherwise not fossilized marine animal (Paris & Nõlvak, 1999), which was part of the epipelagic zooplankton (Vandenbroucke *et al.*, 2010). They are treated under the International Zoological Code of Nomenclature. Eisenack (1931) first described chitinozoans from erratic material in Estonia and lay the foundation for their taxonomy. He chose the name because the material seemed like chitin, but chemical analyses brought no evidence of chitin (Jacob *et al.*, 2007; Voss-Foucart & Jeuniaux, 1972). In a systematic re-evaluation of chitinozoan taxonomy, Paris *et al.* (1999) accepted 56 genera, which are grouped in three families (Fig. 5). The families are as proposed by Eisenack (1931) and emended by Paris (1981): The Lagenochitinidae, which are marked by a prominent chamber that is well differentiated from a neck, which is closed off by a single- or multi-layered prosome; the Conochitinidae, in which chamber and neck are not well differentiated; and the

Desmochitidae, which are lacking a notable neck and are closed by an operculum. A possible chitinozoan was reported from the Cambrian (Shen *et al.*, 2013), but the group only has a notable record starting in the Tremadocian. They diversified rapidly during the Ordovician and are common in marine sediments up to the end-Devonian extinction (Grahn & Paris, 2011). Their widespread and abundant occurrence in many marine sediments during most of their existence qualifies them as biostratigraphic index fossils. Chitinozoan biozonation schemes for the Ordovician have been defined e.g. for "northern" Gondwana (Paris, 1990), Laurentia (Achab, 1989; Achab *et al.*, 2003), Saudi Arabia (Al-Hajri, 1995), and Baltoscandia (Nõlvak, 1999; Nõlvak *et al.*, 2006; Nõlvak & Grahn, 1993).

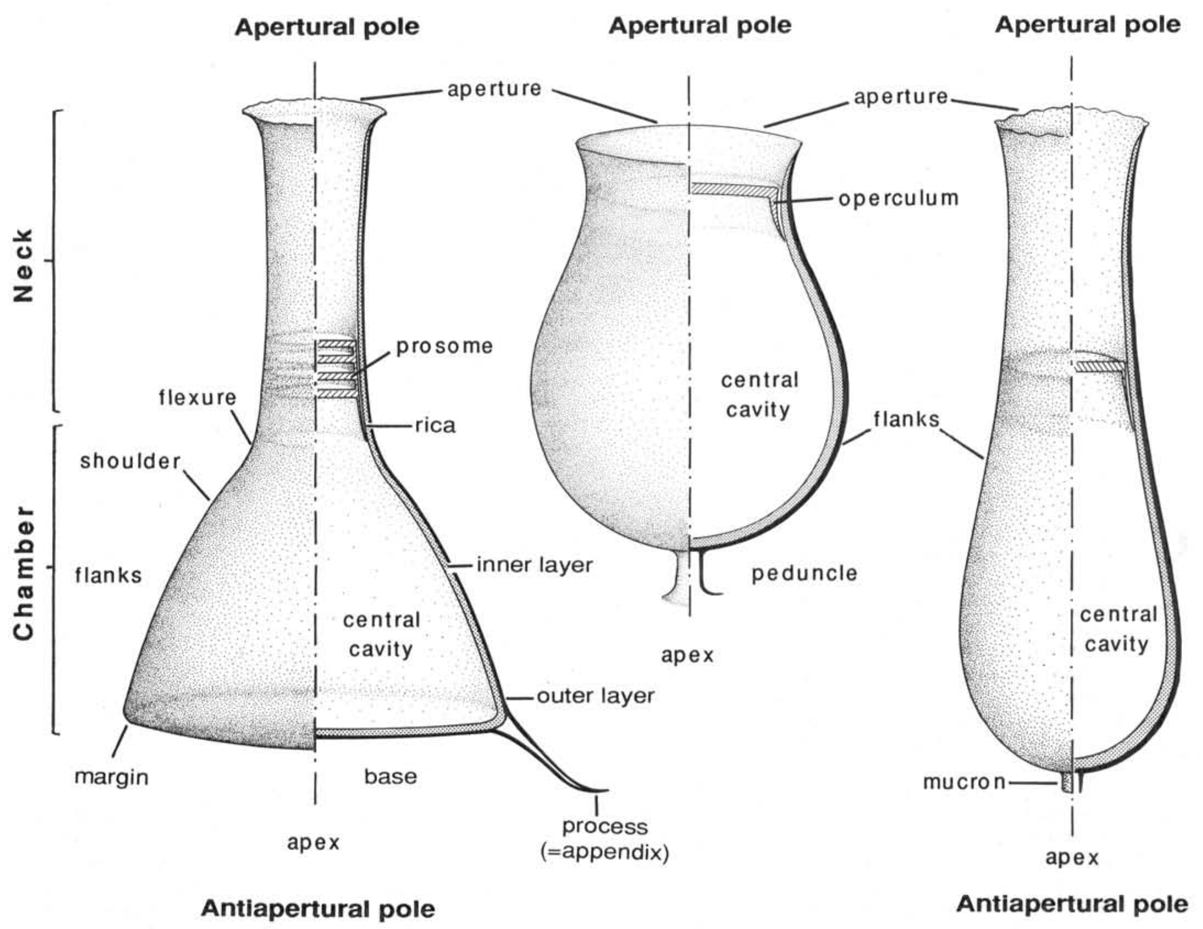

Fig. 5: Basic morphological features of the three chitinozoan families (Paris *et al.*, 1999, modified after Paris, 1981). From left to right: Lagenochitinidae, Desmochitinidae, Conochitinidae.

2.2.3 Small Carbonaceous Fossils

Organic (or carbonaceous) micro- or mesofossils that are commonly ignored in palynological studies or destroyed during maceration were coined SCFs (small carbonaceous fossils) by Butterfield & Harvey (2012). This informal group is more or less analogous to SSFs (small shelly fossils, see Matthews & Missarzhevsky, 1975). They also include organic remains of biomineralizing organisms that normally occur as "shelly" fossils (Butterfield & Harvey, 2012; Butterfield & Nicholas, 1996; Harvey, 2010; Harvey *et al.*, 2012a; Harvey &

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Butterfield, 2011; Martí Mus, 2014). SCFs are often larger, more fragile, and more rare than classical palynomorphs. Because of their fragility, they are preferably extracted with a more gentle method than classical palynomorphs, with as little manipulation as possible (i.e. no stirring, fewer acid treatments; see complementary information to Butterfield & Harvey, 2012). In the Cambrian, they proved useful in extending the stratigraphic and palaeogeographical ranges of certain groups of animals that are rarely preserved as complete body fossils (Butterfield & Harvey, 2012; Smith, 2012; Smith *et al.*, 2015), or that were otherwise unknown from the Cambrian (Butterfield, 1994; Harvey *et al.*, 2012b; Harvey & Butterfield, 2008; Harvey & Pedder, 2013).

2.3 Lagerstätten

A Lagerstätte (pl.: Lagerstätten) is an exceptional fossil deposit. Following Seilacher (1970), Lagerstätten are divided in Konservat- and Konzentrat-Lagerstätten. The former contains fossils with exceptional preservation, e.g. with preserved soft parts that are not normally fossilised. Such fossils need not be very abundant. In contrast, Konzentrat-Lagerstätten are marked by a high concentration of fossils, which are not necessarily preserved in any special way. Konzentrat-Lagerstätten are rather common and not usually labelled as such, while Konservat-Lagerstätten are rare and of particular scientific interest. Consequently, “Lagerstätte” is nowadays used almost synonymously with “Konservat-Lagerstätte”.

The exceptional preservation of fossils in Konservat-Lagerstätten can be attributed to several different types, depending on the taphonomic pathway. In the Cambrian, the most common is the Burgess Shale-type preservation involving carbonaceous films (Butterfield, 1995; Gaines, 2014; Gaines *et al.*, 2008). “Orsten”-type preservation involves phosphatisation of small (<2 mm) cuticular fossils (Maas *et al.*, 2006, and references therein). Pyritisation is responsible for the exceptional preservation of arthropods in the Upper Ordovician Beecher's Trilobite Bed (Briggs *et al.*, 1991).

The Cambrian has an unusually high concentration of Lagerstätten compared to other systems (Allison & Briggs, 1993). According to Gaines (2014), the Cambrian hosts 50 Burgess Shale-type Lagerstätten alone. Van Roy *et al.* (2015) listed 14 Ordovician Lagerstätten (Fig. 1; counted including the Soom Shale, which may be lowermost Silurian; see Vandenbroucke *et al.*, 2009).

The Fezouata Lagerstätte consists in a part of the Lower Ordovician Fezouata Formation in the Anti-Atlas region of Morocco (Martin *et al.*, 2015) (Fig. 3B). It was the first Lower

Ordovician Konservat-Lagerstätte to be found (Van Roy *et al.*, 2010). Only recently were the Afon Gam Biota of Wales (Botting *et al.*, 2015) and the Floresta Formation of Argentina (Aris & Palomo, 2014) discovered. The Fezouata Lagerstätte is remarkable for possibly being the only post-Cambrian Burgess Shale-type Lagerstätte and for preserving a rich, open-marine fauna that includes a mixture of typical elements of the Cambrian Burgess Shale-type faunas and of the more modern Palaeozoic Evolutionary Fauna (Van Roy *et al.*, 2010; 2015).

The Winneshiek Shale (Darriwilian) around the city of Decorah, Winneshiek County, Iowa, USA (Fig. 3C), contains a Konservat-Lagerstätte that so far has yielded eurypterids, phyllocarids, other bivalved arthropods, linguloid brachiopods, conodont elements and apparatusses of sometimes giant sizes, mollusks, bromiolites, and possible jawless fish (Liu *et al.*, 2006; 2009). Unpublished reports also documented the presence of abundant coenobial algae and acritarchs (P. Zippi, 2010). The shale is particularly rich in cuticle fragments, which are probably for the most part eurypterid remains. Presently, the eurypterids of Winneshiek are the oldest known (Lamsdell *et al.*, 2015; Liu *et al.*, 2009). The Winneshiek Shale is still barely studied. It is restricted to a circular area with a diameter of about 5.6 km, with a thickness of 18 to 27 m (Lamsdell *et al.*, 2015). In preliminary reports it is interpreted as deposits in a meteorite crater, the “Decorah impact structure” (Kass *et al.*, 2013a; 2013b; McKay *et al.*, 2010; 2011), in a restricted, brackish, shallow marine environment (Liu *et al.*, 2013). So far only two Konservat-Lagerstätten are known from the Middle Ordovician, the other being the Llanfallteg Formation in south-west Wales (Legg & Hearing, 2015; Whittington, 1993).

2.4 The RALI project

The RALI project (“The Rise of Animal Life (Cambrian-Ordovician) – organization and tempo: evidence from exceptionally preserved biotas”, grant number ANR-11-BS56-0025) is a four year research program funded by the French ANR (Agence National de la Recherche). It is a cooperation between the universities Lille 1 and Lyon 1 and partnered with researchers from across the globe. The RALI project targets the Cambrian to Ordovician episode of biodiversification. In particular, it is centred around three main questions:

1. How and when did marine biodiversity evolve in time and space?
2. Are the current models that identify the Cambrian Explosion and the GOBE as separate events and a change in evolutionary faunas *sensu* Sepkoski (1981, 1984) valid?

3. How did modern ecosystems evolve?

To answer these questions in practice, the project has three main targets:

1. The study of sites of exceptional preservation, which have the potential to give us a more complete view of ancient ecosystems than the more common “shelly” fossils alone.
2. The study of the early food chains through the analysis of fossilized gut contents.
3. The creation of a database on morphological, ecological, and environmental information regarding sites of exceptional preservation and the assessment of these data for the development of biodiversity and the occupation of the ecospace.

2.5 Aim and scope of this thesis

As a part of RALI, and financed by this project, the aim of this thesis work was to provide answers to the questions of RALI with the methods of palynology. Among the many possible specific questions to be researched under the broad topic of palynomorphs in relation to the Cambro-Ordovician biodiversification, this study focuses on three main points:

The biodiversity of Cambrian acritarchs

A major question for the understanding of the evolution of life in the Cambrian and Ordovician is the understanding of food chains, and in particular the base of the food chain. As a main food source of recent marine ecosystems, phytoplankton probably also have had an important role in lower Palaeozoic food chains. The evolution of phytoplankton may have influenced the Cambrian Explosion and was a possible trigger of the GOBE. Consequently, one part of the present study was directed at the biodiversity of acritarchs during the Cambrian, as a proxy for the evolution of phytoplankton. This first involved the compilation of a database with presence/absence data for Cambrian acritarchs, which was derived from a substantial part of the literature. The database was then used to calculate various diversity indices on two different stratigraphic scales, globally and regionally (Fig. 3A), and for both species and genera. The results are critically discussed. A main point of interest was the search for evidence for or against a strong evolutionary link between phytoplankton/acritarchs and marine invertebrates during the Cambrian Explosion and in the prelude of the GOBE during the latest Cambrian.

This part of the thesis resulted in two publications. The first (Nowak *et al.*, 2015a), described in detail the database, the results of the diversity calculations and their implications. These results contributed to a second paper (Servais *et al.*, *recommended for publication after minor revision*), discussing the evolution of phytoplankton during the late Cambrian in the context of the "Ordovician plankton revolution" (see Saltzman *et al.*, 2011; Servais *et al.*, 2008).

Article I: Nowak, H., Servais, T. Monnet, C. Molyneux, S.G. & Vandenbroucke, T.R.A. (2015a) Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: A review of Cambrian acritarch diversity. *Earth-Science Reviews* **151**, 117–131, doi:10.1016/j.earscirev.2015.09.005

Newly calculated diversity curves show a possible link between acritarch and animal diversity during the Cambrian explosion, but also a heavy bias in the acritarch data.

Article II: Servais, T., Perrier, V., Danelian, T., Klug, C., Martin, R.E., Munnecke, A., Nowak, H., Nützel, A., Vandenbroucke, T.R.A., Williams, M. & Rasmussen, C.M.Ø. (*recommended for publication after minor revision*) The onset of the "Ordovician Plankton Revolution" in the late Cambrian. *Palaeogeography, Palaeoclimatology, Palaeoecology*.

A revision of all plankton groups during the latest Cambrian did not provide evidence for a single event such as the SPICE event to have triggered the "Ordovician plankton revolution".

The palynology of the Fezouata Lagerstätte (Lower Ordovician, Morocco)

The Fezouata Lagerstätte is a main focus of the RALI project, as it provides a unique view on an open-marine community during the early stages of the GOBE. In the context of an interdisciplinary effort to re-evaluate the Fezouata Formation as a whole and the Fezouata Lagerstätte in particular, this part of the thesis delivers well correlated information about the palynomorph assemblages in the outcrop area of the Lagerstätten-bearing Fezouata Formation near Zagora and in the subsurface at Adrar Zouggar Mountain (Fig. 3B). Outcrop samples were taken over the course of several field campaigns between 2012 and 2014. I took part in one excursion in late February/early March 2013. The focus is on the biostratigraphy of acritarchs and chitinozoans, which are the most common palynomorphs present. A secondary objective was the search for SCFs. Their presence seemed likely, since the preservation of fossils in the Fezouata Lagerstätte involves the carbonaceous films and Cambrian Konservat-Lagerstätten with a similar type of preservation have yielded SCFs, yet no SCFs were recovered here.

Four papers resulted from this work. First, a short report on the acritarchs in subsurface samples of the Fezouata Formation was published (Nowak *et al.*, 2015b). The chitinozoans from the same borehole and both acritarchs and chitinozoans are described and interpreted in a second paper, with a focus on biostratigraphy, palaeogeography and palaeoenvironment (Nowak *et al.*, *submitted*). The palynological samples yielded numerous conodonts, which are discussed by Lehnert *et al.* (*in preparation*). Finally, palynological results are summarized in the review paper by Martin *et al.* (*in press*).

Article III: Nowak, H., Akodad, M., Lefebvre, B. & Servais, T. (2015b) Discovery of the *messaoudensis–trifidum* acritarch assemblage (upper Tremadocian–lower Floian, Lower Ordovician) in the subsurface of Morocco. *Estonian Journal of Earth Sciences* **64**(1), 80–83, doi:10.3176/earth.2015.14.

Acritarchs from the lower part of the Fezouata Formation in the AZ-1 borehole are assignable to the *messaoudensis-trifidum* assemblage, which is typical for the uppermost Tremadocian-lowermost Floian interval on the Gondwanan margin.

Article IV: Nowak, H., Servais, T., Pittet, B., Vaucher, R., Akodad, M., Gaines, R. R. & Vandenbroucke, T. R. A. (*submitted to Palaeogeography, Palaeoclimatology, Palaeoecology*) Palynomorphs of the Fezouata Formation (Lower Ordovician, Morocco): age and environmental constraints of the Fezouata Biota.

Acritarch and chitinozoan assemblages from the Lagerstätten-bearing Fezouata Formation are described and interpreted, with acritarchs tying in perfectly with the biostratigraphy of graptolites and with the *messaoudensis-trifidum* assemblage known from the Gondwanan margin in the Lower Ordovician, while chitinozoans reveal complications in the chitinozoan biostratigraphy, but also potentially important preservational patterns.

Article V: Lehnert, O., Nowak, H., Sarmiento, G., Servais, T., Gutiérrez-Marco, J.-C. & Akodad, M. (*in preparation for Palaeogeography, Palaeoclimatology, Palaeoecology*) Conodonts from the Lower Ordovician of Morocco – a contribution to age and faunal diversity of the famous Fezouata Lagerstätte

Conodonts derived from palynological residues indicate uppermost Tremadocian to lower Floian biozones for the Lagerstätten-bearing part of the Fezouata Formation in outcrops and subsurface samples.

Article VI: Martin, E.L.O., Pittet, B., Gutiérrez-Marco, J.-C., Vannier, J., El Hariri, K., Lerosey-Aubril, R., Masrour, M., Nowak, H., Servais, T., Vandenbroucke, T.R.A., Van

Roy, P., Vaucher, R. & Lefebvre, B. (2015, *in press*) The Lower Ordovician Fezouata Konservat-Lagerstätte from Morocco: Age, environment and evolutionary perspectives. *Gondwana Research*, doi:10.1016/j.gr.2015.03.009.

Two stratigraphic intervals with exceptionally preserved fossils within the lower Fezouata Formation are identified and dated as upper Tremadocian by graptolites and acritarchs.

SCFs of the Winneshiek Lagerstätte (Darriwilian, Iowa, USA)

The Winneshiek Shale (Fig. 3C) provided excellent prospects for the search for SCFs, since preliminary reports told of large amounts of eurypterid cuticulae and the presence of other arthropods. It is one of currently only two known Middle Ordovician Lagerstätten, arguably representing the peak of the GOBE, and consequently of special interest. Herein, first observations on SCFs of possible crustacean origin and a large filamentous eukaryotic alga are presented.

Article VII: Nowak, H., Harvey, T.H.P., Liu, H., McKay, R.M. & Servais, T. (*in preparation for Lethaia*) Exceptionally preserved arthropodan microfossils of possible crustacean origin from the Middle Ordovician Winneshiek Lagerstätte, Iowa, USA

The Winneshiek Shale contains a surprising amount of possible crustacean mandibles resembling cladoceran branchiopods in certain features. A few possible crustacean filter plates are also recovered.

Article VIII: Nowak, H., Harvey, T.H.P., Liu, H., McKay, M.R., Zippi, P., Campbell D. & Servais, T. (*in preparation for Review of Palaeobotany and Palynology*) Filamentous eukaryotic algae from the Winneshiek Lagerstätte in Iowa (Middle Ordovician).

The presence of giant-celled filamentous algae with a probable affinity to cladophoraceans in the Winneshiek Shale is reported.

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Article I

Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: A review of Cambrian acritarch diversity

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Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: A review of Cambrian acritarch diversity

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ABSTRACT

Most early Palaeozoic acritarchs are thought to represent a part of the marine phytoplankton and so constituted a significant element at the base of the marine trophic chain during the 'Cambrian Explosion' and the subsequent 'Great Ordovician Biodiversification Event.' Cambrian acritarch occurrences have been recorded in a great number of studies. In this paper, published data on Cambrian acritarchs are assembled in order to reconstruct taxonomic diversity trends that can be compared with the biodiversity of marine invertebrates. We compile a database and calculate various diversity indices at global and regional (i.e. Gondwana or Baltica) scales. The stratigraphic bins applied are at the level of the ten Cambrian stages, or of fourteen commonly used biozones in a somewhat higher resolved scheme. Our results show marked differences between palaeogeographical regions. They also indicate limitations of the data and a potential sampling bias, as the taxonomic diversity indices of species are significantly correlated with the number of studies per stratigraphic bin. The total and normalized diversities of genera are not affected in the same way. The normalized genus diversity curves show a slow but irregular rise over the course of the Cambrian. These also are the least biased. A radiation of species and to a lesser extent of genera in the 'lower' Cambrian Series 2 appears to mirror the 'Cambrian Explosion' of metazoans. This radiation, not evident on Gondwana, is followed by a prominent low in species diversity in the upper Series 3 and lower Furongian. Highest diversities are reached globally, and on both Baltica and Gondwana, in the uppermost Cambrian Stage 10, more precisely in the *Peltura* trilobite Zone, preceding a substantial phase of acritarch species extinction below and at the Cambrian/Ordovician boundary. Nearly all the genera present in Stage 10 survived into the Ordovician. The forms that emerged during the Cambrian therefore became the foundation for the more rapid radiation of acritarchs during the 'Great Ordovician Biodiversification Event'.

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1. Introduction

The Cambrian fossil record is marked by the well-known 'Cambrian Explosion' (or radiation), which is characterized by the appearance of most metazoan phyla in a seemingly short interval (e.g. Conway Morris, 2000). Although molecular clock estimates now indicate a Proterozoic origin for many lineages (Erwin et al., 2011), the Cambrian Explosion is still considered to be one of the most important periods in the history of life. It was followed in the Ordovician by the 'Great Ordovician Biodiversification Event' (GOBE), an episode of rising taxonomic diversity in most marine organisms and of increasingly complex ecosystems that were more diverse and differentiated than those of the Cambrian, with a wider range of ecological niches (Webby et al., 2004; Bambach et al., 2007). Whether these two episodes were in fact separate, or should be considered as one long period of diversification, is currently debated (Alroy et al., 2008), as are their possible causes and mechanisms.

Phytoplankton is an important constituent at the base of the food web today and in this capacity may have played a key role in the early Palaeozoic diversification events (Debrenne and Zhuravlev, 1997; Butterfield, 1997). It has been argued that a higher concentration of phytoplankton in the early Palaeozoic oceans triggered the major evolutionary events and had an important impact on metazoan diversification. Butterfield (1997), for example, argued that the interaction between phytoplankton and metazoans fuelled the Cambrian Explosion after the appearance of mesozooplankton. Similarly, Servais et al. (2008, 2010) argued that the evolution of the phytoplankton triggered a 'plankton revolution' through the Cambrian–Ordovician boundary interval at the beginning of the GOBE. The expanding and increasingly diverse phytoplankton could have served as food for the developing zooplankton, but also for various clades of suspension feeders and detritus feeding organisms. Detailed knowledge on the development of biomass, taxonomic and morphological diversity of phytoplankton would be useful to test this hypothesis. Here we concentrate on taxonomic diversity.

The phytoplankton of early Palaeozoic oceans is generally considered to be present among the acritarchs, which are defined as organic-walled microfossils of uncertain biological affinity (Evitt, 1963). Consequently, the acritarchs are a polyphyletic group and have a long stratigraphical range. A number of organisms originally considered to be acritarchs now have established affinities with other groups, including prasinophycean and zygnematacean green algae, cyanobacteria, dinoflagellates, multicellular algae (Butterfield, 2004; Mendelson, 1987), fungi (Butterfield, 2005) and even metazoans (e.g. schizomorphitae: Van Waveren, 1992; Van Waveren and Marcus, 1993; *Ceratophyton*: Fatka and Konzalová, 1995; large spinose Ediacaran microfossils: Cohen et al., 2009). Although technically no longer acritarchs (Evitt, 1963), they are still occasionally referred to as such. Nevertheless, most of the remaining Palaeozoic acritarchs are considered to be cysts of marine, generally planktonic unicellular algae, which are often globally distributed. We here use the term 'acritarchs' to include all organic-walled microfossils of possible phytoplankton origin, including acritarchs *s.s.* and organic microfossils that are now attributed to the green algae and cyanobacteria. Where preserved, they are often recovered in large numbers, even from small samples, resulting in an abundant record and frequent application in biostratigraphy (e.g. Martin and Dean, 1981, 1988; Moczydłowska, 1991, 1998; Vanguestaine and Van Looy, 1983).

Biomarker evidence suggests that Palaeozoic acritarchs may include forms that have a close biological affinity with (or be evolutionary precursors of) dinoflagellates (Moldowan and Talyzina, 1998; Talyzina et al., 2000). However, the oldest unambiguous dinoflagellates in the fossil record are from the Triassic (e.g. Fensome et al., 1996a) and an alternative view is that the Palaeozoic acritarchs represent a "green" phytoplankton lineage (Martin et al., 2008). Observations of recent dinoflagellates have shown that only some species form organic-walled cysts with the potential to fossilize (Dale, 1976), and may do so at more than one stage in their life cycle (Fensome et al., 1996a). If, by analogy, Palaeozoic acritarchs are also cysts, perhaps of various algal groups, there is a clear implication that they only represent a part of the phytoplankton.

A further difficulty is that acritarch taxa are morphospecies rather than true biological species. In some instances, morphological gradations from one Palaeozoic acritarch taxon to another have been demonstrated, suggesting ecophenotypic variation rather than speciation (Servais et al., 2004b). If so, the number of taxa recorded would overestimate the number of biological species. Conversely, for the rather featureless sphaeromorph acritarchs, often identified simply as 'sphaeromorphs' or '*Leiosphaeridia* spp.', the number of taxa recorded probably underestimates biological diversity. Despite these limitations, acritarchs remain the main source of information for phytoplankton in the Cambrian, long before the appearance of planktonic algae forming calcitic and siliceous skeletons during the Mesozoic (Bown, 2005).

Various Palaeozoic acritarch diversity curves have been published previously. Detailed global curves are available for the Carboniferous (Mullins and Servais, 2008), Lochkovian to Tournaisian (Klug et al., 2010) and the Permian (Lei et al., 2013). Regional diversity curves have been published for the Ordovician on the Yangtze Platform (South China) and North Africa (Algeria, Tunisia and Libya; also including the latest Cambrian; Servais et al., 2004a), for 'northern Gondwana' (including North Africa, Turkey, Saudi Arabia and several peri-Gondwanan microcontinents; Vecoli and Le Hérissé, 2004) and for Baltica (Hints et al., 2010). Li et al. (2007) published a diversity curve for genera in the Ordovician of South China, North China and Tarim.

Acritarch diversity curves that include the Cambrian have been published by Tappan and Loeblich (1972, 1973; genera, Precambrian to present); Vidal and Knoll (1982; species, upper Riphean to lower Cambrian); Knoll (1994; species, Proterozoic to lower Cambrian); Strother (1996; Precambrian and Phanerozoic, using data of Downie, 1984, and Fensome et al., 1990), Vidal and Moczydłowska-Vidal (1997; species, Proterozoic to Cambrian), Moczydłowska (1998; species, Cambrian in Upper Silesia; and 2011; species, Ediacaran to basal Ordovician, global and Baltica); Zhuravlev (2001; genera, Cambrian to Tremadocian); Katz et al. (2004; species, Proterozoic to Neogene, and genera, Cambrian to Neogene); Huntley et al. (2006a, 2006b; genera, Proterozoic to Cambrian), Strother (2008; genera, Phanerozoic), and

Servais et al. (2008; species, middle Cambrian to Llandovery). Katz et al. (2004) and Strother (2008) used the Palynodata database (see Fensome et al., 1996b) to create their diversity curves. Palynodata had been compiled by a consortium of oil companies and scientific institutions over the course of three decades and was discontinued in 2006. Mullins et al. (unpublished) compiled the PhytoPal database of acritarch occurrences covering the interval from the Cambrian to the Triassic (mainly Ordovician to Devonian), data that were partly used by Servais et al. (2008); Klug et al. (2010) and Moczydłowska (2011).

All these publications present a (usually global) total diversity (see 2.3). Knoll (1994) and Knoll et al. (2006) also discussed the diversity of species in single assemblages through time between the Proterozoic and the early Cambrian. The resolution varies between a single value for the whole Cambrian (Tappan and Loeblich, 1972, 1973; Strother, 1996) and more than 20 intervals (Zhuravlev, 2001).

Acritarch diversity analyses that include the Proterozoic-Cambrian transition at sufficient resolution show fairly high global total diversities in the late Neoproterozoic, followed by decreasing diversity towards the end of the Ediacaran (Vidal and Knoll, 1982; Knoll, 1994; Vidal and Moczydłowska-Vidal, 1997; Knoll et al., 2006). Several studies found a diversification during the early Cambrian to a peak around the late early/early middle Cambrian (Strother, 1996; Vidal and Moczydłowska-Vidal, 1997; Moczydłowska, 1998; Zhuravlev, 2001). The Ordovician, when it is included, is marked by generally higher diversity than the Cambrian.

Diversity studies on Cambrian acritarchs published so far have had limitations in the choice of sources and in the analytical methods they applied, which may have allowed possible biases to go undetected, making them vulnerable to a certain degree of criticism. The goal of this study is to produce a robust database of acritarch occurrences in the Cambrian by compiling as much data as is feasible, in order to approximate their standing diversity using various methods, to identify evolutionary trends, and to test the results for biases. In particular, we address whether the Cambrian Explosion is reflected in acritarch diversity and whether the GOBE was preceded by a diversification of acritarchs, a temporal relation which would be a primary requirement in support of a cause-and-effect hypothesis. If phytoplankton had an effect on or was affected by these radiations, it might be expected that this would be reflected in acritarch diversity, and that, in turn, acritarch diversity might indicate general trends in phytoplankton biodiversity, assuming that other effects could be ruled out.

2. Materials and methods

2.1. Source data

The literature on Cambrian acritarchs includes over 500 publications, but many studies do not include descriptions or precise biostratigraphical data. Occurrence data for acritarchs in this study are derived from 103 studies (see Supporting material S1, S2). All available publications with consistent information on the presence of acritarch taxa in the Cambrian were included in the database, but only 72 of these studies reported assemblages with stratigraphic information that could be correlated precisely to any of the stratigraphic units we use (see 2.2., Fig. 1). We only included the latter in our subsequent diversity analysis.

Of the 72 source publications, 39 describe data from Gondwana (including various microcontinents on its periphery, most importantly 12 from Avalonia), 31 from Baltica, 11 from Laurentia, 11 from South China, 5 from Bruno-Silesia (or the Brunovistulicum), 4 from the Holy Cross Mountains (or the Małopolska 'Block'), 2 each from Tarim and Siberia, 1 from Kara and 1 from North China. Fig. 2 shows the palaeogeographical positions of study areas of publications included in our analysis, using the base maps of BugPlates (Torsvik, 2009). The only distinct regions with sufficiently extensive records to allow individual diversity analyses for most of the Cambrian are Baltica and that part of (peri-)Gondwana that includes northwestern Africa, Avalonia, Iberia and Sardinia and which was positioned near the South Pole during the Cambrian (Hartz and Torsvik, 2002).

Many published studies only list selected, biostratigraphically useful taxa or those typical of an assemblage. As a consequence, it is possible that we have undersampled the full range of species and, by the nature of the fossil record, their actual stratigraphical ranges in the Cambrian. Nevertheless, we consider our database to be representative of the current state of research.

2.2. Database

Our database (Supplementary Table S1) contains exactly 6000 entries reporting the presence/absence (not abundance) of acritarch taxa within the studied stratigraphic intervals. Each entry contains information on the identification of the taxon in question, the entry's source study, study area and stratigraphic position (with lower and upper limits). Taxonomic information includes genus name; species epithet or placeholder; qualifiers such as '?', 'cf.' and 'aff.', where applicable, for either the genus or species; authorship; and the original identification if it has been revised. Generally, we relied on the identifications and age-assignment in the original studies or published later revisions. Obvious and reported synonymies were taken into account (see Supplementary Table S3). The applied names follow the latest usage, without any intention on our part to validate or revise them. This approach purely serves to create a taxonomic framework that reflects the current state of research with as much consistency and as little redundancy as possible.

We use two schemes of stratigraphic subdivisions or bins in the database. One scheme corresponds to the ten stages of the International Chronostratigraphic Chart (state 2014; Cohen et al., 2013, updated), and the other to fourteen biozones (Fig. 1). The latter are mainly trilobite biozones. The Terreneuvian ('pre-trilobite' Cambrian) stages are dated by trace fossils or small shelly fossils (Peng et al., 2012). The first appearance of the trace fossil *Trichophycus* (or alternatively *Treptichnus*, *Phycodes* or *Manykodes*) *pedum* marks the base of the Cambrian System, the Terreneuvian Series and the Fortunian Stage (Brasier et al., 1994); the base of the upper stage in the Terreneuvian Series (Cambrian Stage 2) has not yet been defined. The choice of stratigraphic bins was a compromise guided by the resolution required to address our research question, the available data, and the maximal precision with which data can be attributed to a given stratigraphic interval in the Cambrian. Due to imperfect correlation, some data sets could be assigned to biozones but not stages or vice versa.

In order to calculate origination and extinction (see Section 2.3) for the basal and top Cambrian bins, we had to consider the presence of acritarch taxa during Proterozoic and post-Cambrian times. Data were derived from some of the sources mentioned above (Section 2.1., Figs. 1, 2), the acritarch and prasinophyte index of Fensome et al. (1990), and, for the post-Cambrian, the unpublished PhytoPal database by Mullins et al.

2.3. Methods

Diversity can be measured in different ways and for any taxonomic rank. In the case of acritarchs, treated as *incertae sedis*, only species and genera have a formal rank. Both are included in our analysis. Acritarch genera counted herein include reports of species assigned under open nomenclature (e.g. as 'sp.') to a genus or with an uncertain specific identification, but exclude species that are only tentatively assigned to a genus (see Supplementary Table S3). Species counted exclude those with uncertain identification, but include records that are only tentatively assigned to any particular genus (see Supplementary Tables S6-S11). After this selection process and under the stratigraphic constraints discussed above (see Section 2.2.), our dataset records the ranges of 173 genera and 404 species.

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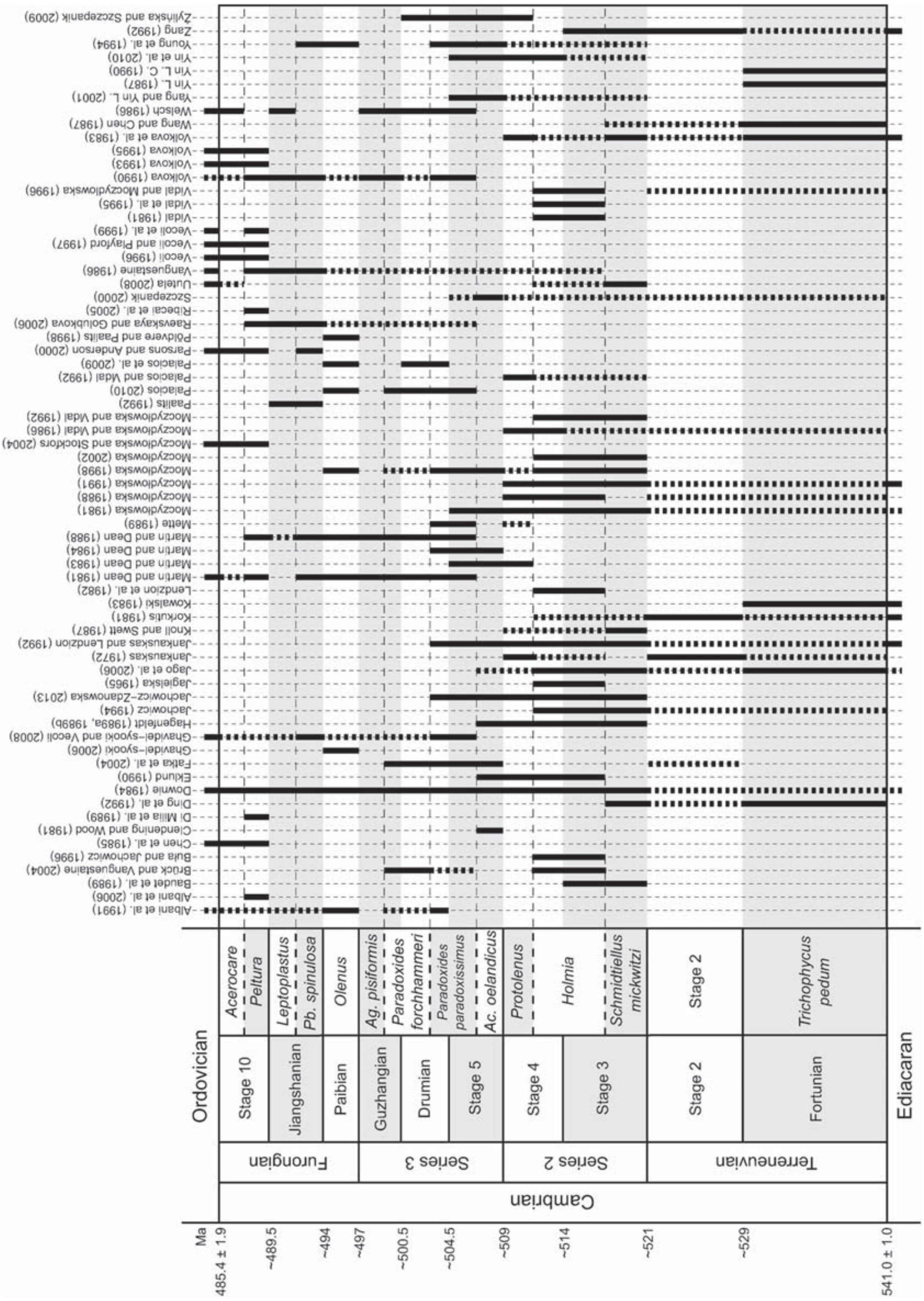

Fig. 1. Cambrian stratigraphic scheme and stratigraphic ranges of source studies used for diversity analyses. Chronostratigraphy according to Cohen et al., 2013, updated. *Ac.* = *Acadoparadoxides*. *Ag.* = *Agnostus*. *Pb.* = *Parabolina*. For complete references of source studies see Supplementary information S2.

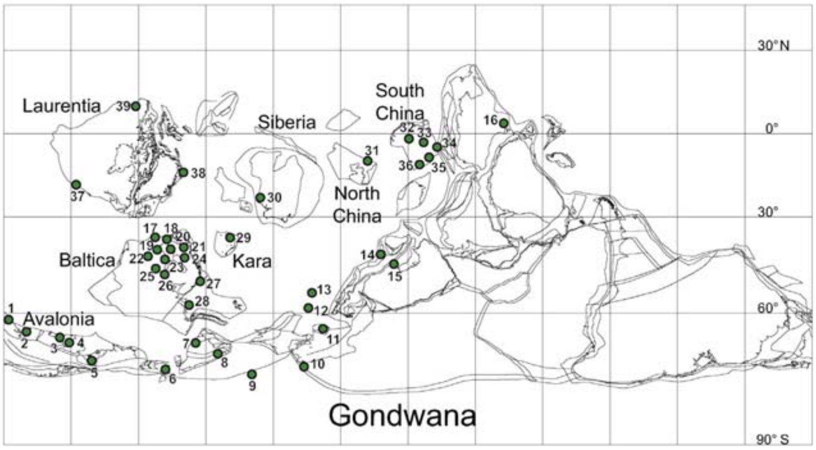

Fig. 2. Palaeogeographical reconstruction for the mid Cambrian Period (510 Ma) with study areas marked. Base map produced with BugPlates (Torsvik, 2009). 1 Nova Scotia, Canada (Palacios et al., 2009); 2 Eastern Newfoundland, Canada (Martin and Dean, 1981; Martin and Dean, 1983; Martin and Dean, 1984; Martin and Dean, 1988; Parsons and Anderson, 2000); 3 County Wexford, Ireland (Brück and Vanguestaine, 2004); 4 Wales (Young et al., 1994); 5 Belgium (Vanguestaine, 1986); 6 Sardinia, Italy (Ribecai et al., 2005); 7 Sierra Morena, Spain (Mette, 1989); 8 Cantabrian Mountains, Spain (Palacios and Vidal, 1992; Albani et al., 2006; Palacios, 2010); 9 N Algeria (Vecoli, 1996; Vecoli and Playford, 1997; Vecoli et al., 1999); 10 Ghadames Basin, Libya/Tunisia (Albani et al., 1991); 11 Barrandian area, Czech Republic (Fatka et al., 2004); 12 Upper Silesia (Bruno-Silesia), Poland (Jachowicz, 1994; Buła and Jachowicz, 1996; Moczydłowska, 1998; Jachowicz-Zdanowska, 2013); 13 Holy Cross Mountains (Małopolska High), Poland (Jagielska, 1965; Lendzion et al., 1982; Kowalski, 1983; Żylińska and Szczepanik, 2009); 14 Central Alborz Mountain Range, Iran (Ghavidel-syooki, 2006); 15 Zagros Basin, Iran (Ghavidel-syooki and Vecoli, 2008); 16 South Australia (Jago et al., 2006); 17 Baltic Poland (Moczydłowska, 1981, 1988, 1991; Moczydłowska and Vidal, 1986; Jankauskas and Lendzion, 1992; Szczepanik, 2000); 18 Bornholm, Denmark and Skåne, Sweden (Vidal, 1981; Moczydłowska and Vidal, 1992); 19 Lithuania (Jankauskas, 1972); 20 Östergötland and Öland, SE Sweden (Vidal, 1981; Di Milia et al., 1989; Eklund, 1990); 21 SW Sweden and SE Norway (Vidal, 1981; Vidal and Moczydłowska, 1996); 22 Belarus (Jankauskas and Lendzion, 1992); 23 Estonia (Paalits, 1992; Põldvere and Paalits, 1998; Uutela, 2008); 24 Swedish Caledonides, Sweden (Moczydłowska, 2002; Vidal and Moczydłowska, 1996); 25 Moscow Syneclise, Russia (Volkova, 1990; Volkova, 1995); 26 Leningrad Oblast, Russia (Volkova, 1993); 27 Digermul Peninsula, Norway (Welsch, 1986); 28 Kolguev Island, Russia (Moczydłowska and Stockfors, 2004); 29 Severnaya Zemlya, Russia – Kara (Raevskaya and Golubkova, 2006); 30 NE Siberia (Vidal et al., 1995); 31 Jilin, China (Chen et al., 1985); 32 Hubei, China (Ding et al., 1992; Zang, 1992); 33 Guizhou, China (Yang and Leiming, 2001; Yin et al., 2010); 34 Yunnan, China (Yin, 1990; Zang, 1992); 35 Sichuan, China (Wang and Chen, 1987); 36 Shaanxi, China (Yin, 1987); 37 Grainger County, Tennessee, USA (Clendening and Wood, 1981); 38 East Svalbard, Norway (Knoll and Swett, 1987); 39 Mackenzie Mountains, Canada (Baudet et al., 1989).

Taxa are counted as present in a stratigraphic interval in one of four ways (Fig. 3): as crossovers ranging through the entire interval; ranging into and going extinct in that interval; originating within the interval and ranging beyond its upper boundary; and as singletons, with a range confined to an interval, meaning that they originate and go extinct within the interval (Foote, 2000).

The actual number of coexisting taxa is the standing diversity (Cooper, 2004), and can only be estimated for palaeontological data. The sampled-in-bin diversity (Figs. 4, 5) gives the total count of taxa reported from a given stratigraphic interval. This index often underestimates diversity due to the incompleteness of the fossil record and sampling bias. Total diversity (Figs. 4, 5, 8, 9) is calculated by interpolating discontinuous taxon ranges from established occurrences (Foote, 2000), i.e., taxa not recorded from an interval are counted as being present if they occur in intervals below and above. With complete data, total diversity is likely to exceed the standing diversity at any specific point in time, because it does not account for extinctions within an interval (Cooper, 2004). Normalized diversity (Figs. 4, 5, 9) is calculated as the number of species ranging through an interval (crossovers), plus half the number of taxa that originate and/or become extinct in that stage (Sepkoski, 1975; Cooper, 2004). According to Cooper (2004), normalized diversity is a good approximation of the mean standing diversity in a stratigraphic bin.

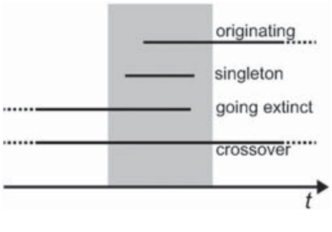

Fig. 3. Classes of taxa (in regards to ranges) present in a stratigraphic interval. After Foote (2000).

Indices of origination and extinction represent, respectively, the number of species originating and becoming extinct in a stratigraphic interval. Turnover in an interval is the sum of origination and extinction events. These indices of taxonomic change can be calculated as including or excluding singletons. In Fig. 6, singletons are excluded.

The use of stages and trilobite zones as the stratigraphic divisions in our analysis means that bins in both schemes are inevitably of different durations, and longer bins may have a higher diversity than shorter bins simply because they are sampling longer intervals, while at the same time obscuring short-term excursions. As the Cambrian stages vary in duration from about three million years (e.g. Guzhangian, Paibian) to twelve million years (Fortunian), a considerable effect may be expected. To correct for a possible bias resulting from these unequal interval lengths, rates of origination, extinction and turnover have been computed. They are equal to the origination, extinction and turnover indices divided by the stage duration in Myr (from Cohen et al., 2013 updated; Fig. 6 B, D).

Vidal and Moczydłowska-Vidal (1997) first applied poly-cohort survivorship to Cambrian acritarchs. Poly-cohort survivorship measures the percentage of species in a cohort, i.e. species present in a given stratigraphic interval that are still present in later intervals (Fig. 7A). In contrast, poly-cohort prenascence (also called backward survivorship) measures the proportion of a cohort present in earlier intervals (Fig. 7B; e.g. Raup, 1978; Foote, 2001). Poly-cohorts of survivorship and prenascence respectively are calculated for all stratigraphic bins considered herein and plotted on a logarithmic scale. The slope of the

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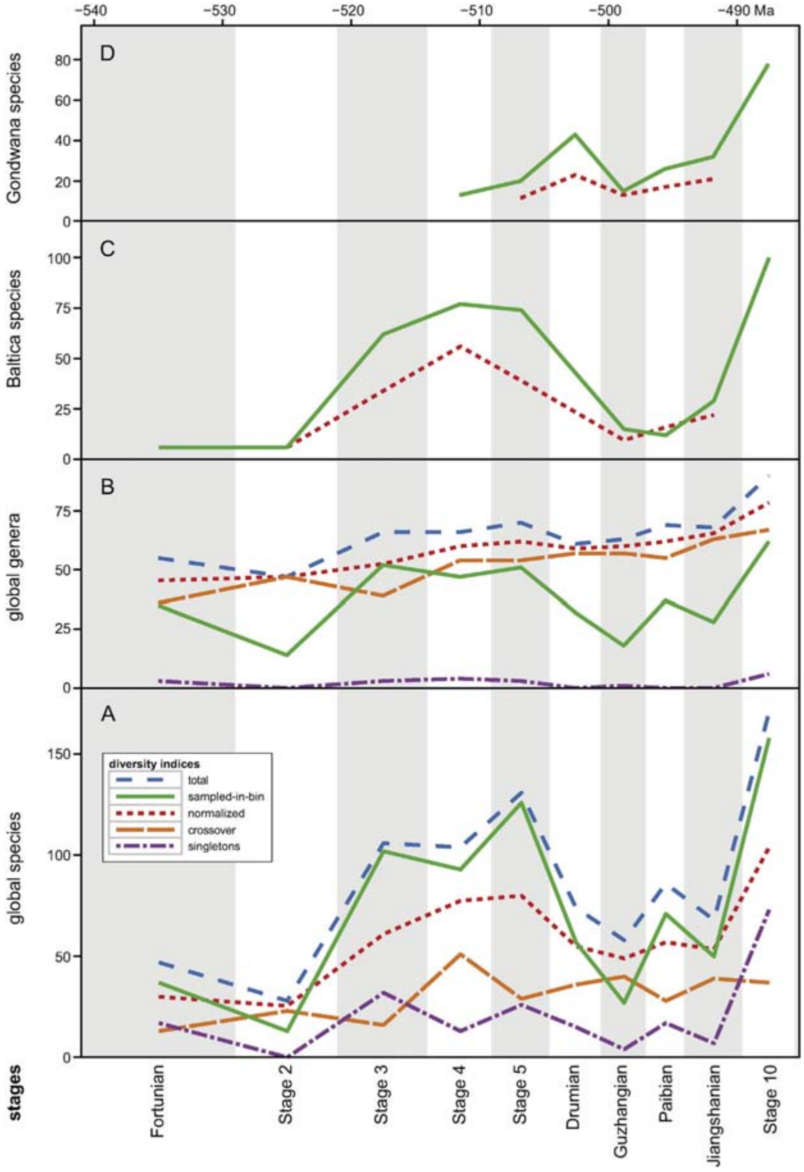

Fig. 4. Global and regional taxonomic diversity curves of Cambrian acritarchs based on stages. A, Global species diversity. B, Global genus diversity. C, Baltica species diversity (no data available for the Drumian). D, Gondwana species diversity (no data available for the Fortunian, Stages 2–3).

cohort curves then represents the rate of extinction or origination for each cohort, with a linear curve (on a logarithmic scale) implying constant rates, while changes over time or between cohorts can reveal changes in rates or biases.

We evaluate the effect of sampling bias and test for evolutionary links between acritarchs and marine invertebrates (diversity values for marine invertebrate taken from the supporting information of Na and Kiessling, 2015) by calculating Spearman's ρ (*rho*) or r_s – a non-parametric rank order correlation coefficient (e.g. Press et al., 1992) – for correlations between diversity indices and the number of studies per interval (Fig. 9) and between the sampled-in-bin genus diversities of acritarchs and animals (Fig. 11), respectively. This metric is commonly used to identify bias in the fossil record (e.g. Dunhill et al., 2012; Na and Kiessling, 2015). The value of r_s varies between −1 and 1 for perfect negative and positive correlation, respectively, with 0 indicating absence of correlation. The statistical significance is given by the probability value p, which is derived from permutation tests. A correlation is accepted as strong if the coefficient is high (> 0.75) and significant if the probability value is low (< 0.05). In some cases, this might indicate a bias. The results are here rounded to two and to three significant digits for r_s and p, respectively. We also investigate the changing strength of correlation through the studied stratigraphic intervals by applying a moving-window approach (Fig. 11B).

Subsampling methods are often used in biodiversity analyses in order to address sampling bias. These methods standardize for number of occurrences, number of studies, taxon frequency, or rock volume

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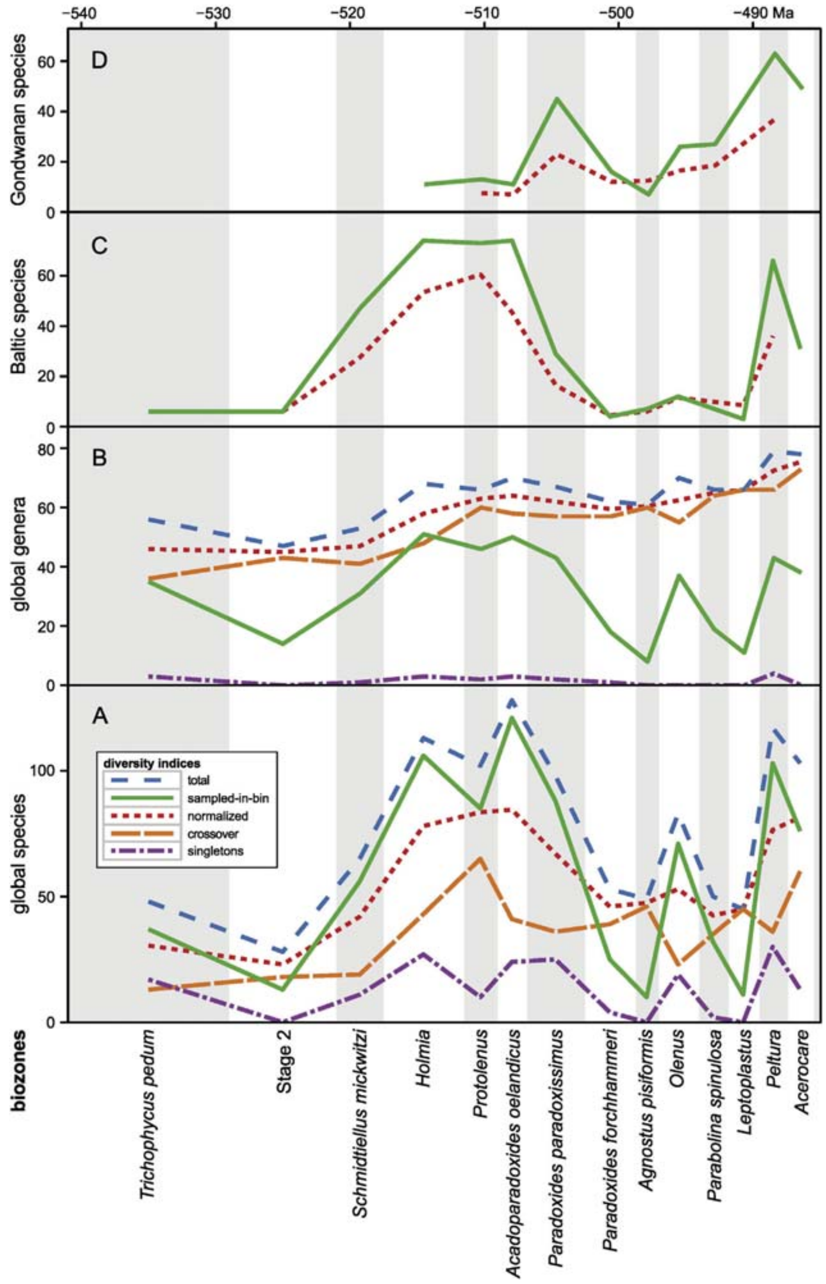

Fig. 5. Taxonomic diversity based on biozones. A, Global species diversity. B, Global genus diversity. C, Baltica species diversity (no data available for the *Parabolina spinulosa* zone). D, Gondwana species diversity (no data available for the *Trichophycus pedum* zone, Stage 2, the *Schmidtiellus mickwitzi* and *Leptoplastus* zones).

(Alroy, 2010; Hannisdal and Peters, 2011). The resulting trends are usually less biased than diversity based on raw counts, but they can introduce new distortions, depending on the premise of the respective approach (Alroy, 2010). The applicability of such methods on the Cambrian acritarch record might be explored in the future. Here we test for the existence of biases with other methods.

The analyses are performed with a customized program using the statistical environment R (version 3.0.2; R Core Team, 2013).

3. Results

3.1. Global

3.1.1. Diversity by stages

Global diversity curves through the ten Cambrian stages are shown in Figs. 4A and B, for species and genera respectively. Relatively few species range from the Proterozoic into the Cambrian and global total

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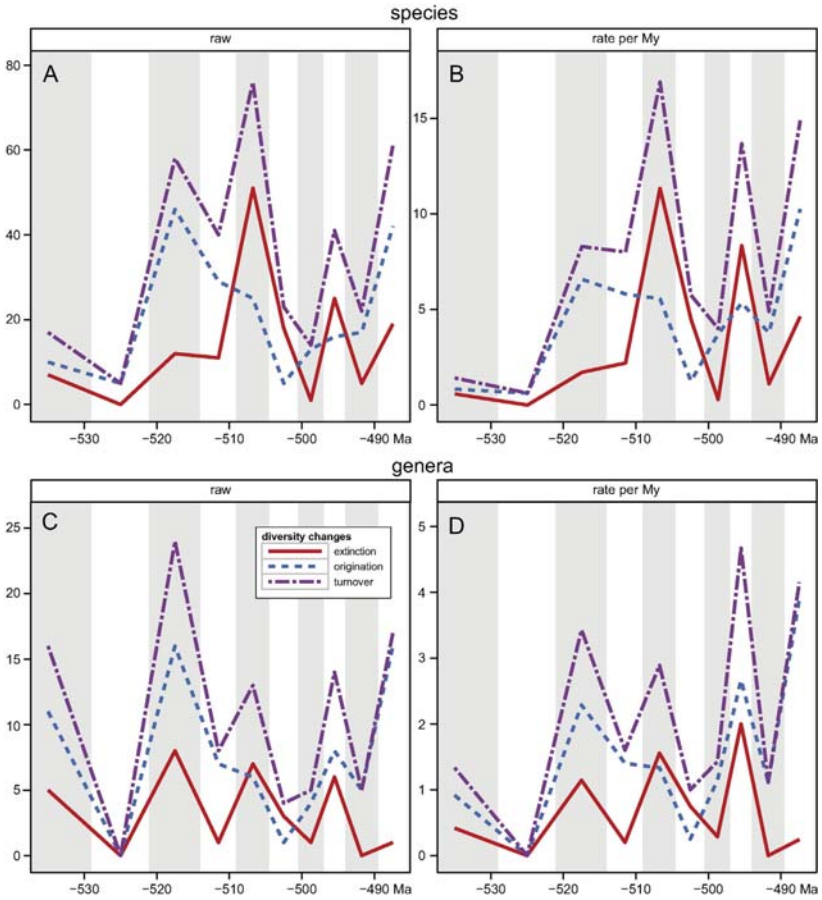

Fig. 6. Taxonomic changes of global species and genus diversity. A, B, species. C, D, genera. A, C, raw data. B, D, rates of taxonomic changes per stage duration [Myr].

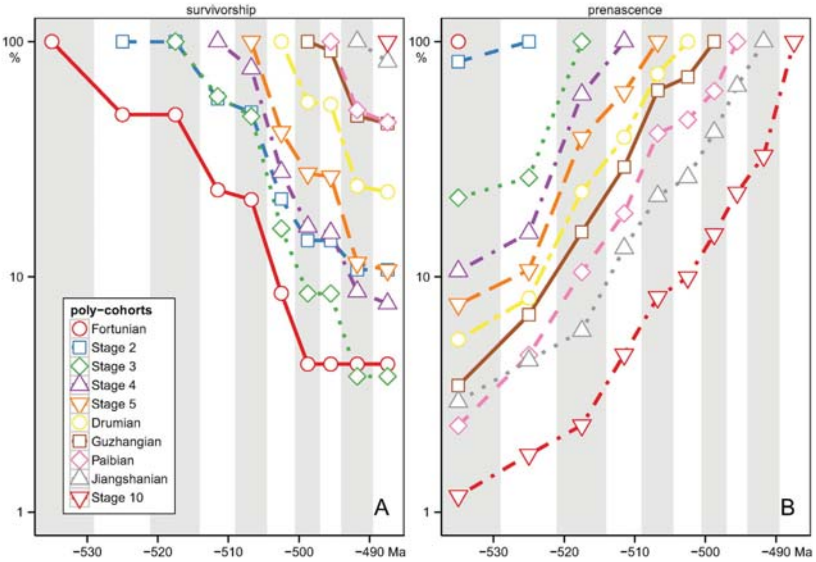

Fig. 7. Poly-cohort analyses. A, cohort survivorship. B, cohort prenascence.

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species diversity (Fig. 4A) is at its lowest in the Terreneuvian Series (Fortunian Stage and Stage 2). It is high in Stages 3, 4 and 5 and in Stage 10. The upper Series 3 (Drumian and Guzhangian stages) and the lower Furongian Series (Paibian and Jiangshanian stages) are marked by low global species diversity. Normalized species diversity peaks are present in Stages 5 and 10. The number of crossover species rises unsteadily over the course of the Cambrian. Singletons are mostly minor constituents, except in Stage 10 where they constitute more than a third of the total diversity.

Sampled-in-bin genus diversity (Fig. 4B) follows trends similar to those of the sampled-in-bin species diversity (Fig. 4A). The total genus diversity, incorporating a high number of range-through extensions for genera that are not present in a stage, but which are present in underlying and overlying stages, rises more or less steadily from Stage 2 onwards, with a minor drop between Stage 5 and the Drumian, barely hinting at the main trends of the species curve. This effect is even more conspicuous in the normalized diversity curve. The highest point of global genus diversity is reached in Stage 10. The proportion of crossovers is high in relation to the total genus count and in comparison to taxonomic changes. Singletons are rare or absent. Perhaps somewhat counter-intuitively, total genus diversity is higher than total species diversity in the Terreneuvian stages and the Guzhangian Stage (see Discussion). They are equal in the Jiangshanian Stage.

3.1.2. Diversity by biozones

The biozonal curves are similar to the stage curves. Using trilobite biozones as stratigraphic bins above Stage 2 (Fig. 5), total and sampled-in-bin species diversity rises from the base of the Cambrian to highs between the *Holmia* and *Paradoxides paradoxissimus* zones, followed by low values between the *Paradoxides forchhammeri* and *Leptoplastus* zones, with a peak in the *Olenus* Zone, and reaching another peak in the *Peltura* Zone. Diversity drops slightly from the *Holmia* Zone to the *Protolenus* Zone, in the Jiangshanian between the *Parabolina spinulosa* and *Leptoplastus* zones, and from the *Peltura* Zone to the *Acerocare* Zone in Stage 10. The first two falls in diversity are also evident on the stage curves, although not so pronounced; the last, in Stage 10, is not. The high number of singletons in Stage 10 on the stage scale is reduced to moderate numbers on the biozone scale.

In six of fourteen biozones (corresponding to the Terreneuvian stages and parts of Series 3 and the Furongian), total genus diversity is higher than total species diversity (Fig. 8). In two more (the *Schmidtiellus mickwitzi* and *Olenus* zones), it is barely lower.

3.1.3. Taxonomic changes

Origination indices for species and genera reach peaks in Stages 3 and 10 (Figs. 6A, C). The rate of origination per Myr is only moderate for Stage 3, and that for Stage 10 appears higher in comparison (Figs. 6B, D). The number of originating genera is also high in the Fortunian, while the rate of origination is relatively low. Otherwise, the rates of taxonomic changes per Myr are similar to the raw indices. Species extinctions are by far highest in Stage 5, discounting the extraordinarily high number of singletons in Stage 10 (Fig. 4A). Almost no extinctions of species or genera occur in the Fortunian, Stage 3 and Guzhangian stages. Stages 5 and 10 contain the highest number of species turnovers from the raw data (Fig. 6A). Corrected for stage duration, turnover is also high in the Paibian Stage (Fig. 6B).

Poly-cohorts of survivorship and prenascence produce almost parallel and relatively straight curves (Fig. 7), indicating that rates of origination and extinction are relatively constant throughout the Cambrian. The poly-cohorts of survivorship for the Terreneuvian stages have a gentler slope than younger ones, indicating a greater number of long-ranging species. Otherwise the poly-cohorts show no drastic differences in diversification or extinction trends between cohorts or over time.

3.2. Regional trends

The regional diversity curves are incomplete due to the limited sources and difficulties in correlations. The curves for genera are not figured or discussed separately, as they are very similar to the species curves, albeit with lower values (Supplementary Table S12, S13).

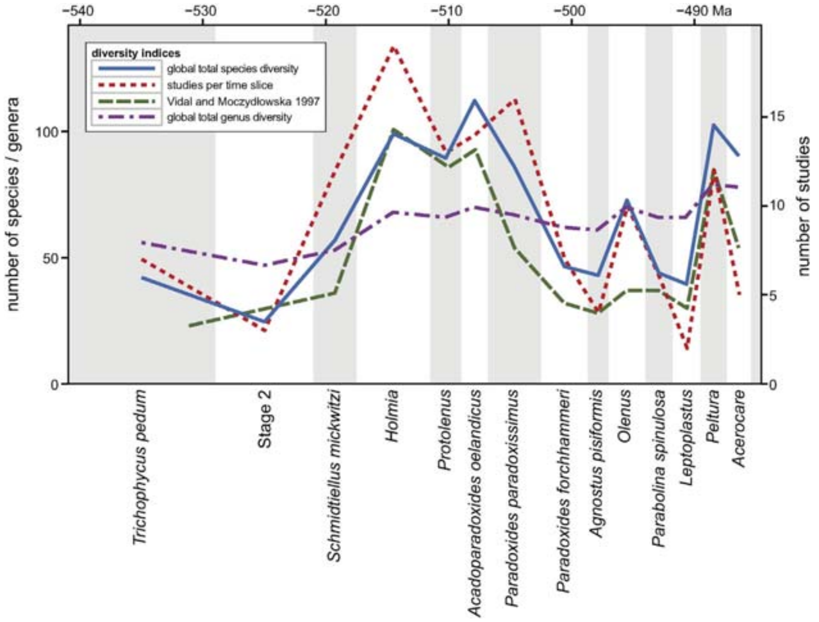

Fig. 8. Comparison of global species and genus diversities with the distribution of studies and a previously published diversity curve.

3.2.1. Baltica

The diversity curve for Baltica (Figs. 4C, 5C) mostly mirrors the global trends. Notable differences from the global curve are the overall lower diversity, its exceptionally low and unchanging values in the Fortunian Stage and Stage 2, and a slight rise in the Jiangshanian Stage, preceding the ultimate diversity maximum in Stage 10. No data could be assigned to the Drumian. In the biozonal curve, the *Olenus* Zone marks a minor diversity peak and is separated by a gap in the record in the *Parabolina spinulosa* Zone and a minor diversity low in the *Leptoplastus* Zone from the point of maximum diversity in the *Peltura* Zone. This is followed by a lowered diversity in the latest Cambrian *Acerocare* Zone.

3.2.2. Gondwana

There are no published data from the Terreneuvian Series of Gondwana, so acritarch diversity at that level cannot be evaluated. Also, we could not assign any data with certainty to Stage 3, the *Schmidtiellus mickwitzi* Zone and the *Leptoplastus* Zone. Species diversity on the Gondwana margin (Figs. 4D, 5D) is very low in Stages 4 and 5, in contrast to the high diversity of the Baltic and global curves. Above Stage 5, Gondwanan diversity is similar to, or higher than that on Baltica. Diversity peaks in the Drumian Stage (Fig. 4D) or in the *Paradoxides paradoxissimus* Zone (Fig. 5D), but corresponds to declining diversity in the global and Baltica curves. In parallel to the situation on Baltica, the Guzhangian and Paibian stages are marked by relatively low diversities, followed by a slight rise in the Jiangshanian Stage and a strong rise to an overall maximum in Stage 10 (Fig. 4D). The same trend is seen on the biozonal curve (Fig. 5D), except that the late Cambrian peak in the *Peltura* Zone is followed by a fall in the *Acerocare* Zone.

3.3. Distribution of studies over time

The number of studies in each of the stratigraphic intervals considered is very irregular and particularly low for Stage 2, the *Agnostus pisiformis* Zone, the *Leptoplastus* Zone and the *Acerocare* Zone (Fig. 8). The distribution of studies over the Cambrian has a conspicuous correlation with species diversity (Fig. 8), as shown by the strong and significant correlation for both total ($r_s = 0.95$; $p < 0.001$) and normalized ($r_s = 0.93$; $p < 0.001$) species diversity based on stages (Figs. 9A, B). The correlation is weaker, but significant for species on a biozonal level (total: $r_s = 0.76$; $p = 0.002$; normalized: $r_s = 0.57$; $p = 0.032$, Fig. 9C) and for genus total diversity based on stages ($r_s = 0.78$; $p = 0.008$). In contrast, the correlation is both weak and not significant for normalized diversity of genera by stage ($r_s = 0.52$; $p = 0.121$) and total diversity of genera by biozone ($r_s = 0.35$; $p = 0.214$). The Gondwanan total species diversity based on biozones ($r_s = 0.55$; $p = 0.098$) and normalized species diversity based on stages ($r_s = 0.58$; $p = 0.306$) also only show weak and not significant correlations. Global normalized genus diversity by biozone shows no correlation ($r_s = -0.11$; $p = 0.708$, Fig. 9D).

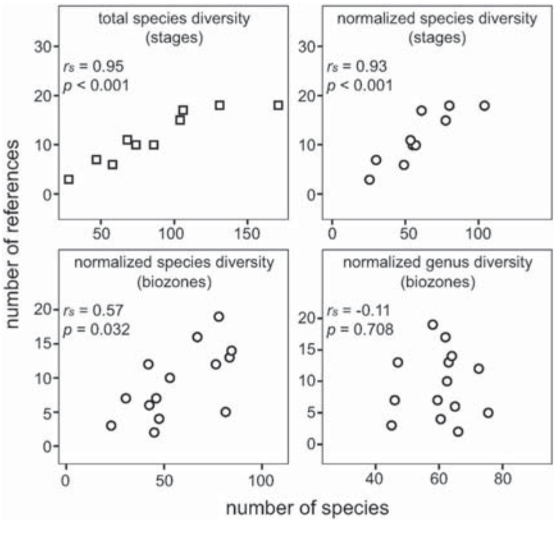

Fig. 9. Correlation of taxonomic (global species per stage) and monographic (number of references per stage) diversity.

4. Discussion

4.1. Global diversity

The total species diversity curve presented here is strikingly similar to that published by Vidal and Moczydłowska-Vidal (1997), although the latter was based on fewer sources and diversity levels are mostly higher in our curves (Fig. 8). The same basic trends – rising diversity in the 'lower' Cambrian followed by low diversity and subsequent rise at the end of the Cambrian – also appear in Strother (1996) and Zhuravlev's (2001) diversity curves. This does not exclude the possibility of biases, but would at least imply consistent biases, such as the concentration of productive studies in certain areas and stratigraphic intervals. In particular, the northwestern part of Baltica is disproportionally well studied and studies on Gondwana are essentially limited to the western and southern margins (Fig. 2). Also, studies on the pre-trilobite Cambrian are usually poorly dated. In fact, the uneven availability of index fossils in general might present a bias, since an important amount of data remains simply unusable due to a lack of stratigraphic constraints.

Considering the low number of studies that deal specifically with Stage 2 and the *Agnostus pisiformis*, *Leptoplastus* and *Acerocare* zones, all of which coincide with decreased diversity, results from these units should be regarded with some caution. The conspicuous correlation between total species diversity and the number of studies per stratigraphic bin (Figs. 8, 9) suggests the influence of an important sampling and/or preservational bias.

The same would be true for the sampled-in-bin genus diversity, but in this case the interpolation of ranges in the total diversity curve changes the picture profoundly. A high number of genera that are missing from the low diversity intervals of Stage 2 and from the Drumian to Jiangshanian stages (and the corresponding biozonal units) are present in the preceding and succeeding higher diversity intervals. These genera are inferred to range through the low diversity intervals and so are also inferred to contribute to total generic diversity in those intervals. The result is a decoupling of the total and sampled-in-bin diversity curves (Figs. 4B, 5B), indicating a significant incompleteness of the record. This would certainly also affect species diversity and perhaps even more severely.

As a consequence of the obvious incompleteness of the record, it is conceivable that the total genus diversity in the affected intervals is still underestimated and that the diversification of genera actually continued throughout the whole Cambrian at a more or less constant rate (Figs. 4B, 5B). A further consequence of the interpolation of generic occurrences to construct the total global genus diversity curves is that the total genus diversity actually exceeds total species diversity in the less extensively studied intervals of the Terreneuvian Series and parts of Series 3 and the Furongian Series (Fig. 8). This is an artifact of the data, as well as highlighting some of the limitations, and is explained by the generally longer ranges of genera being more likely to span gaps in the record. It might be argued that if a genus is inferred to be present in a low diversity interval, based on its interpolated range, then at least one species of that genus should also be present. The anomaly of genus diversity exceeding species diversity would be removed by inferring the presence of at least one species per genus, but the true number of missing species would be unknown.

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The normalized genus diversity curve also indicates a more or less steady, if slow, diversification (Fig. 4B). Regression analysis indicates that normalized genus diversity is the least biased (Fig. 9D). Genera are typically easier to identify than species since they are defined by broader characteristics, and can often be determined when the species is unknown to the author or the preservation is too poor to identify it. Taxonomic inflation may also be less of a problem at the generic level for the same reasons. This means that the record of genera is potentially more complete and the ranges more accurate than those of species. Generic diversity can therefore be considered more robust than species diversity. However, it cannot show the full range of diversity and may be a poor proxy for species diversity, because the number of species in a genus varies greatly and is not constant over time. Furthermore, the possibility of polyphyly needs to be considered for genera even more so than for species. Even so, based on current knowledge, the generic record hints at an increasing diversification trend through the Cambrian. Prenascence analysis of species also suggests an overall stable origination pattern (Fig. 7B).

Global sea level is generally considered to have risen more or less constantly throughout the Cambrian (Miller et al., 2005; Haq and Schutter, 2008), a plausible cause being the formation of mid-ocean ridges following the breakup of Pannotia in the late Neoproterozoic (Miller et al., 2005; Scotese, 2009). A correlation between long-term sea-level changes on Palaeozoic and Mesozoic phytoplankton diversity has previously been reported, based on diversity curves for various groups, including acritarchs (Katz et al., 2004). During transgressions, flooded continental areas, which are the most favorable habitats for phytoplankton, increase and so provide more niche space and opportunities for diversification, following a species-area relationship (e.g. Sepkoski, 1976; Katz et al., 2004). The Cambrian acritarch record would be consistent with that idea. Flooding of continental shelves also controls the accumulation of sedimentary rocks and provides a general explanation for the correlation between biodiversity in the fossil record and available rock volume (Hannisdal and Peters, 2011).

Bambach et al. (2004) noted that proportional extinction among metazoan genera during most of the Cambrian and Early Ordovician was unusually high compared to the rest of the Phanerozoic. They identified two phases of declining diversity due to low origination; the late Botomian and the early late 'middle' Cambrian. Na and Kiessling (2015) found that per-capita rates of extinction exceeded origination in Stage 3, the Drumian, and Stage 10. Acritarch genera show such a signal only in the Guzhangian and Drumian. The sampled-in-bin diversities of Cambrian animal (based on Na and Kiessling, 2015) and acritarch genera are neither strongly nor significantly correlated ($r_s = 0.55$; $p = 0.098$; Fig. 11A).

4.2. Regional trends

As shown in this paper and previously by others (Yin and Xue, 2002; Molyneux et al., 2013) from more limited sources, regional differences do exist in the currently available data. Even for acritarchs in the Cambrian, the global diversity does not necessarily reflect regional trends (or vice versa), as for example on Gondwana in stages 4 and 5, where diversity is particularly low, in contrast to the high contemporary diversity on Baltica (Figs. 4, 5, Supplementary Table S15). Such differences are not evident above Stage 5. In a similar fashion, Moczydłowska's (1998) curve for Upper Silesia shows diversification in the lower part of the Cambrian up to the *A. oelandicus* biochron, with no earlier peak (see Supplementary Table S15). As pointed out by Molyneux et al. (2013), important taxa were present on both Baltica and Avalonia. The primary difference between Gondwana and Baltica, at least for the Cambrian, therefore lies not in the differentiation of microfloras. The differences in diversity are quite probably at least enhanced by poor sampling of the lower Cambrian of Gondwana. They may also indicate differences in the local palaeoenvironment, rather than discrete provinces (see e.g. Lei et al., 2012, and references therein).

4.3. Cambrian explosion

The apparent rapid diversification of acritarch species in Stage 3 parallels the radiation of metazoans (Sepkoski, 1997; Na and Kiessling, 2015; Fig. 10). Such a correlation could point to a link between phytoplankton and metazoans. For the Cambrian in total, the correlation between metazoans and acritarchs is moderate ($r_s = 0.55$) and not significant ($p = 0.098$) (Fig. 11A). In contrast, applying a moving window to each set of eight successive stages, results in a good and significant correlation ($r_s = 0.88$, $p = 0.004$) for the interval from Stage 2 to the Jiangshanian Stage (9), inclusive (Fig. 11B). This correlation thus supports the presence of a more or less partial, but important link between acritarch and metazoan diversities during the time of the Cambrian Explosion. This result may be more or less modulated by a possible sampling bias, because most acritarch diversity indices are strongly and significantly correlated with the distribution of studies over time (Fig. 9). The dramatic increase in diversity in Stage 3 follows the particularly poorly covered Stage 2, one of the stages where total genus diversity exceeds species diversity (Fig. 8). The latter proves

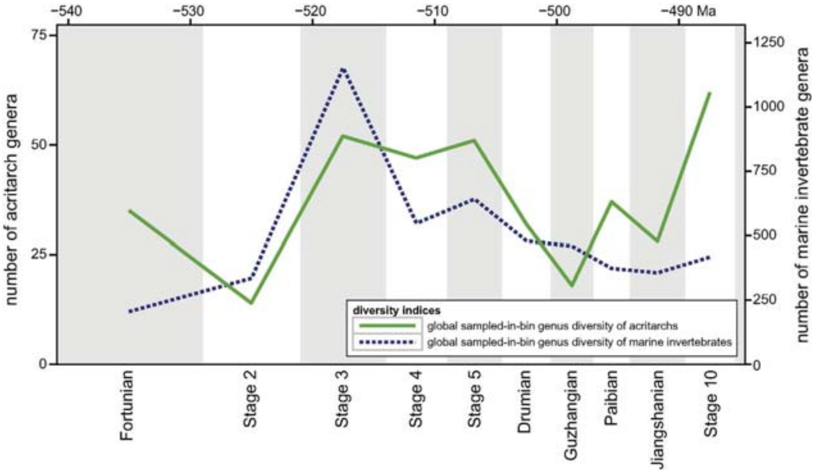

Fig. 10. Comparison of global sampled-in-bin genus diversity of acritarchs and marine invertebrates. Values for invertebrates taken from the supporting information of Na and Kiessling (2015).

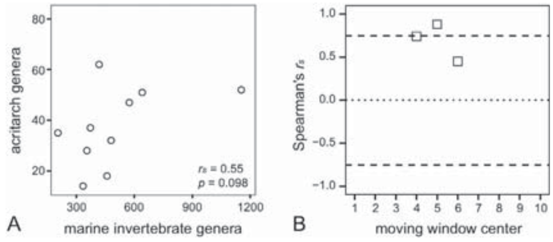

Fig. 11. Correlation of global sampled-in-bin genus diversity of acritarchs and marine invertebrates. Values for invertebrates taken from the supporting information of Na and Kiessling (2015). A, scatterplot of acritarch vs. marine invertebrate diversity. B, Spearman's r_s calculated with a moving window for successive intervals, each comprising eight stages; values above 0.75 or below −0.75 (dashed lines) indicate strong correlation. The middle square indicates strong and significant correlation ($r_s = 0.88$, $p = 0.004$) for the middle set of eight stages, from Stage 2 to the Jiangshanian Stage (9).

that this unit is critically undersampled and the following increase in diversity at least exaggerated. The normalized genus curve, which we find to be the least biased, indicates that acritarchs diversified without a notable peak. These trends, supported by the prenascence cohorts (Fig. 7B), suggest that there is no evidence for a distinct or sudden origination phase in the first half of the Cambrian. This does not negate the possibility of important interactions between certain groups of acritarch-producing organisms and metazoans, but the relation between the Cambrian Explosion and the diversity of the acritarchs as a whole remains unclear.

4.4. Furongian diversification and the GOBE

Servais et al. (2008) perceived a rise in phytoplankton diversity and disparity following the SPICE $\delta^{13}C_{carb}$ event, which broadly coincides with the Paibian Stage and the *Olenus* trilobite Zone (Saltzman et al., 2011). In our results, the Jiangshanian Stage, which follows the SPICE event, is indeed marked by a slight rise in diversity in the regional species curves for both Baltica and Gondwana (Fig. 4 C, D). This rise is not reflected on the global curves (Fig. 4A), which show a decline in diversity from the Paibian Stage to the Jiangshanian Stage, but it is in the origination index, which exceeds the extinction even at a global scale (Fig. 6A). It does not show up in the total or sampled-in-bin diversity curves on a global scale because more species went extinct within or at the end of the Paibian but are still counted in that stage, and because these are minor fluctuations (Figs. 4A, 5A). There is no evidence that the Jiangshanian was a time of great innovation, the amount of originating genera being very low. Many new genera with innovative morphologies that reach into the Ordovician do appear later in Stage 10, several million years after the SPICE event and without any obvious connection. The biozonal curve even shows a time of exceptionally low origination (and extinction) in the upper Jiangshanian *Leptoplastus* Zone, separating the minor lower Jiangshanian diversification from the massive origination phase in Stage 10, although this is certainly related to the very low number of studies treating the *Leptoplastus* Zone as such (Fig. 8). By contrast, the diversity maximum in Stage 10 appears globally and on both Baltica and Gondwana (Figs. 4C, D), which makes this short-lived phenomenon credible. It is tempting to see the sudden rise in diversity as a precursor of the GOBE, but at the finer scale of trilobite biozones, the diversity is already seen to fall from the *Peltura* Zone to the *Acerocare* Zone (Fig. 5B, C). Only about half of the species recorded from Stage 10 range into the Tremadocian. Thus the Cambrian seems to end with a phase of species extinction. However, few genera go extinct at the Cambrian/Ordovician boundary. Animal genera do show a comparatively high per-capita extinction rate in Stage 10 (Na and Kiessling, 2015). Metazoan and acritarch genus extinctions seem to be generally unrelated in the Cambrian (see 4.1.). Among the acritarch genera surviving the transition, several bore morphological traits that emerged during the late Cambrian (Servais et al., 2008) and would be important contributors to later assemblages (such as the 'galeate' acritarchs: Servais and Eiserhardt, 1995; Servais et al., 2004b). The latest Cambrian can be seen as a time of phytoplankton turnover, preceding but distinct from the radiation of acritarchs during the Ordovician.

5. Conclusions

Our new, more complete dataset on Cambrian acritarchs provides new insights into the global and regional diversification of phytoplankton in the Cambrian oceans. Global acritarch species diversity starts on a comparatively low level at the base of the Cambrian, rises in parallel to the radiation of metazoans to a high in stages 3 to 5 (or the *Holmia* to *Paradoxides paradoxissimus* zones), then drops considerably to an extended low until it peaks sharply in Stage 10 (more precisely in the *Peltura* Zone). Genera show an irregular increase in total and normalized diversity throughout the Cambrian, indicating that the low species diversity in Stage 2 and the upper Series 3 to lower Furongian interval is at least in part due to an incomplete record. Correlation analysis shows normalized genus diversity to be the least biased. The regional curves are markedly different in Series 2 and Stage 5; while diversity is high on Baltica, it is low on Gondwana. This difference may be attributed to the limited record on Gondwana and perhaps palaeoenvironmental differences rather than distinct provinces. After Stage 5, the regional diversities are similar. A diversity maximum in the *Peltura* Zone and subsequent fall in the *Acerocare* Zone is mirrored on both Baltica and Gondwana. The end of the Cambrian is marked by an extinction of species, while nearly all genera present in Stage 10 survived into the Ordovician.

Our acritarch diversity curves mirror the diversity curves of marine invertebrates to some extent. The correlation between both diversities has statistical significance only when the first and last stage of the Cambrian are excluded. Taken at face value, rising diversity in Stage 3 mirrors that of the metazoans (Cambrian Explosion), but the acritarch diversity trends might be attributed to sampling bias. The relationship between the two groups remains uncertain. Similarly, although the end of the Cambrian coincides with an extinction-led turnover of acritarch species, morphological innovations from the Cambrian, particularly among genera, might well have paved the way for the rapid diversification of acritarchs during the Ordovician that can be viewed as a part of the Great Ordovician Biodiversification Event.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.earscirev.2015.09.005.

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Article II

The onset of the "Ordovician Plankton Revolution" in the late Cambrian

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The onset of the 'Ordovician Plankton Revolution' in the late Cambrian

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ABSTRACT

The ‘Great Ordovician Biodiversification Event’ comprises the rapid diversification of marine organisms during the Ordovician Period. It is now clear that this adaptive radiation started for some organisms already in the Cambrian and continued for others beyond the end of the Ordovician, making the ‘Great Ordovician Biodiversification Event’ part of a long-term late Proterozoic and Early Palaeozoic radiation, that in part is expressed by the fossil record as the ‘Cambrian Explosion.’ A significant diversification of different groups of the plankton is observed in the late Cambrian – Early Ordovician interval, leading to the subsequent ‘Ordovician Plankton Revolution.’ The possible causes of this ‘plankton revolution’ are currently debated. They include changes in palaeoclimate, palaeogeography or tectonic and volcanic activity, as well as a modified nutrient supply. In this context, the Steptoean Positive Carbon Isotope Excursion $\delta^{13}C_{carb}$ (SPICE) event in the late Cambrian (Paibian Stage, Furongian Series) has been related to a major increase in atmospheric O_2 and to increased oceanic nutrient availability. Here we analyse the diversification of the planktonic groups during the late Cambrian and Early Ordovician, in particular in relation to the SPICE event. Our analyses include the changing diversities of the phytoplankton (acritarchs), diverse groups of zooplankton (e.g., radiolarians, graptolites, chitinozoans, etc.) and the switch to a planktonic mode of life of fossil groups (e.g., arthropods, molluscs, etc.) that were part of the Cambrian benthos and that later occupied pelagic niches. In addition, we focus also on data indicating evidence for a late Cambrian to Ordovician origin of planktotrophy in invertebrate larvae. It can be concluded that none of the diversifications of the different planktonic organisms can be related directly to the SPICE event. However, a long term (10-20 million years) oxygenation pulse related to the SPICE event might have fuelled the explosion of phytoplankton diversity observed in the latest Cambrian – Early Ordovician that led to completely modified trophic structures permitting an increase in diversity and abundance of plankton-feeding groups during the Ordovician.

Keywords:

Plankton

SPICE

late Cambrian

Early Ordovician

Ordovician Plankton Revolution

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1. Introduction

In a simplified view, marine animal diversity changes during the Phanerozoic include two major radiations (the Early Palaeozoic and the Early Mesozoic radiations) and five mass extinctions, of which the Permian/Triassic extinction, considered the most serious in terms of species-diversity loss, clearly stands out. Both the classical Sepkoski-type biodiversity curves of marine faunas (e.g., Sepkoski, 1978, 1979, 1981, 1984, 1988) and the more recent standardized curves provided by the Paleobiology Database (PBDB, e.g., Alroy et al., 2002, 2008) show a clear long-term radiation of marine organisms during the Early Palaeozoic. In the Sepkoski-type biodiversity curves, this major radiation took place in the Cambrian and Ordovician, with a Palaeozoic 'plateau' being reached at the end of the Ordovician. In the more recent curves of the PBDB a much longer and continuously increasing diversity trend started already in the late Proterozoic and only ended in the Early Devonian (e.g., Alroy et al., 2008).

The Early Palaeozoic radiation can either be seen as including two separate events, the 'Cambrian Explosion' and the 'Great Ordovician Biodiversification Event' (GOBE), or as a continuous, stepwise evolution of faunal changes, including the rise of three Evolutionary Faunas, the Cambrian, Palaeozoic and Modern Faunas (e.g., Sepkoski and Miller, 1985). The question of whether the 'Cambrian Explosion' and the 'Great Ordovician Biodiversification Event' are two separate events or a single one is a current matter of debate.

The 'Cambrian Explosion' is considered to be a relatively short period (during the early-middle Cambrian) when most animal phyla that we know today have their first fossil record (e.g., Erwin et al., 2011; Smith and Harper, 2013). The GOBE, on the other hand, is an event that covered most of the Ordovician and that represents an 'explosion' in diversity of marine organisms at the family, genus, and species level (e.g., Harper, 2006). Several authors considered the GOBE as a sum of diversification events (e.g., Miller, 2004), because the diversification of individual fossil groups did not take place at the same time, and not on the same palaeocontinents. Other authors pointed out that the Ordovician radiation was clearly a follow-up to the 'Cambrian Explosion' (e.g., Droser and Finnegan, 2003).

In terms of ecological shifts, the late Precambrian microbial-dominated ecosystems were replaced during the early Cambrian by benthos dominated communities with most marine groups of the Cambrian biota limited to shallow water environments representing benthic/nekto-benthic communities (e.g., Burzin et al., 2001). It was only during the Ordovician that the water column was more completely filled with planktonic and nektonic organisms and that pelagic habitats were colonized to develop modern marine ecosystems (e.g., Servais et al., 2010).

The term 'Ordovician plankton revolution' has increasingly been used in the last decade. Signor and Vermeij (1994) already noted that a review of the fossil record suggests that the diversification of the plankton and suspension-feeding marine animals began in the late Cambrian and continued into the Ordovician, pointing out that the ultimate cause of these changes is uncertain, but that it appears likely that the plankton became a refuge from predation and bioturbation. Nützel and Frýda (2003) first coined the term 'Palaeozoic plankton revolution' to indicate that the plankton was fundamentally restructured during the Palaeozoic. Subsequently, Nützel et al. (2006) provided the first empiric evidence for a late Cambrian to Ordovician switch to planktotrophy in invertebrate larvae, confirming Peterson's (2005) assumption, based on molecular clock data, that planktotrophy had evolved in several clades during the latest Cambrian to Middle Ordovician. Servais et al. (2008) indicated that the Ordovician Biodiversification represented important changes in the marine trophic chain, with an ‘Ordovician plankton revolution’ profoundly modifying the marine food web. They pointed out that after the Steptoean Positive Carbon Isotope Excursion (SPICE) $\delta^{13}C_{carb}$ event in the late Cambrian (Paibian Stage of the Furongian Series) the organic-walled phytoplankton (acritarchs) underwent a major change in morphological disparity and taxonomical diversity, triggering the important changes in the marine food webs, with the development of planktotrophy in larval stages and the rise of suspension feeders.

More recently, Saltzman et al. (2011) correlated the late Cambrian SPICE $\delta^{13}C_{carb}$ event with a pulse of atmospheric oxygen that can be correlated with the onset of the GOBE and the plankton and animal radiation that began 40 million years after the so-called ‘Cambrian Explosion.’ Saltzman et al. (2011) argued that it is possible that the oxygenation event during the SPICE led to a promotion of dinoflagellate-like taxa of the organic-walled microphytoplankton that are the dominant primary producers overall throughout much of the Palaeozoic, triggering the expansion of ecologically diverse plankton groups that provided few food sources for the expanding animal biota.

The main objective of the present paper is to review the literature and to summarize recent results in order to precisely position in time the onset of the ‘Ordovician plankton revolution.’ What are the changes that took place in the plankton during the late Cambrian and Early Ordovician? Was there a ‘plankton revolution’ and when may this have occurred precisely? What was the duration of the onset of this ‘plankton revolution?’ Did the SPICE event trigger the plankton revolution and can this event be correlated with the diversification of the different planktonic groups?

In order to examine when the different planktonic groups diversified and when they became an important component of the marine environment, the fossil record of the phytoplankton and of all zooplanktonic groups is here reviewed in detail. In addition, the data on the

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development of planktotrophic larval stages of marine invertebrates are also reviewed. A major question is the search of the cause(s) of the changes in the marine trophic webs. Might the 'Ordovician plankton revolution' be the result of a biological escalation or was it triggered by an environmental event, such as a pulse of atmospheric oxygen in the late Cambrian, or both?

2. What is the plankton?

2.1. Definitions – modern plankton

The modern global oceans are dominated in abundance and biomass by the plankton that plays a major role in marine trophic chains (e.g., Le Quéré et al., 2005). The plankton represents all organisms that live in the water column but that cannot freely swim. The term plankton comes from the Greek πλανκτός (*plankton* = drifter) and therefore indicates that the planktonic organisms (plankters) drift, or passively float, with the water currents and within the water column, although some plankton groups are somewhat mobile (most planktonic arthropods, molluscs or cnidarians can swim, but such movements are usually limited to vertical migrations). The nekton, in contrast, represents all organisms that can (freely) swim against a current and move largely independently of water currents.

On the other hand, benthic organisms are those that live close to or are attached to the seafloor, and that are usually not swimming in the water column. Some organisms considered as nektobenthic live near the seafloor (demersal habitat, see below) but are also able to swim, although usually not in open waters.

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Furthermore, some organisms have benthic-planktonic life cycles, with a part of their life in the benthos, and another part in the plankton. Benthic or nektobenthic organisms that have a planktonic mode at the beginning of their life are classified within the meroplankton, in contrast to the holoplankton that includes all organisms of which the entire lifecycle is planktonic.

In terms of size, the plankton ranges from the bacterioplankton (smaller than 1 µm) and the picoplankton (usually 1-2 µm in diameter) to macro-scale (of a size up to several tens of cm or even meters) zooplankton predators (e.g., jellyfish). Plankton occurs at all depths within the oceans, although such organisms are most common in the photic zone. Plankton distribution is primarily controlled by upwelling zones and by the nutrient supply in the oceans. Plankton is also distributed following temperature and salinity zones, but many species have wide biogeographical distributions.

The plankton is broadly divided into three major trophic categories, the bacterioplankton, the phytoplankton and the zooplankton. The bacterioplankton mainly consists of bacteria, while the phytoplankton is basically composed of prokaryotic and eukaryotic algae. The phytoplankton constitutes the major part of the 'marine floras', the term phytoplankton meaning 'drifting plants' (from the Greek φυτόν*, phyton* = plant, and πλανκτός, *plankton* = drifter). The phytoplankton is therefore generally considered to represent the autotrophic component of the plankton, in contrast to the zooplankton that constitutes the heterotrophic part of it (although some parts of the phytoplankton can also be heterotrophic, such as dinoflagellates, for example, who are represented by autotrophic, heterotrophic and mixotrophic taxa).

It is usually accepted that the phytoplankton is an essential part of the modern marine food chain, but the bacterioplankton and picoplankton also play an essential role, with the picoplankton being considered the essential part of the biomass in modern oceans (e.g., Buitenhuis et al., 2012). Although the marine phytoplankton only represents about 1% of the total photosynthetic biomass at a given time, single-celled algae in the oceans are responsible for about 50% of the total primary production (e.g., Falkowski, 2012).

The zooplankton includes both metazoans and unicellular protozoans that are critical intermediaries (primary and secondary consumers) in the flow of energy and biomass through marine ecosystems. Some zooplanktonic organisms have a strictly planktonic lifestyle as they float or drift in the water column during all their life (holozooplankton), while others (merozooplankton) have during their life cycle both a planktonic (usually during their larval stage) and a nektonic lifestyle, because they are able to swim and move independently of currents during one part of their life (as adults).

In terms of marine life habitats, the different zooplanktonic organisms live both in demersal (the zone close to the seafloor) and pelagic (the water column between the demersal zone and the surface, i.e., open waters) environments. The modern marine zooplankton consists of different groups, including arthropods, rhizarians, actinopodes, ciliophores, cnidarians, rotifers and other groups (e.g., CMarZ, 2004).

The definition of the terms plankton and nekton vary. We note that several groups referred to as zooplankton include good swimmers, and in the context of this study these are not treated as planktonic organisms.

2.2. The fossil record of plankton and its significance in Palaeozoic palaeocology

Understanding ancient food chains and macroevolutionary patterns in the marine realm during geological time is dependent on an analysis of the fossil plankton. However, the fossil record

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of the plankton is mostly incomplete. The smaller parts of the plankton are usually not preserved. At best, some groups can be identified by geochemical biomarkers. The bacterioplankton has almost no fossil record, while the picoplankton is to small to be observed under a light microscope and remains largely unobserved, although very small organic-walled microfossils fall in the size-range of the picoplankton, indicating that the picoplankton was already present during the Early Palaeozoic (see below). Despite these occurrences, the importance of the picoplankton in ancient food chains is far from understood. Moreover, the geological history of virioplankton is almost completely unknown, although viruses are very abundant in modern seawater.

The phytoplankton is considered a major part of the base of modern marine food chains. It can be divided into a calcareous part (e.g., coccolithophores), a siliceous part (e.g., diatoms) and an organic-walled part (e.g., dinoflagellates). However, none of these modern groups of phytoplankton is present in the fossil record before the Mesozoic. The major part of the phytoplankton in the Palaeozoic is represented by the organic-walled fraction, attributed to the ‘acritarchs,’ calcareous and siliceous phytoplankton being usually absent in the fossil record. The analysis of the diversity and abundance of the acritarchs is thus a possible key to understand the presence of Palaeozoic phytoplankton and the functioning of ancient ecosystems. However, the knowledge of the diversity of the phytoplankton does not give any information about the amount of the biomass produced.

The Palaeozoic zooplankton was very different from the modern. Two of the major zooplanktonic groups in the Palaeozoic are the radiolarians and graptolites. Radiolarians are already present in the Cambrian but they only rise in diversity during the Ordovician, and they become a dominant part of the zooplankton only much later. Graptolites are very well known as the stratigraphical index fossils in the Ordovician and Silurian, their planktonic life-style making them excellent biostratigraphical markers. They are essentially benthic in the

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Cambrian and are considered to become planktonic in the Early Ordovician. A further group of Early Palaeozoic microfossils attributed to the plankton are the enigmatic chitinozoans, of which the diversity increased rapidly during the Early Ordovician. The diversity changes of all these groups are compiled here in order to understand the timing of the onset of the 'Ordovician plankton revolution.'

The fossil record of arthropod zooplankton is extremely poor for most of the Phanerozoic. The analysis of the fossil record of arthropods indicates that a zooplanktonic lifestyle has arisen independently across several arthropod groups already during the Cambrian. Most probably some groups of the molluscs also belonged to the macrozooplankton during some geological periods. Several groups of Ordovician cephalopods most probably had a planktonic mode of life and need to be integrated in the study of the Early Palaeozoic plankton.

Klug et al. (2010) presented some patterns of the diversity and the proportional abundance of demersal/nektobenthic organisms, plankton and nekton in the Palaeozoic, based on both Sepkoski's data resolved to geological stages (Sepkoski, 2002) and on occurrence counts from the Paleobiology Database resolved to 10 million year intervals.

Figure 1 illustrates the proportional abundances of the different groups, based on the original study of Klug et al. (2010). According to the different datasets, the proportion of the plankton clearly increased significantly in the late Cambrian, and particularly in the Early to Middle Ordovician. The nekton became abundant during the Devonian and was dominant since the Carboniferous, leading Klug et al. (2010) to coin the term 'Devonian nekton revolution.' Several major palaeoecological shifts thus took place, and it would be interesting to relate these changes to extrinsic or intrinsic parameters.

In addition, many benthic animals have larvae that display a planktonic mode of life and that often feed on phytoplankton. As already indicated in the landmark paper by Signor and

Vermeij (1994), the relationships between the plankton and the benthos have changed through geologic time, and most probably in a notable way during the Early Palaeozoic radiation, in particular between the 'Cambrian Explosion' and the GOBE, i.e., somewhere during the late Cambrian.

In order to realize the importance of the plankton in the Early Palaeozoic and to establish when the onset of the 'Ordovician plankton revolution' may have taken place, the data of the first appearance and of the diversifications of the different phytoplanktonic and zooplanktonic groups are reviewed in the following chapters, with a focus to the late Cambrian-Early Ordovician interval, when the relative abundance of the plankton significantly increased (Figure 1; Klug et al., 2010).

3. The fossil record of Early Palaeozoic phytoplankton

3.1. Palaeozoic picoplankton and phytoplankton

The life of the global ocean is fuelled by the microorganisms referred to as phytoplankton, ranging in size from the tiny picoplankton to larger organisms that can be identified under the microscope (e.g., Falkowski, 2004). However, determining the net primary production in the oceans of ancient ecosystems is extremely difficult because the fossil record is very incomplete. Nevertheless, some broader trends can be proposed. It is possible to roughly estimate the areas of high versus low productivity in ancient oceans. Models are also proposed to locate oligotrophic versus eutrophic areas. Such estimates can be made both in space (due to the knowledge of palaeocontinental distribution) and in time, in particular by using multiproxy approaches that rely on palaeontological, geochemical, and sedimentological data (e.g., Saltzman, 2005). Moreover, the presence and abundance of

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consumers such as suspension feeders and planktotrophic larvae also provides indirect evidence for sufficient primary production in the oceans.

The knowledge of Palaeozoic picoplankton and phytoplankton is very patchy. Most palaeontologists usually consider the phytoplankton (coccolithophorids, diatoms, dinoflagellates in the Mesozoic and Cenozoic) as the main component at the base of the marine trophic chains, but the smaller parts, including the bacterioplankton and the picoplankton, also play an essential role, that is almost impossible to quantify in ancient geological periods.

The tiny picoplankton (0.2 and 2.0 µm in diameter) and even smaller bacterial fraction of the plankton, commonly classified as the bacterioplankton, constitutes an important part of the food source for zooplanktonic organisms (e.g., Hisatugo et al., 2014). The cyanobacteria, a phylum of the bacteria, but also erroneously called blue-green algae, are another large, heterogeneous group of principally photosynthetic prokaryotic organisms that are widely considered as another major component of the modern phytoplankton. In the Precambrian, the cyanobacteria were an important component of microbial-dominated ecosystems, for example in the form of stromatolites (e.g., Allwood et al., 2009). The relative proportions of the different groups of bacterioplankton, picoplankton and phytoplankton in the primary production are difficult to estimate, but they undoubtedly changed through geological time, and most probably during the Early Palaeozoic.

The fossil record is usually only documented by the visible part of the phytoplankton. The observation with optical microscopes is generally limited to the investigation of larger phytoplankton, i.e., 20 µm or greater in diameter. The diversity curves of the organic-walled microphytoplankton (both the dinoflagellates since the Mesozoic and the acritarchs in the Palaeozoic) therefore represent only the diversities of the fraction of the phytoplankton that is greater than 20 µm. The smaller fraction (< 20 µm) remains mostly unknown, although a few studies document the presence of the tiny microphytoplankton or even picoplankton in the fossil record. With the help of the scanning electron microscope such very small organic-walled microfossils, often between 5 and 10 µm in diameter, have been observed, for example, in the Cretaceous by Schrank (2003) and in the Silurian by Munnecke and Servais (1996), as well as Servais et al. (2009a). These observations indicate that such specimens may be extremely abundant, and that their importance in the primary production in ancient oceans was probably of great significance. Such organisms, although almost completely absent in the fossil record, were thus most probably a significant part of the food source for the zooplankton or for planktotrophic larvae.

3.2. The Palaeozoic fossil record of calcareous and siliceous phytoplankton

Different phytoplanktonic groups live today in the oceans. Most of these 'modern' groups only evolved during the Mesozoic, and the presence of various phytoplanktonic organisms in the Palaeozoic or Precambrian remains debated. The three major groups today are the coccolithophores (that produce calcareous exoskeletons built up by calcified scales named coccoliths), the diatoms (that produce siliceous tests) and the dinoflagellates (that generally produce organic-walled cysts).

The coccolithophores are the main constituents of modern calcareous microphytoplankton, besides several other microalgal groups. They build calcareous exoskeletons and played an essential role in ancient marine carbonate-forming palaeoenvironments, as they are well known to be a main component of Cretaceous chalk (e.g., Stanley et al. 2005). Coccolithophores appear to have evolved during the early Mesozoic with the first definite specimens in the fossil record found in the Triassic (Gardin et al., 2012). Dinoflagellates usually produce organic-walled resting cysts, but a few taxa also produce calcified exoskeletal structures during their life cycle (e.g., Elbrächter et al., 2008). The presence of calcareous phytoplankton (i.e., of calcareous cysts that have been produced by phytoplanktonic organisms) before the Permian/Triassic extinction event is debated. Munnecke and Servais (2008) and Servais et al. (2009a) reported different types of calcareous microfossils, named calcispheres and nannospheres, from the Silurian carbonate platform of Gotland. The comparison with calcareous microplankton from the Mesozoic and Cenozoic indicated that some morphotypes from the Silurian are comparable with coccospheres, while others show similarities with calcareous dinoflagellates. The observation that many of these calcareous microfossils occur in almost all sedimentary facies indicates that they probably belong to calcareous micro- and nannoplankton. Munnecke and Servais (2008) concluded that calcareous plankton most probably existed already during the Palaeozoic, and even in the Early Palaeozoic, but that it could only be observed if the material was not subject to late stage diagenesis that destroys the microstructures necessary to recognise the morphological parameters typical of calcareous phytoplankton cysts. Versteegh et al. (2009) proposed the term Calcitarcha to include all these calcareous microfossils with unknown biological affinities, in analogy to the Acritarcha, defined by Evitt (1963) who included all organic-walled microfossils of unknown biological affinities (that could not be related with certainty to the dinoflagellates). Calcareous cysts produced by phytoplanktonic organisms were therefore possibly already present during the Early Palaeozoic, but detailed investigations are mostly absent, and the fossil record of such groups is sparse. To date, calcareous phytoplankton groups have not been reported from the Cambrian and Ordovician, but it is possible that future investigations in well preserved calcareous environments may provide evidence of Calcitarcha in the Early Palaeozoic.

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The most common group of phytoplankton producing siliceous skeletons are the diatoms (the radiolarians being the major group of zooplankton producing siliceous skeletons). The first occurrence of diatoms in the fossil record is in the Jurassic, but diatoms only became abundant during the Lower Cretaceous (e.g., Sims et al., 2006). A few dinoflagellate taxa produce siliceous cysts, but they are extremely rare (e.g., Harding and Lewis, 1995). So far, there are no records of siliceous phytoplankton from the Palaeozoic and likely they did not exist.

3.3. The fossil record of organic-walled phytoplankton (acritarchs) in the Cambrian and Ordovician

The acritarchs *sensu lato* provide the most complete fossil record of Palaeozoic phytoplankton, but even this record does not fully document the autotrophic part of the plankton in the Cambrian and Ordovician oceans. Evitt (1963) defined the acritarchs as a ‘catch all’ entity that groups nearly all organic-walled microfossils of unknown origin. A number of organisms originally classified within the acritarchs now have established affinities with other groups, including prasinophycean and zygnematacean green algae, cyanobacteria, etc. (e.g., Colbath and Grenfell, 1995; Servais, 1996; Servais et al., 1997). However, most of the remaining Palaeozoic acritarchs are considered to be cysts of marine, generally phytoplanktonic unicellular algae. Some acritarchs show greatest similarities with organic-walled cysts of dinoflagellates, displaying some of the typical morphologies of the dinoflagellates (e.g., Lister, 1970; Le Hérissé, 1989) and showing comparable palaeoecological and palaeogeographical distribution patterns (e.g., Li et al., 2004; Molyneux et al., 2013). However, in order to be identified as a fossil dinoflagellate cyst, an organic-walled microfossil must display some characteristic features, such as a paratabulation, a

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cinculum, a sulcus, and an operculum. Many organic-walled microfossils in the Palaeozoic do not display these features (and even several modern dinoflagellate species do not produce cysts with these morphological criteria). As a consequence, their biological affinity is uncertain and they are classified within the acritarchs. Nevertheless, most Palaeozoic acritarchs are probably the resting cysts of phytoplanktonic organisms, most similar to modern dinoflagellates (e.g., Martin, 1993; Servais et al., 2004a). Such interpretations are also suggested by the discovery of biogeochemical markers typical of dinoflagellates in the Palaeozoic rock record, including the Cambrian (e.g., Moldovan and Talyzina, 1998).

As the precise biological affinities of the acritarchs are (by definition) unknown, acritarch diversity curves thus only reflect indirectly, and not precisely, phytoplankton cyst diversity curves. In addition, although most acritarch morphotypes most probably represent the cysts of phytoplanktonic organisms, some Cambrian acritarchs are probably not planktonic, and can be attributed to benthic or nektobenthic organisms (Figure 2).

Nonetheless, the acritarchs can be interpreted as representing an important part of the marine phytoplankton in the Early Palaeozoic and therefore they constituted a significant element at the base of the marine trophic chain during the ‘Cambrian Explosion’ and the subsequent GOBE. An increasing phytoplankton biomass would have served as food for the developing zooplankton, but also for various clades of suspension feeders and detritus feeding organisms (e.g., Servais et al., 2010).

Several Palaeozoic acritarch diversity curves are available in the literature. A few studies covering the late Proterozoic and the entire Palaeozoic have been published by Tappan and Loeblich (1973), Strother (1996), Servais et al. (2004), Katz et al. (2004) and Strother (2008), just to name a few. Katz et al. (2004) and Strother (2008) created their diversity curves using the Palynodata database (see Palynodata and White, 2008): Palynodata were compiled by a consortium of oil companies and scientific institutions over the course of three decades, but this process was discontinued in 2006. Mullins et al. (2006) compiled another database (the PhytoPal database) of acritarch occurrences covering the interval from the Cambrian to the Triassic. A common trend in all these diversity curves is a continuous increase of acritarch diversity between the late Precambrian and the Ordovician, with a peak in the Middle Ordovician. Diversities remained high until the Late Devonian, when a relatively rapid acritarch diversity decline took place, associated by some authors as a 'phytoplankton blackout' (e.g., Riegel, 2008; but see also Servais et al., in press).

Several diversity analyses have focused on the late Precambrian to Ordovician evolution of acritarch diversity. Vidal and Moczydłowska (1997) published a species diversity curve from the Neoproterozoic and the Cambrian. Zhuravlev (2001) used acritarch genera to draw a diversity curve of the Cambrian to the earliest Tremadocian, while Huntley et al. (2006a, 2006b) published both taxonomic diversity and morphological disparity curves of Proterozoic to Cambrian acritarch genera. Moczydłowska (2011) published a species diversity curve from the Ediacaran to basal Ordovician, using some of the data of the PhytoPal database. These Cambrian diversity curves show a peak in the early-middle Cambrian, reflecting somehow the numerous studies on levels associated with the 'Cambrian Explosion' and a rapid increase at the end of the Cambrian. Servais et al. (2008) focused on the Cambrian-Ordovician transition, with a species diversity curve from the middle Cambrian to early Silurian (Llandovery), documenting this increase of acritarch diversity during this period.

Nowak et al. (in press) produced the most complete database of acritarch occurrences for the Cambrian, with the aim to produce acritarch diversity curves using various statistical methods (Figure 3). The main objective of Nowak et al. (*op. cit.*) was to address whether the 'Cambrian Explosion' is reflected in acritarch diversity and whether the GOBE was preceded by a diversification of acritarchs, in particular in relation to the SPICE event and the possible global oxygenation of ocean waters during the late Cambrian postulated by Saltzman et al. (2011). A comparison of the database by Nowak et al. (*op. cit.*) with the most recent dataset of Na and Kiessling (2015) on the diversity of Cambrian marine invertebrates (based on the Paleobiology Database) shows that a radiation of acritarch species and to a lesser extent of genera in the lower Cambrian Stage 3 appears to mirror the 'Cambrian Explosion' of metazoans. This radiation is followed by a prominent low in species diversity in the upper Series 3 and lower Furongian. Subsequently, the diversity increases, with peak levels reached globally in the uppermost Cambrian Stage 10 (more precisely at the level of the *Peltura* trilobite Biozone), preceding a substantial phase of acritarch species extinction below and at the Cambrian/Ordovician boundary. By contrast, nearly all the genera present in Stage 10 survived into the Ordovician. The diversity maximum in Stage 10 appears globally and for both the Baltica and Gondwana palaeocontinents, suggesting a consistent phenomenon.

Of particular interest are the diversity changes of the acritarchs during the SPICE event. Nowak et al. (*op. cit.*) noted that the Jiangshanian, which follows the SPICE event, is marked by a slight rise in diversity at the regional level (Baltica and Gondwana), but that this rise is not reflected on the global curve, which shows a decline in diversity from the Paibian Stage to the Jiangshanian Stage. Thus, there is no evidence that the Jiangshanian was a time of great innovation, as the numbers of newly originating genera was low. Importantly, many new genera with new morphologies that progress into the Ordovician first appear late in Stage 10, i.e., post-dating the SPICE event considerably and with no apparent causal mechanism. Although the sudden rise in diversity in Stage 10 might seem like the beginning of the GOBE, the Cambrian appears to end with an extinction of acritarch species. Their diversity already drops between the *Peltura* and the *Acerocare* trilobite biozones, and only about half of the species recorded from Stage 10 range into the Tremadocian. On the other hand, many of the typical Early Ordovician acritarch genera find their origin clearly in the late Cambrian, such as the ‘diacromorphs’ or the ‘galeate’ acritarchs (Servais and Eiserhardt, 1995). The latest Cambrian was therefore a time of phytoplankton turnover that preceded and established the foundations for the radiation of acritarchs during the GOBE, but was nevertheless distinct from it (Nowak et al., *op. cit.*).

Although the fluctuations in diversity, as well as the origination and extinction of several morphotypes are not completely understood, a general tendency of a marked increase of phytoplankton diversity can be observed between the late Cambrian and the Early Ordovician (Figure 3).

4. The fossil record of Early Palaeozoic zooplankton

4.1. The fossil record of Radiolaria

Radiolaria (radiolarians) are one of the most important groups of zooplankton in the fossil record (e.g., De Wever et al., 2001). They are mostly rhizarians. The fossil record of radiolarians dates back to the Cambrian and, because radiolarians are usually considered to feed on phytoplankton, it is important to understand if their fossil record shows major changes in diversity in the critical late Cambrian-Early Ordovician interval.

Since Haeckel (1887) three different lineages of protozoans with living representatives are included in the Radiolaria. These are the polycystines, which secrete an aesthetically pleasing siliceous skeleton, the Acantharea which secret a skeleton in celestite (strontium sulphate: $SrSO_4$), and the Phaeodarea, that produce highly porous siliceous tests or loosely

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attached skeletal elements. The single cell of all the above three groups is subdivided in two parts by an organic membrane, called central capsula.

By grazing on the phytoplankton and thus controlling their population size, radiolarians play an important role in modern oceanic food webs. They are locally abundant, depending on the water mass conditions, especially with respect to nutrients. It can be summarized that polycystins are known to be abundant in upwelling areas, both coastal and equatorial (e.g., Anderson, 1983).

From an ecological point of view, radiolarians live in all depths of the water column, although every species is rather specialized in its trophic strategy. The symbiont-bearing species are usually restricted to the surface waters, while there are other species that prefer to live closer to the nutricline, feeding on picoplankton, while a substantial number of species live in the deeper parts of the water column, feeding on suspended organic particles.

Molecular data confirm the close phylogenetic relationship of polycystines and acantharians, both lineages forming the rhetarian clade, deeply rooted in the recently established monophyletic rhizarian supergroup. However, pheodarians are now included within a diverse cercozoan clade (Bass et al., 2005).

Acantharians have no fossil record (as their celestite skeleton is not preserved), and pheodarians are only known since the Cretaceous (Takahashi, 2004). However, the polycystine radiolarians have a much older fossil record, and they allow examination of radialorian evolution during the Palaeozoic. The oldest currently known fossil polycystine radiolarians come from a Botomian (early Cambrian) pelagic sedimentary sequence preserved in the Altai Mountains (Korovnikov et al., 2013). Polycystines probably diversified and became widespread after their first appearance in the early Cambrian, because by the late

Cambrian they were abundant enough to contribute to oceanic sedimentary oozes (Tolmacheva et al., 2001).

Polycystine radiolarians diversified progressively during the Early Paleozoic, but the fossil record remains particularly poor. Nevertheless, they may have the potential to provide some insights regarding the plankton response to palaeoclimatic, palaeoceanographic and global biogeochemical changes. Only a limited number of studies have attempted to produce biodiversity curves of polycystine radiolarians (e.g., Danelian and Johnson, 2001; Renaudie and Lazarus, 2013). Most of the previous studies focused on specific time intervals that coincide with either major or minor mass extinction events (e.g., Erbacher and Thurow, 1997; Hori, 1997; Kiessling and Danelian, 2010; Musavu-Moussavou et al., 2007; Yao and Kuwahara, 1997).

Radiolarian diversity data for the Cambrian-Ordovician interval are patchy, especially for the Cambrian. One of the best-preserved Cambrian polycystine radiolarian assemblages comes from middle Cambrian levels of Australia (Won and Below, 1999) that can be attributed to Cambrian Stage 5. The diversity of this assemblage is represented by 6 genera and 18 species, all of them being part of the archeoentactinid, palaeospiculid and aspiculid families of archaeospicularian radiolarians.

Although some late Cambrian radiolarians are reported from China (Dong et al., 1997) it is the pelagic carbonate sequence of western Newfoundland that provides an observational window on late Cambrian radiolarian diversity and faunal changes during the Cambrian-Ordovician transition. The thorough taxonomic studies conducted initially by Won and Iams (2002) and Won et al. (2005) were more recently supplemented by data from Pouille et al. (2014), who recognized three successive radiolarian assemblages for the late Cambrian-early Tremadocian interval. These studies only cover the interval of the Jianshanian, Cambrian

Stage 10, and the early Tremadocian, but do not report radiolarians from the Paibian, when the SPICE event was recorded. The Jiangshanian *Subechidnina* assemblage is composed of 7 genera and 22 species. The stratigraphically younger *Ramuspiculum* assemblage, known from the Cambrian Stage 10, includes 8 genera and 21 species, while the earliest Tremadocian *Protoentactinia kozuriana* assemblage is composed of 6 genera and 20 species.

There are so far no records of diverse radiolarian assemblages between the middle Cambrian report from Australia (Won and Below, 1999) and the late Cambrian and Early Ordovician report from Newfoundland (Pouille et al., 2014). Although taxonomic richness appears to have remained more or less at the same level as in the middle Cambrian, it is interesting to highlight that only two genera are in common with the middle Cambrian fauna from Australia.

The current knowledge of the polycystine radiolarian record appears to suggest that their taxonomic richness remained at more or less the same level during the middle Cambrian-earliest Ordovician interval. However, a detailed look at the pattern of changes in radiolarian diversity in the latest Cambrian unveils a two-step faunal change, each one of them being approximately correlated with negative excursions of the carbon isotope curve.

As a continuous radiolarian record through the middle and late Cambrian interval is far from complete, and as data from the Paibian are not yet available, it is not possible to attest if the SPICE event had an impact on radiolarian diversity in late Cambrian planktonic ecosystems. However, in spite of the sparse character of the Cambrian radiolarian record, no ‘explosion’ in diversity is recorded when middle and late Cambrian radiolarian assemblages are compared. The diversity of radiolarian assemblages only increased later, with a continuously increasing number of genera during the Ordovician (Noble and Danelian, 2004). However, the record remains too patchy to draw definite conclusions.

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4.2. The fossil record of the Graptoloidea

Graptolites were a major macrozooplanktonic group of the Early Palaeozoic. They include the first abundant, well-preserved fossil record of macrozooplankton in Earth history. They constitute a very well studied fossil group, and serve as biostratigraphical index fossils for Ordovician and Silurian strata. Although graptolites have a fossil record extending back to the Cambrian, the first planktonic graptoloids were earliest Ordovician. The occurrence of selected planktonic graptoloid species serves for the definition of the Global Boundary Stratotype Section and Point (GSSP) of a number of Ordovician and Silurian series and stages, including the Ordovician-Silurian boundary. Being particularly well studied for biostratigraphical purposes, the graptolites show clear onshore-offshore trends of distribution as well as depth-facies preference, occupying the mesopelagic and epipelagic zones, but also neritic (inshore) biotopes (e.g., Vandenbroucke et al., 2009; Cooper et al., 2012).

The graptoloids were colonial pterobranch hemichordates. By analogy with modern pterobranchs, it is assumed that the graptolites filtered food particles from the ocean waters, probably phytoplankton (or picoplankton). Graptolites may therefore have been primary consumers. The graptolites belong to one of the classes of the Graptolithina, that include several other groups, such as the Dendroidea, that are considered to be benthic and sessile. Maletz (2014) revised the systematic position of the colonial or pseudocolonial Pterobranchia (Cephalodiscida and Graptolithina) and revised the stratigraphical occurrence of the Pterobranchia with a first occurrence in the middle Cambrian Series 3, although a clonal, colonial organization of the tubaria can only be recognized in the basal Drumian (Stage 6 of the Cambrian). Maletz (2014) indicated that palaeontological data provide evidence that the oldest fossil hemichordates are from the Burgess Shale, but the record of pterobranchs from the Chinese Kaili Formation appears to be slightly older. A possible pterobranch has also been described from the early Cambrian Chengjiang biota of China (Hou et al., 2011).

Graptolites underwent a significant ecological innovation at the beginning of the Ordovician, as planktonic forms were presumably derived from their benthic ancestors. The graptolites are clearly one of the major players in the GOBE, but as the first planktonic graptolites only appear in the earliest Ordovician these diversity changes cannot be linked directly with the late Cambrian SPICE event, that occurred some 8 to 10 millions years earlier.

4.3. The fossil record of the chitinozoans

The chitinozoans are an enigmatic group of organic-walled microfossils that are important for biostratigraphical correlation. They have been used in Ordovician and Silurian stratigraphy where they complement graptolites and conodonts, in particular for intercontinental correlation (e.g., Webby et al., 2004).

Chitinozoans are very widespread, but their biological affinity remains unknown. They are considered as reproductive bodies, possibly egg cases, of marine invertebrates, called chitinozoophorans (e.g., Paris and Nõlwak, 1999; Grahn and Paris, 2011). Chitinozoans are generally preserved as isolated individuals, but they have also been found in chains of monospecific individuals (sometimes with attachment structures between individuals) or in aggregate masses, sometimes within an organic cocoon-like envelope (e.g., Gabbott et al., 1998). The animals that produced the chitinozoans, the chitinozoophorans, are interpreted as small soft-bodied, probably wormlike organisms, possibly a few millimetres to a few centimetres in length. They most probably occupied pelagic and nektopelagic environments from the Ordovician to the Devonian (e.g., Vandenbroucke et al., 2010). Grahn and Paris (2011) considered that they most likely fed on phytoplankton. Achab and Paris (2007) and

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Grahn and Paris (2011) revised the biodiversification of the chitinozoans in detail. The chitinozoans occupied the planktonic niche from the Early Ordovician onward, with first occurrences in the fossil record in the early (but not earliest) Tremadocian. Chitinozoans are commonly found together with graptolites, suggesting that graptolites and chitinozoophorans lived in partially overlapping environments, occupying nearshore and offshore habitats. In contrast to the graptolites, the chitinozoans displayed their highest diversity at high palaeolatitudes and in less distal environments (e.g., Vandenbroucke et al., 2010; Grahn and Paris, 2011).

For many years, it was believed that chitinozoans were apparently not present in the Cambrian and that they only occupied their pelagic niche after the Cambrian/Ordovician boundary. A few hypothetical records of older chitinozoans have been published, such as the presence of Precambrian vase-shaped microfossils, tentatively attributed to the chitinozoans by Bloeser et al. (1977). These microorganisms were subsequently attributed to testate amoebae (e.g., Porter et al., 2003). More recently, Shen et al. (2012) reported three phosphatised flask-shaped vesicles recovered from the Duyan fauna of China, attributed to Cambrian Stage 5. They tentatively attributed the specimens to *Eisenackitina*? sp., which would date the oldest occurrence of the chitinozoans some 20 million years earlier. Shen et al. (2012) noted that the exceptional occurrence within an Orsten-type Lagerstätte might imply a benthic mode of life for these organisms. However, both the origin of the chitinozoophorans and the passage from a possible benthic to a planktonic mode of life during the late Cambrian remains uncertain.

Therefore, chitinozoophorans were a major component of the Ordovician to Devonian zooplankton. Together with the graptolites, they rapidly diversified in the earliest Ordovician. Chitinozoans disappear at the end of the Famennian (Late Devonian). It has been suggested that their ecological niche was invaded by more efficient organisms and that their usual food supplies disappeared, or were no longer sufficient (Grahn and Paris, 2011). As with the graptolites, they contribute to the 'Ordovician plankton revolution,' but they were apparently absent in the late Cambrian, and are therefore not directly related to environmental changes associated with the SPICE event.

4.4. The fossil record of planktonic arthropods

Arthropods are invertebrate animals that have an articulated body, jointed legs and usually a chitinous or calcitic shell that undergoes ecdysis. They have been extremely diverse since the early Cambrian (e.g., Minelli et al., 2013), with trace fossil and a body fossil records extending to the early Cambrian.

Trilobites are clearly a species-rich fossil group of the Cambrian, but even when the fossil record is extended to non-biomineralised groups, arthropods are the most numerically abundant and diverse phylum in Early Palaeozoic Lagerstätten (Briggs et al., 1994; Hou et al., 2004). Most of the arthropod groups known at present also have their origin in the Cambrian and these include all major classes of crustaceans that are the only group present in modern plankton (Rota-Stabelli et al., 2013). However, the origin and evolution of planktonic arthropods is not entirely understood, as many arthropods belong to the meroplankton, being present in the plankton for only the first part of their life cycle.

Perrier et al. (2015) reviewed the evolution of the marine arthropod zooplankton, their fossil record, and the palaeoecology of the different groups. Arthropod zooplankton are rare in the fossil record, with virtually no occurrences from post-Carboniferous strata and, except for those groups with mineralized skeletons, most planktonic arthropods are known almost exclusively from Konservat-Lagerstätten, with a majority of these having been described from

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the Cambrian. Nevertheless, new insights on arthropod evolution are available through the study of the 'Small Carbonaceous Fossils' (SCFs, see Harvey et al., 2012). Some SCFs in the Cambrian represent groups such as branchiopods, copepods or ostracods, but they are so far only known from a few disarticulated appendages, which precludes a detailed reconstruction of their lifestyle. In addition, because studies of SCFs have mostly concentrated on Cambrian material, the Phanerozoic record of these arthropods is strongly biased, with virtually no record of copepods, for example, between the Cambrian and Recent (Selden et al., 2010).

There is now sufficient evidence to suggest that the zooplankton food web was already well developed by the early Cambrian, and arthropods are likely to have been present within the plankton from that time onwards (e.g., Signor and Vermeij, 1994; Rigby and Milsom, 2000; Butterfield, 2001; Peterson et al., 2004; Vannier, 2007; Vannier et al., 2009). However, most of these arthropods probably never occupied pelagic niches and only lived in the lower levels of the water column (and therefore likely possessed demersal habitats).

Other small putative mesozooplankton in the Cambrian include species of the bradoriids that probably originated in benthic shelf settings in the early and middle Cambrian (Siveter and Williams, 1997; Williams and Siveter, 1998), possibly migrating into the water column during intervals of widespread shelf dysoxia in the Drumian and Guzhangian stages of Cambrian Series 3 (Collette et al., 2011; Williams et al., 2015).

Other records of arthropod macrozooplankton in the Cambrian are meagre. *Isoxys,* with its light carapace, appendages adapted for swimming, a flap-like telson, powerful prehensile frontal appendages, a well-developed digestive system and large spherical eyes, is probably one of the best candidates as a macrozooplankton predator (Vannier and Chen, 2000; Vannier et al., 2009). Although *Isoxys* is not cosmopolitan at the species level like some Cambrian bradoriids, evidence from functional morphology, taphonomy and palaeogeographic distribution suggests that it may have been a widespread predator, living near the seafloor (Vannier et al., 2009).

The presence of pan-arthropod top predators (e.g., Radiodonta) in the early Cambrian (Series 2) water column is well documented. These animals reached metre-scale lengths in the Cambrian and Ordovician (e.g., Van Roy and Briggs, 2011) and were present until at least the Early Devonian (Kühl et al., 2009). The functional morphology of the frontal appendages suggests that some anomalocaridid taxa were durophagous predators, whilst others fed on soft-bodied organisms (Daley et al., 2013). Two taxa from the early Cambrian (Vinther et al., 2014) and Early Ordovician (Van Roy et al., 2015) most probably were microphagous suspension feeders. The appendages of these large (up to up to 2 m long) anomalocaridids were probably used for sweep-net capture of food items down to 0.5 mm, which is within the size range of mesozooplankton such as copepods and branchiopods.

The first putative malacostracan crustaceans entered the water column only during the Early Ordovician. Based on its cosmopolitan palaeogeographic distribution and its associated faunas, the putative phyllocarid *Caryocaris*, recorded from the Tremadocian onward, has been interpreted as a microphageous/opportunistic mid-water zooplanktonic animal that probably occupied the same niches as Ordovician pelagic trilobites (Vannier et al., 2003).

Although trilobites were already diverse during the Cambrian (e.g., Fortey and Owens, 1997), there are only a few adult forms that have been interpreted as pelagic. On the contrary, the Ordovician bears a wider range of what are generally agreed to be pelagic trilobite species (e.g., Fortey, 1974, 1975, 1985; Fortey and Owens, 1999). Some of these occur across inner and outer shelf facies.

The presence of a great diversity of lifestyles and feeding strategies in Early Palaeozoic arthropods suggests that the planktonic food web was already complex perhaps as early as the

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early-middle Cambrian, implying that arthropods were present at several trophic levels from primary consumer to tertiary predator. However, it appears also that during the Cambrian many planktonic niches remained unoccupied, at least until the late Cambrian. The arthropods only filled these niches progressively during the Ordovician.

The review of the literature clearly indicates that radical changes in arthropod zooplankton evolution cannot be related directly to the SPICE event. Several zooplanktonic groups are present in the fossil record since the early-middle Cambrian. Bradoriids, bivalved arthropods, copepods and branchiopods, as well as agnostids were clearly present in the water column of the Cambrian ocean before the SPICE event. Pelagic trilobites and phyllocarids, however, only strongly diversify in the Ordovician (see also Figure 2).

4.5. The fossil record of planktonic (pelagic) cephalopods

Modern cephalopods are swimming animals and are therefore considered as living in the free water column (i.e., numerous species clearly belong to the nekton, especially Decabrachia). Today they occupy nearly the entire spectrum of marine environments, with different life habits corresponding to the different habitats. Being more mobile, cephalopods have commonly played the consumer-role, similar to some of the larger arthropods described from Cambrian Lagerstätten. For this reason, cephalopods and arthropods were probably the largest animals in Cambrian and Ordovician oceans, although arthropods (e.g., Butterfield, 2001; Van Roy and Briggs, 2011; Vinther et al., 2014; Van Roy et al., 2015) and cephalopods (e.g., Dzik, 1981; Holland, 1987; Kröger, 2003, 2005, 2007; Mutvei et al., 2007; Klug et al., 2010) occupied different niches that changed over time. Both groups also produced relatively gigantic (metre-scale) forms in the Cambrian and Ordovician (e.g., Teichert and Kummel, 1960; Braddy et al., 2007; Van Roy and Briggs, 2011; Vinther et al., 2014; Klug et al., 2015;

Van Roy et al., 2015).

The precise moment of the first occurrence of cephalopods in the fossil record has been disputed (e.g., Kröger et al., 2011, 2013). Currently, the majority of specialists agree that the sister group of the cephalopods has to be sought in the monoplacophorans (e.g., Kröger et al., 2011). Although the origin of the group is not fully understood, cephalopods are clearly present in the latest Cambrian. They displayed cm-long breviconic shells with several simple chambers and a narrow siphuncle (e.g., Dzik, 1981; Holland, 1987; Kröger, 2007). These early forms are known from the late Cambrian of North America and China (Holland, 1987), from two distinct regions located in tropical palaeolatitudes. The combination of shell characters and their early wide distribution underlines the plausibility that these forms were indeed planktonic drifters, most likely feeding on planktonic organisms of smaller size. Occurrences in South China indicate the presence of late Cambrian and early Tremadocian cephalopods in off-shore shelf carbonates, interpreted as deposited below normal storm wave base, representing in some cases clearly neritic habitats (e.g., Chen and Qi, 1982; Zou, 1987). However, late Cambrian cephalopods are not known from deeper water settings, and the oldest cephalopods from deeper water environments are from the middle Tremadocian (Kröger et al., 2009).

A planktonic mode of life of Ordovician cephalopods with orthoconic or cyrtoconic shells appears likely. Based on the fact that many Ordovician cephalopods with orthoconic shells had thick siphuncles, Kröger (2003) suggested that these may have been vertical migrants in the water column. The presence of apical endosiphuncular or endocameral deposits has been considered as an aid to move the shell into a position to facilitate horizontal swimming (e.g., Holland, 1987), but this hypothesis needs further testing. Simultaneously with the increase in siphuncular disparity, from the late Cambrian to the Late Ordovician (see Kröger, 2003), cephalopod shell geometry disparity also increased. The independent evolution of coiled

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shells in several Ordovician cephalopod clades documents an ecological transition from an essentially planktonic to a nektonic habit (Kröger, 2005), anticipating similar coiling events in the 'Devonian Nekton Revolution' (Klug and Korn, 2004; Klug et al., 2010).

The probable change in the mode of life from benthic to planktonic in the late Cambrian at the monoplacophoran-cephalopod-transition and from planktonic to nektonic lifestyles early in the Ordovician within several cephalopod clades, may reflect the rich supply of planktonic food sources developing in the later part of the Cambrian. Kröger et al. (2009) summarized data that suggest that the exploitation of the pelagic realm by several independent invertebrate clades began synchronously during the latest Cambrian to Middle Ordovician. Possibly this might be linked to new food supplies from primary producers.

The origin of planktonic/nektonic cephalopods occupying pelagic niches and offshore environments occurs during the time interval of the late Cambrian to Early Ordovician, although a direct link with the SPICE event cannot be demonstrated.

5. The development of planktotrophy in marine invertebrate larvae

Several marine invertebrate organisms begin their lifecycle with a planktonic phase (meroplankton) and several marine invertebrate clades produce free-swimming larvae or hatchlings that feed on the smaller parts of the plankton. Such larvae and hatchlings play an important role in the study of the evolution of the Early Palaeozoic plankton. They clearly form a significant part of the plankton, and, on the other hand, if they are plankton feeding (planktotrophic), they are amongst the primary consumers grazing the phytoplankton.

Marine invertebrates may hatch from the fertilized egg (direct development) or they may have biphasic life cycles and hatch as a larva (indirect development). The definition of larvae is

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basically the presence of a profound morphological and ecological transformation (metamorphosis) of a hatchling into a larger juvenile animal (Strathmann, 1986). Planktonic larvae and other hatchlings that do not undergo metamorphosis enhance dispersal and gene flow between populations. They either feed on plankton (planktotrophic larvae) or do not feed but live on yolk or other parental energy resources (lecithotrophic larvae). These ontogenetic pathways vary from clade to clade. For instance, planktotrophic larval development is unknown in modern brachiopods (e.g., Lüter, 2001), although it is common in higher gastropods and bivalves, but absent in other mollusc classes (e.g., Nützel, 2014). Planktotrophic larval development is most common in modern tropical and subtropical shallow waters but rare in species from higher latitudes and deep water (e.g., Thorson, 1950; Jablonski and Lutz, 1980, 1983).

There is currently a detailed debate about the time periods when planktotrophic larval development evolved and whether it is ancestral in Eumetazoa or Bilateria or not (e.g., Nützel, 2014). This is also relevant for the discussion about the onset of the 'Ordovician plankton revolution' because the timing of the evolution of planktotrophic larval development has implications for the overall evolution of primary productivity and food chains in the plankton. Planktotrophic larvae are mostly primary consumers of phytoplankton although larvae may also feed on zooplankton (e.g., Richter, 1987). Sufficient and continuous primary production by phytoplankton is therefore a prerequisite for planktotrophic larval development. The question is whether planktotrophic larval development was present as early as the early Cambrian or even the late Proterozoic (e.g., Nielsen, 2013) or whether it evolved later and independently in several evolutionary lineages.

The notion that larval planktotrophy is an original trait of eumetazoans or bilaterians has previously been rejected based on the phylogenetic distribution of planktotrophy (Signor and Vermeij, 1994; Haszprunar et al., 1995; Haszprunar, 1995; Peterson, 2005). Thus, basal clades lack planktotrophic larvae, including basal mollusc clades. Chaffee and Lindberg (1986) also argued that Cambrian molluscs were too small to produce large numbers of planktonic larvae, which suffer high mortality rates (but see also, Mus et al., 2008 and discussion by Nützel, 2014). Therefore, Chaffee and Lindberg (1986) concluded that planktotrophy in molluscs evolved during the late Cambrian/Ordovician transition.

Nützel et al. (2006) found that the early (Cambrian) ontogenetic parts of univalved mollusc shells, amongst them probably early gastropods, are clumsy and large at a defined shell length at 100 µm. They suggested that this reflects yolk-rich early ontogeny and thus either direct or non-planktotrophic larval development. By contrast, Ordovician/Silurian shelly assemblages yield numerous moulds of gastropod protoconchs with small initial parts suggesting the presence of planktotrophic larvae. Nützel et al. (2006, 2007) concluded that in molluscs, including gastropods, planktotrophic larval development evolved at the Cambrian/Ordovician transition (for a contrasting opinion see Freeman and Lundelius, 2007). Based on the study of relatively well-preserved helcionellids, Parkhaev (2014) corroborated the assumption that planktotrophic larval development is absent in Cambrian molluscs and concluded that Cambrian univalved molluscs (helcionellids) had either direct or lecithotrophic larval development. Similarly, the oldest known bivalve, *Pojetaja runnegari*, likely had a non-planktotrophic (lecithotrophic) larval development according to Runnegar and Bentley (1983) (but see Freeman and Lundelius *op. cit.*, postscript, for a different opinion).

Freeman and Lundelius (1999, 2005, 2007) proposed that a planktotrophic larval development is common in Early Palaeozoic brachiopods and that the presence of planktotrophic larva is probably a basal and universal character across brachiopod groups. However, seemingly all living brachiopods have a non-planktotrophic early ontogeny, either a lecithotrophic larva or direct (Lüter, 2001, and references therein). The proposed plesiomorphic presence of a planktotrophic larval development in Brachiopoda is in conflict with the fact that all living members (or at least articulate brachiopods) lack planktotrophic larvae. The presence of exclusively lecithotrophic early ontogenetic stages in all recent representatives of craniiform and rhynchonelliform brachiopods suggests that the stem species of both groups had a lecithotrophic early ontogeny although the ontogeny of the numerous fossil representatives is either unknown or insufficiently known (Lüter, written communication 2015).

In conclusion, there is no evidence for Cambrian molluscs with planktotrophic larval development. This is also suggested by the phylogenetic distribution of planktotrophic larval development in molluscs and also in other invertebrates and in Eumetazoa as a whole. Planktotrophic larvae evolved independently in several evolutionary lineages during the late Cambrian and Ordovician (see also Signor and Vermeij, 1994; Haszprunar et al., 1995; Haszprunar, 1995; Peterson, 2005; Nützel et al., 2006, 2007; Nützel, 2014). However, more observations on well-preserved early ontogenetic hard parts are needed to corroborate this assumption.

It is evident that the evolution of larval planktotrophy is an important part of the establishment of planktonic food chains. Palaeozoic morphological trends in gastropod larval shells, i.e., the change from open coiling to tight coiling and increasing larval ornament, suggest an increasing predation pressure in the plankton and this was originally termed the ‘Palaeozoic Plankton revolution’ in analogy with Vermeij’s (1977) 'Mesozoic Marine Revolution' (Nützel and Fryda, 2003; Nützel et al., 2006; Seuss et al., 2012; Nützel, 2014).

An explanation for the convergent evolution of planktotrophy in the larva of several different invertebrate groups remains debatable. Increasing primary production could have triggered this, as well as increasing predation pressure in the benthos by burrowers and suspension feeders, which forced hatchlings to escape to the plankton (see Strathmann, 1986; Signor and Vermeij, 1994; Nützel et al., 2006).

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In conclusion, it appears evident that an important ecological shift took place with the development of planktotrophy. This significant additional step took place during the late Cambrian – Early Ordovician interval (see also Peterson, 2005), i.e., it clearly is part of the 'Ordovician plankton revolution.' However, the exact timing when these changes took place is imprecisely known.

6. Nutrients and the trophic structure of the oceans between the 'Cambrian Explosion' and the 'Great Ordovician Biodiversification Event'

The objective of this section is to place the late Cambrian and Ordovician in a general context of nutrient availability in the oceans, though noting at present that there is only limited data available to assess this.

The Palaeozoic positive carbon isotope excursions of which nine shifted $\delta^{13}C_{carb}$ by $\geq 3‰$, each having a duration of a few million years, are considered to represent significant palaeoceanographic events, commonly modeled as episodes of increases in oceanic nutrient availability (e.g., Kump and Arthur, 1999; Goddéris and Joachimski, 2004). Analyses of the geological processes that took place during the SPICE event are therefore important to assess whether an increased nutrient availability in the late Cambrian oceans fuelled the 'Ordovician plankton revolution' and ultimately the GOBE.

The proliferation of phytoplankton that serves as the food supply for both planktotrophic larvae and planktotrophic (heterotrophic) zooplankton, depends on the availability of nutrients. Phytoplankton obtains energy through photosynthesis and primarily need macronutrients such as nitrate, phosphate and silicic acid and the micronutrient iron. The abundances of these nutrients in the oceans change in time and space. Phytoplankton usually blooms in spring and summer, and is abundant in upwelling zones where nutrient supply is usually high.

The huge increase of biodiversity during the GOBE, including the 'Ordovician plankton revolution,' may ultimately have been fuelled by tectonism, as evidenced by strontium isotope ratios that indicate increased continental weathering. Strontium isotope ratios have been used as a qualitative indicator of nutrient runoff from the continents: increasing strontium isotope ratios reflect orogeny and enhanced continental weathering, which inputs the heavier isotope ^{87}Sr to the oceans, as opposed to ^{86}Sr input which associated with increased rates of seafloor spreading and hydrothermal weathering (e.g., Cárdenas and Harries, 2010). Strontium isotopes exhibit strong positive excursions during the Pan-African Orogeny (Neoproterozoic-Cambrian) (e.g., McKenzie et al., 2011). Some of the highest, if not the very highest strontium isotope ratios of the Phanerozoic also occur during the Cambrian presumably in response to widespread tectonism and orogeny associated with the Pan-African Orogeny and the rifting of Rodinia/Pannotia (Montañez et al., 2000). However, for the late Cambrian – Early Ordovician interval, precise Sr ratios are not available so far, and only general trends have been published (see Figure 3).

Nutrient input in the oceans is also related to volcanism. Some of the greatest volumes of volcanic rocks of the entire Phanerozoic erupted in the Middle Ordovician, possibly in response to a mantle plume (e.g., Barnes, 2004; Servais et al., 2009b; Lefebvre et al., 2010). Mafic volcanic rocks are associated with higher phosphorus concentrations (Hartmann et al., 2014) and satellite data indicate that phytoplankton blooms are stimulated by ash outfall (Duggen et al., 2007; see also Botting, 2002). Models indicate that silicate weathering rates are similar to out-gassing rates of volcanic and metamorphic CO_2 and that intervals of continental dispersion are characterized by high rates of out-gassing and runoff due to intensification of the hydrologic cycle, whereas supercontinent stasis is associated with low out-gassing rates, high aridity resulting from the development of supercontinents, and low

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chemical weathering fluxes (Tardy et al., 1989; Gibbs et al., 1999).

From about 470 million years ago during the Ordovician, the origin and diversification of land plants and their consequences may also have played a critical role in the weathering of the continents, nutrient runoff, and the evolution of the marine biosphere. Spores and cryptospores provide evidence of land plants at least as early as the Mid Ordovician-Silurian, and likely produced widespread rudimentary soils in place of microbial soil crusts (e.g., Boucot and Gray, 2001; Wellman et al, 2013; Gerrienne et al., submitted). Lenton et al. (2012) also argued that the terrestrialisation by land plants cooled the Ordovician oceans. However, the impact of the land plants most probably did not influence the onset of the 'Ordovician plankton revolution,' as the first land plants appeared only several tens of million years after the massive occurrence of plankton in the fossil record.

During the late Cambrian – Early Ordovician interval, presumably accelerated nutrient runoff could have supported greater primary productivity. Increased tiering above and below the sea bottom, as evidenced by the fossil record, and the presence of abundant planktotrophic larvae suggest greater food availability in the marine realm (Droser and Bottjer, 1988, 1989; Bottjer et al., 2000). Increased nutrient availability may have contributed to the alteration of life history traits and the initial evolution of the benthos into the plankton (Elser et al., 1996; Main et al., 1997; Sterner and Elser, 2002; Nützel et al., 2006). All of these conditions together probably provided optimal conditions for metazoan evolution and diversification. Greater food availability above (in the form of plankton) and below (in the form of dead organic matter at the sea bottom) would have supported expanding populations, potentially leading to their migration and genetic isolation (see also Allmon and Martin, 2014). Other energy-based mechanisms may have also driven biodiversification (Brown, 1995; Maurer, 1999; Evans et al., 2005a,b, 2006).

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In conclusion, there is evidence to suggest that there may have been an increase of nutrients available in the global oceans during the Cambrian and Ordovician (see also Cárdenas and Harries, 2010; Allmon and Martin, 2014). However, future research is needed, including models of oceanic current distribution and upwelling zones and climate (e.g., Nardin et al., 2011; Servais et al., 2014; Pohl et al., 2014, this volume), to fully understand the development of trophic webs during the Early Palaeozoic radiation.

7. Isotope geochemistry and oxygen evolution in the Cambrian-Ordovician

Saltzman et al. (2011) related a pulse of oxygenation to the SPICE event and correlated this to the GOBE and the 'Ordovician plankton revolution.' What might the SPICE event mean in terms of plankton evolution?

The Cambrian and Early and Middle Ordovician interval is associated with several $\delta^{13}C_{carb}$ isotope excursions, though these are of relatively small magnitude, with values varying typically between -1.5‰ and +1.5‰ through this interval (Saltzman, 2005; Bergström et al., 2009; Munnecke et al., 2010). The chief exception is the SPICE event in the late Cambrian (Paibian Stage, Furongian Series). This excursion, with a $\delta^{13}C_{carb}$ amplitude of up to 5‰, is known from sections in Australia, China, Kazakhstan, North America, and Siberia (Glumac and Walker, 1998; Saltzman et al., 1998, 2000, 2004; Kouchinsky et al., 2008; Gill et al., 2011). Coeval positive excursions in organic matter ($\delta^{13}C_{carb}$) have been reported from Baltica (Ahlberg et al., 2009) and Avalonia (Woods et al., 2011). The onset of the excursion coincides more or less with the FAD of the cosmopolitan agnostid *Glyptagnostus reticulatus* and with a time of significant faunal changes on different palaeocontinents, amongst these being the extinction of the marjumiid trilobites (see summary in Gradstein et al., 2012). The early Furongian is characterised by an initial global transgression which lead to the deposition of black shales in Avalonia, Baltica, and Argentina (Alvaro et al., 2013), followed by a major glacio-eustatic regression and the deposition of sand- and siltstones or quartz-rich carbonates (Sauk II-Sauk III event; Saltzman et al., 2004, Lindsay et al., 2005; Buggisch, 2008).

As for most other Palaeozoic $\delta^{13}C_{carb}$ excursions the ultimate cause of the SPICE is a matter of debate. Saltzman et al. (2000) highlighted the fact that sedimentological evidence for glaciation is lacking, and proposed thermal contraction of the deep-ocean water coupled with increased storage of groundwater in continental reservoirs as a cause for the global regression. The lack of large ice sheets that could have changed the ratio of silica to carbonate weathering rates by covering up silicate terranes containing organic matter at high latitudes, suggests that burial of organic carbon in black shales was the likely cause of the $\delta^{13}C_{carb}$ excursion (Saltzman et al., 2004). There is, however, no indication of enhanced deposition of black shales during the SPICE (Saltzman, 2005; Ahlberg et al., 2009). Munnecke et al. (2003) pointed out that the SPICE shared many similarities with Late Ordovician and Silurian $\delta^{13}C_{carb}$ excursions, and argued that a change from humid to arid climate in low latitudes and thus a change from chemical to physical continental weathering might have increased the availability of quartz grains (see also Bickert et al., 1997, and Kozłowski and Sobień, 2012).

Gill et al. (2007, 2011) document a positive sulphur isotope excursion both from carbonate-associated sulphate ($\delta^{34}S_{CAS}$) and pyrite ($\delta^{34}S_{pyrite}$) in phase with the $\delta^{13}C_{carb}$ excursion. This is interpreted as indicating enhanced pyrite burial (with preferential removal of ^{32}S) stimulated by large-scale marine organic carbon burial during the SPICE. A decrease and minimum in molybdenum (Mo) and Mo/TOC ratios in the Andrarum 3 core of Scandinavia corresponding to the initiation and peak of the carbon and sulphur isotope excursions, respectively, indicate the transient spread of marine anoxia (Gill et al., 2011). Based on a carbon and sulphur mass balance model Saltzman et al. (2011) interpreted the coeval carbon and sulphur isotope excursions as an indicator of a major increase in atmospheric O_2. On a first view, oceanic anoxia seems to contradict an atmospheric oxygenation event, but deposition and burial of organic matter can plausibly be linked to both increase and decrease in marine oxygenation (Thompson and Kah, 2012). Because the bacterial decomposition of organic matter in the water column removes O_2 from sea-water and, consequently, from the atmosphere, the non-decomposition and burial of organic matter acts in the opposite direction, and oxygen becomes available to build up in the atmosphere. On the other hand, if black shale deposition is triggered by ocean stratification, i.e., by effective decoupling of the ocean-atmosphere system, the long-term effect would include an increase in global anoxia (Thompson and Kah, 2012).

The most prominent feature of the immediate aftermath of the end-Ordovician (e.g., Delabroye et al., 2011), end-Devonian (e.g., Buggisch and Joachimski, 2006), end-Permian (e.g., Payne et al., 2004), and end- Triassic extinction events (e.g., van de Schootbrugge et al., 2009) is the occurrence of large (> +3 ‰) to very large (> +5 ‰) positive carbon isotope excursions measured from carbonates and organic carbon. These positive excursions are invariably associated with anoxic conditions in the oceans, and are most readily explained as the result of massive carbon burial during times of enhanced primary productivity (Kump and Arthur, 1999).

9. Discussion

The analysis of early-middle Cambrian (Series 2 and 3) Lagerstätten indicates that formerly benthic organisms began to enter the plankton (e.g., Butterfield, 2001). The exceptionally preserved assemblages in these ecosystems were characteristic of shallow-water shelf communities. It is evident that some arthropods from these communities were able to swim (see Perrier et al., 2015, for a review), and they could thus be attributed to the nekton (or to nekto-benthic organisms), or at least to the plankton (unable to swim against currents). However, these arthropods did not leave shallow shelf environments, although a few organisms probably started to live in deeper shelf and slope environments (e.g., Burzin et al., 2001). The pelagic zones were probably not fully occupied during the 'Cambrian Explosion,' but only much later. The main zooplankton captured by the fossil record during the early and middle Cambrian was thus composed of arthropods, together with a first sporadic record of radiolarians.

Figure 2 summarizes the evolution of the most important fossil groups belonging (partly or entirely) to the plankton. This figure includes some qualitative data on the presence or absence of selected groups of organisms. Between the benthic (at the sea-floor) and planktonic (drifting, with limited swimming capacities), the demersal category includes organisms living in the water column near the sea floor.

The acritarchs include various microorganisms present in the fossil record as organic-walled microfossils. As a polyphyletic group, they include (for all geological periods) several kinds of small organisms, living in benthic, demersal and pelagic habitats, and including cysts of phytoplanktonic organisms. The chitinozoans are possibly already present in the Cambrian Series 3, but the organisms producing them clearly are planktonic after the Cambrian-Ordovician boundary. The zooplanktonic radiolarians first appear in the early Cambrian, and they become common in the late Cambrian, before diversifying progressively in the Ordovician. The graptolites were entirely benthic during the Cambrian; but Ordovician graptoloids were clearly planktonic. Among the arthropods, a number of groups are considered to belong to the zooplankton. The bradoriids are one of the few groups of which some taxa appear to have adopted a planktonic lifestyle during Cambrian Series 3, while other bradoriids are benthic. The recent findings as SCFs of copepods and branchiopods indicates that these crustaceans already existed in the early and middle Cambrian, though their lifestyles cannot be precisely constrained for this time period. The agnostids include taxa that may have been planktonic during Cambrian Series 3 and the Furongian, but not later. Trilobites were clearly benthic in the Cambrian, but a few taxa moved into the plankton during the late Cambrian, and pelagic taxa became common in the Ordovician. The phyllocarids are a group of crustacean arthropods that may have occupied pelagic niches from the Tremadocian onward. The cephalopods entered the pelagic realm somewhere during the late Cambrian. Originally living near the sea floor they became active swimmers and predators at the top of the Ordovician food chain.

Figure 3 attempts to quantify the presence of different marine organisms with a planktonic lifestyle from Cambrian Series 3 to the Early Ordovician. The quantitative data (based on published diversity counts, see Legend of Figure 3) of several groups are plotted against the chronostratigraphical scheme, the values of $\delta^{13}C_{carb}$ and $^{87}Sr/^{86}Sr$, and the sea-level curve, as well as against the most recent biodiversity curve of marine invertebrate genera recently published by Na and Kiessling (2015). In addition, radiolarians and planktonic arthropods are plotted here, based on qualitative data only, based on the review presented above.

At a geological scale, in the context of the Palaeozoic or the entire Phanerozoic, the increase of the plankton during the late Cambrian – Early Ordovician might be viewed as a relatively short ‘event’ (see also Figure 1). It appears to have developed over several (tens of) millions of years, assuming that this record is not distorted by an absence of fossil data for the plankton. At a smaller scale, with a focus on the interval of the late Cambrian and Early Ordovician (Figure 3), the onset of the ‘Ordovician plankton revolution’ appears to have been stepwise, and not a sudden event triggered by a single geological or palaeoecological parameter. Between the rapid increase of acritarch (phytoplankton) diversity starting in the Jianshanian, and the rapid onset of the diversification of the cephalopods, graptolites and chitinozoans in the Tremadocian, it appears that a few million years elapsed.

Of particular interest is the lack of correlation between the different planktonic groups and the SPICE $\delta^{13}C_{carb}$ event. Saltzman et al. (2011, fig. 6) suggested that the SPICE event triggered the 'Great Ordovician Biodiversification Event' (GOBE). They correlated the SPICE event with the onset of the GOBE, based on both the global compilation of marine invertebrate genus level diversity of Alroy (2010) and the diversity compilation of South China by Rong et al. (2007). Our compilation of data shows that the SPICE event does not closely correlate with the diversifications of the planktonic groups examined, nor with a dramatic change in the most recent diversity curve calculated for all marine invertebrates. Based on Na and Kiessling's (2015) dataset, it would be possible to consider the Jiangshanian Age as the time of the onset of the GOBE, but not the Paibian Age, when the SPICE event took place. In conclusion, there seems to be no clear correlation between the SPICE event and the fossil record of plankton colonisation.

However, oxygen levels during the SPICE event likely increased in response to enhanced photosynthesis. If so, the question then becomes: What triggered the increase of photosynthesis? One possible cause is increased nutrient availability, as reflected by the broad rise of strontium isotope ratios during the late Proterozoic and into the Cambrian (Figure 3) and which surpassed values for the Cenozoic, when orogenic uplift of major mountain chains was quite pronounced (Montañez et al., 2000; see Figure 3). Rising inorganic nutrient levels may have also enriched food sources (plankton and the pelagic rain of dead organic matter) with inorganic nutrients such as phosphorus and trace elements necessary for nucleic acid synthesis (DNA and especially the ribonucleic acids of ribosomes involved in protein synthesis) and biochemical pathways, including those of photosynthesis. The subsequent rise of sea level into the Cambrian (see Figure 3) would have produced a much more widespread photic zone on the shelf into which nutrients continued to be added (as indicated by strontium isotopes). Depths of bioturbation also began to increase, possibly in

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response to both oxygen and the pelagic rain of dead organic matter.

As noted previously, the positive carbon isotope excursion ($\delta^{13}C_{carb}$) of the SPICE event may also be associated with oceanic nutrient availability (e.g., Kump and Arthur, 1999; Goddéris and Joachimski, 2004). Increasing nutrient and food availability in the water column may therefore have provided conditions that produced a refuge from bioturbation and benthic predation. These trends may have been further stimulated by volcanic and tectonic activity later in the Ordovician, as discussed above. Furthermore, biodiversification may have experienced a significant lag following one or both of the SPICE and volcanic/tectonic events. Analyses of the geological processes that took place during the SPICE and subsequent volcanic events may therefore be critical to understanding the 'Ordovician Plankton Revolution', and the GOBE.

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Figure Captions

Figure 1:

Macroecological changes in the Palaeozoic (modified after Klug et al., 2010) as reflected in diversity changes as well as the relative abundance of demersal organisms (Cephalopoda: Actinocerida, Ascocerida, Discosorida, Ellesmerocerida, Endocerida, Lituitida, Oncocerida; Arthropoda: Radiodonta, Eurypterida; Vertebrata: Galeaspida, Osteostraci, Pteraspidomorphi, Thelodonti; Cephalochordata), plankton (Graptoloidea, Dacryoconarida, Homoctenida, Orthocerids, Bactritida) and nekton (Ammonoidea, Gnathostomata, most coiled nautiloids) in the Palaeozoic. Note the radical change in diversity in the three macroecological groups. A, curves based on Sepkoski (2002). B, Data from the Paleobiology Database (10 myr intervals).

Figure 2:

Qualitative presence/absence data of phytoplankton and zooplanktonic groups in the middle-late Cambrian - Early Ordovician. 3, Cambrian Series 3; F, Furongian; L, M, U, Lower, Middle and Upper Ordovician. For explanation see text.

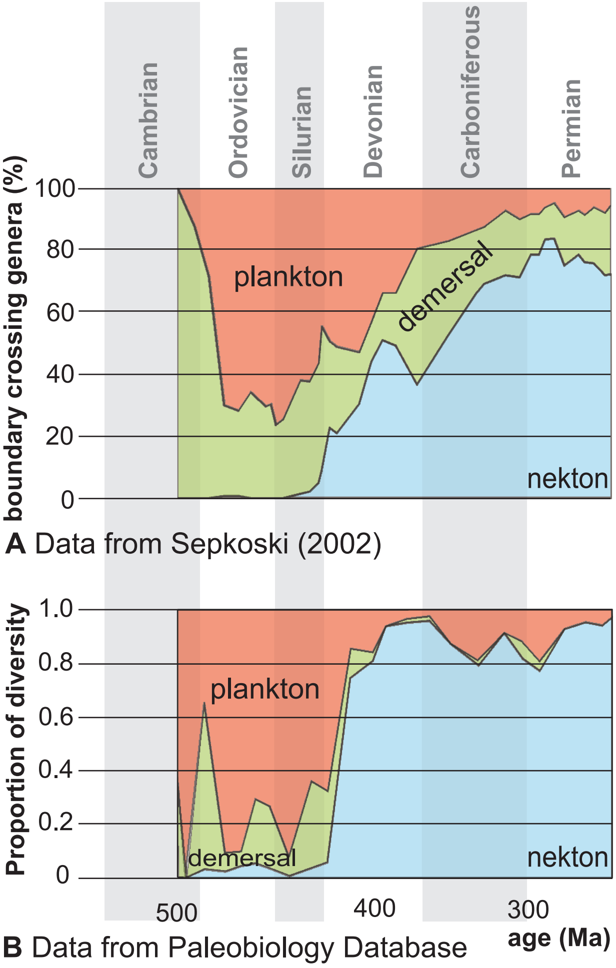
Figure 3:

Middle-late Cambrian - Early Ordovician biodiversity estimates, geochemical proxies and sea level. Columns left to right:

- chronological table based on Gradstein et al. (2012);
- biodiversity of marine invertebrate genera based on the shareholder quorum subsampling method (Na and Kiessling, 2015);

- origin and diversity of major planktonic groups (based on published diversity curves; except for radiolarians and arthropods) : acritarchs, Nowak et al. (in press) and Servais et al. (2008); cephalopods, Kröger et al. (2009, 2011); graptolites, Cooper et al. (2012); chitinozoans, Achab and Paris (2007);
- $\delta^{13}C_{carb}$ isotope curve, compiled from Saltzman et al. (2011)and Bergström et al. (2009);
- $^{87}Sr/^{86}Sr$ curve based on Montañez et al. (2000) and Gradstein et al. (2012);
- relative sea-level curve based on Nielsen (2004) and Gradstein et al. (2012).

Figure 1



A Data from Sepkoski (2002)

B Data from Paleobiology Database

Figure 2

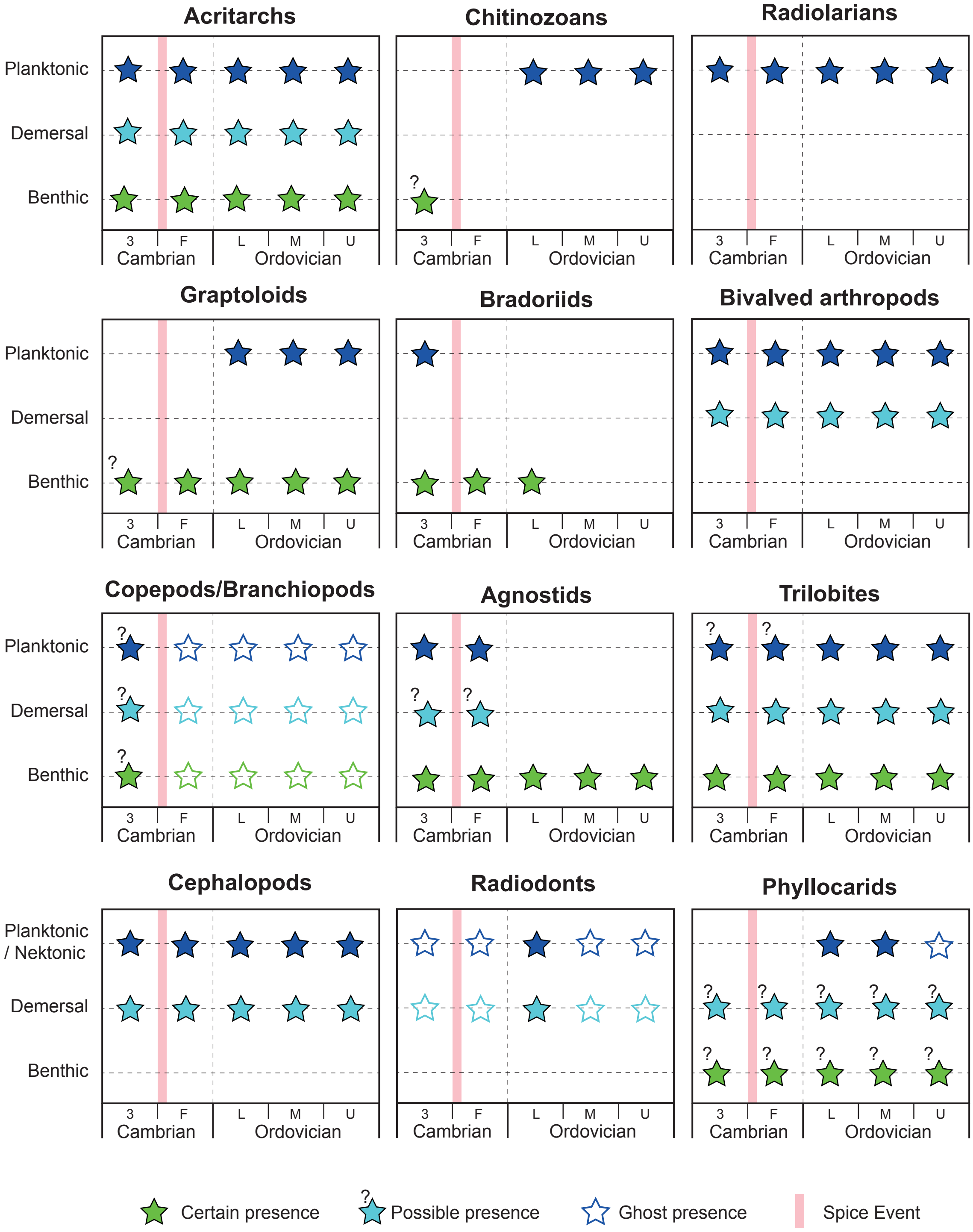


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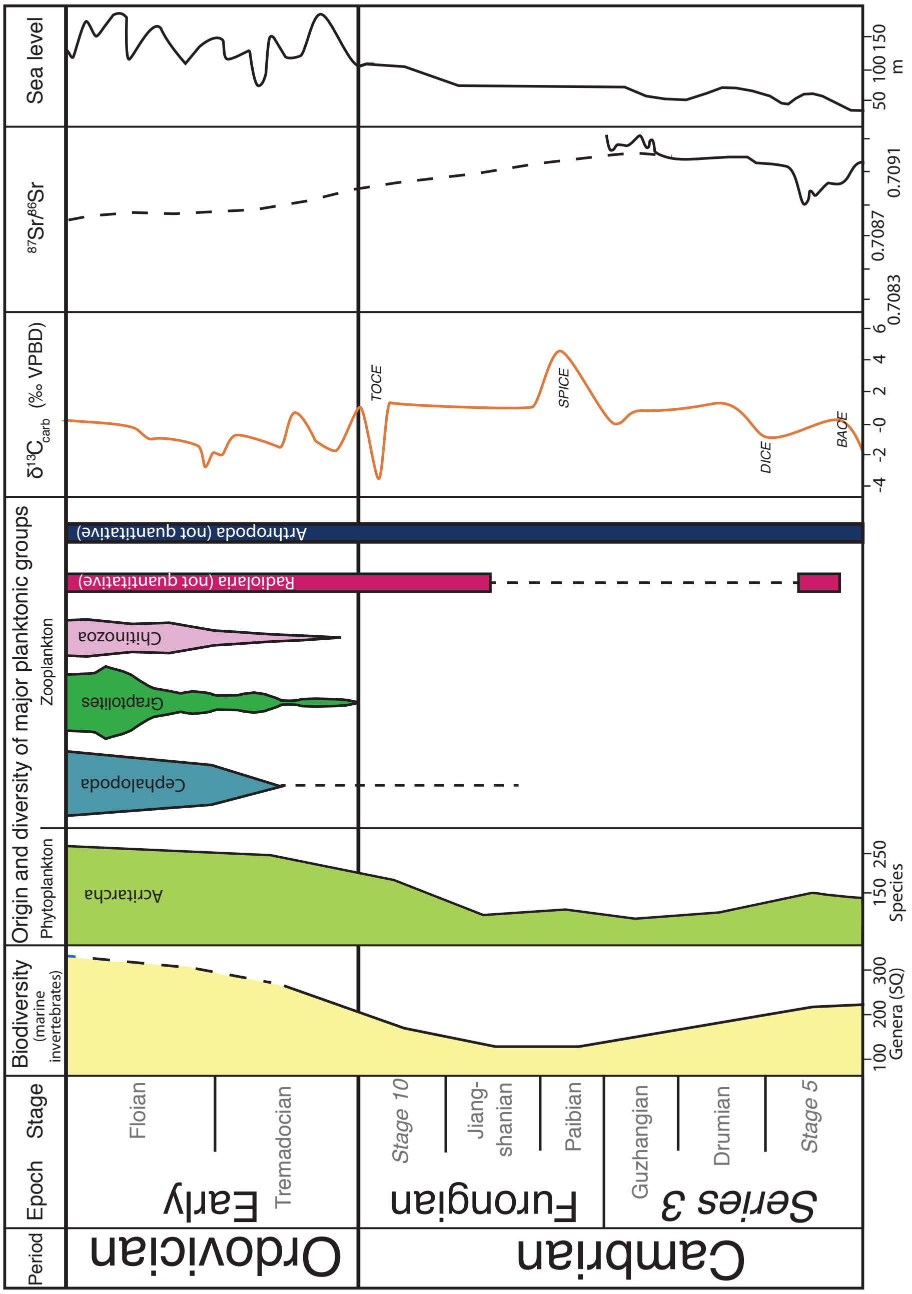
Figure 3



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Article III

Discovery of the *messaoudensis–trifidum* acritarch assemblage (upper Tremadocian–lower Floian, Lower Ordovician) in the subsurface of Morocco

Nowak, H., Akodad, M., Lefebvre, B. & Servais, T.

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Discovery of the *messaoudensis–trifidum* acritarch assemblage (upper Tremadocian–lower Floian, Lower Ordovician) in the subsurface of Morocco

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Abstract. The upper Tremadocian to lower Floian *messaoudensis–trifidum* acritarch assemblage was first described from the Skiddaw Group of England and subsequently from several localities on the Gondwanan margin that were positioned in high southern latitudes during the Early Ordovician. It is here reported for the first time from North Africa, from the Fezouata formations (Tremadocian to Floian) in the AZ-1 borehole, southeastern Morocco. The assemblage is comparable with that from the Skiddaw Group, with *Cymatiogalea deunffii*, *C. messaoudensis*, *C. velifera*, *Caldariola glabra glabra*, *Stelliferidium trifidum* and *Veryhachium lairdii* s.l. The Moroccan assemblage indicates a late Tremadocian age.

Key words: acritarchs, Lower Ordovician, Morocco, Anti-Atlas, biostratigraphy.

INTRODUCTION

The *messaoudensis–trifidum* acritarch assemblage is known from upper Tremadocian to lower Floian (Lower Ordovician) strata in many localities on the Gondwanan margin (Servais et al. 2003). It was first described as the 'Watch Hill assemblage' from the Watch Hill Formation of the Skiddaw Group in the English Lake District by Molyneux & Rushton (1988). Its seven most common species, considered to be the diagnostic taxa, are *Cymatiogalea messaoudensis* Jardiné et al., 1974, *Stelliferidium trifidum* (Rasul, 1974) Fensome et al., 1990, as well as *Acanthodiacrodium*? *dilatum* Molyneux in Molyneux & Rushton, 1988, *Caldariola glabra* (Martin, 1972) Molyneux in Molyneux & Rushton, 1988, *Cymatiogalea deunffii* Jardiné et al., 1974, *Stellechinatum sicaforme* Molyneux in Molyneux & Rushton, 1988 and *Vavrdovella areniga* s.l. (Vavrdová, 1973) Loeblich & Tappan, 1976 (cited in Molyneux & Rushton 1988 as '*Tetraniveum arenigum* (Vavrdová) Vavrdová 1976'). The assemblage was renamed the '*messaoudii–trifidum* assemblage' (and subsequently the '*messaoudensis–trifidum* assemblage' by Servais & Molyneux 1997) and divided into five sub-divisions by Cooper et al. (1995). The stratigraphical range of the assemblage has been correlated with the British and Baltic *Araneograptus murrayi* to *Tetragraptus phyllograptoides* graptolite zones (Molyneux et al. 2007). Reports have been published on its presence from other locations in England, Wales, Ireland, the Isle of Man, Argentina, Belgium, Germany, Spain and Turkey (Molyneux et al. 2007). Common palaeogeographical reconstructions place all these localities at high southern latitudes during the Early Ordovician (Servais et al. 2003; Molyneux et al. 2007). So far the assemblage has not been effectively reported from North Africa, although *Cymatiogalea messaoudensis* was originally described from the Algerian Sahara (Jardiné et al. 1974). Snape (1993), in an unpublished PhD thesis, recognized an association comparable to the one reported by Molyneux & Rushton (1988), marked by the co-occurrence of *Cymatiogalea deunffii*, *C. messaoudensis*, *Stelliferidium trifidum* and *Vogtlandia coalita* Martin in Dean & Martin, 1978, from surface samples of the Moroccan Lower Fezouata Formation.

The Lower and Upper Fezouata formations consist mainly of argillites and, together with the overlying Zini Sandstones and the Tachilla Formation, comprise the Outer Feijas Shale Group (Tremadocian to Darriwilian). The Fezouata formations range in age from the Tremadocian to the early Floian, with the lower formation disconformably overlying Cambrian sediments. Outcrops of the Fezouata formations are found in the Draa valley

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near the city of Zagora, in the central Anti-Atlas region, and they are also known to extend further to the southwest in the subsurface (Destombes et al. 1985). Recently the formations gained attention after the discovery of fossils with exceptional preservation (Van Roy et al. 2010) and are currently being studied under the auspices of the French 'Agence Nationale de la Recherche' (ANR) RALI (Rise of Animal Life) project. Palynomorphs from the Fezouata formations have previously been studied by Deunff (1968a, 1968b, in Destombes et al. 1985), Elaouad-Debbaj (1984, 1988) and Snape (1993).

MATERIALS AND METHODS

The AZ-1 (or Adrar Zouggar-1) borehole was drilled for petroleum exploration by Petrofina in 1963 to 1964 on Adrar Zouggar Mountain, about 300 km southwest of Zagora. It had a total depth of 3398.13 m. The interval between 624 and 1134.8 m was assigned to the Fezouata formations without discrimination between the lower and upper parts. Sixteen well cutting samples from that interval (see Table 1) were each treated partly according to standard palynomorph extraction procedures and partly using a low manipulation technique similar to that described by Butterfield & Harvey (2012). The residue was filtered at 51 µm (for the standard technique) or 63 µm (for the low manipulation technique) and 15 µm mesh sizes. Slides were produced from the 15–51 µm or 15–63 µm fractions and examined under a light microscope.

All specimens figured herein are housed at the Evo-Eco-Paleo Department of University Lille 1 (France).

RESULTS

The lowermost sample (1129.5 m) and the samples from 905 m upwards yielded no or very few, poorly preserved acritarchs (see Table 1). The seven remaining samples from 1100.65 to 930.0 m provided comparatively rich and diverse acritarch assemblages. Chitinozoans are also abundant in all levels except for the lowermost sample. Graptolite prosiculae and nema fragments occur sporadically. Scolecodonts are very rare. The residues produced by both techniques are comparable in terms of palynomorph richness.

Several, but not all species typical of the *messaoudensis–trifidum* assemblage of the Skiddaw Group are present, including four out of the seven diagnostic taxa: *Cymatiogalea deunffii* Jardiné et al., 1974 (Fig. 1B), *C. messaoudensis* Jardiné et al., 1974 (Fig. 1C), *Caldariola glabra glabra* (Martin, 1972) Molyneux in Molyneux & Rushton, 1988 (Fig. 1A) and *Stelliferidium trifidum* (Rasul, 1974) Fensome et al., 1990 (Fig. 1F). The other taxa recorded are *Cymatiogalea velifera* (Downie, 1958) Martin, 1969 (Fig. 1D), *Veryhachium lairdii* s.l. Deflandre, 1946 ex Loeblich, 1970 (Fig. 1G), *Impluviculus milonii* (Deunff, 1968b) Loeblich & Tappan, 1969 (Fig. 1E), *Vulcanisphaera frequens* Górka, 1967 (Fig. 1H) and various species of *Acanthodiacrodium*, *Actinotodissus*, *Baltisphaeridium*, *Cymatiogalea*, *Leiofusa*, *Goniosphaeridium*, *Impluviculus*?, *Leiosphaeridia*, *Micrhystridium*, *Multiplicisphaeridium*, *Polygonium*, *Priscogalea*, *Solisphaeridium*, *Stellechinatum*? and *Stelliferidium*.

The occurrence of *Cymatiogalea velifera* and the absence of *Coryphidium* and *Veryhachium trispinosum* (Eisenack, 1938) Stockmans & Willière, 1962 would be

Table 1. Occurrences of palynomorph groups and selected acritarch species in the Fezouata formations of borehole AZ-1

	Depth (m)															
	1129.5	1100.65	1077	1038	1014	999	965	930	905	874	749	734	699	669	653	634
Acritarchs	+	+	+	+	+	+	+	+	+	+				+	+	+
Chitinozoans		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Graptolites		+			+		+				+			+	+	
Scolecodonts						+					+					
Caldariola glabra glabra		+					+									
Cymatiogalea deunffii			+													
Cymatiogalea messaoudensis							+									
Cymatiogalea velifera			+	cf.			+									
Impluviculus milonii			+													
Stelliferidium trifidum		+	+	+	+	+	+	cf.								
Veryhachium lairdii s.l.			+	cf.			+									
Vulcanisphaera frequens		+	+	cf.												

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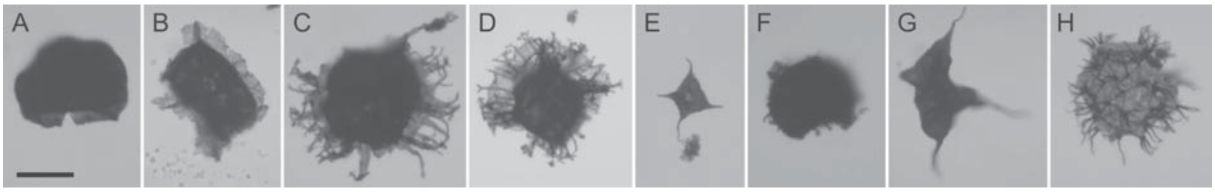

Fig. 1. Selected acritarchs from borehole AZ-1. **A**, *Caldariola glabra glabra* (Martin, 1972) Molyneux in Molyneux & Rushton, 1988, 965 m. **B**, *Cymatiogalea deunffii* Jardiné et al., 1974, 1077 m. **C**, *Cymatiogalea messaoudensis inconnexa* Servais & Molyneux, 1997, 965 m. **D**, *Cymatiogalea velifera* (Downie, 1958) Martin, 1969, 965 m. **E**, *Impluviculus milonii* (Deunff, 1968b) Loeblich & Tappan, 1969, 1077 m. **F**, *Stelliferidium trifidum* (Rasul, 1974) Fensome et al., 1990, 999 m. **G**, *Veryhachium lairdii* s.l. Deflandre, 1946 ex Loeblich, 1970, 1077 m. **H**, *Vulcanisphaera frequens* Górka, 1967, 1077 m. Scale bar = 20 μm.

consistent with an attribution to the *messaoudensis–trifidum* subassemblages 1 and 2 and thus indicate a late Tremadocian age, corresponding to the *Araneograptus murrayi* or *Hunnegraptus copiosus* graptolite zones (Molyneux et al. 2007).

DISCUSSION

The presence of the *messaoudensis–trifidum* assemblage in Morocco adds further evidence to the importance and wide distribution of this assemblage in high southern latitudes during the Early Ordovician. It allows for correlation of the studied part of the AZ-1 borehole with surface samples from the Zagora area and with other regions. The late Tremadocian age in the borehole fits well with the established age of the Lower Fezouata Formation from the outcrop areas (Destombes et al. 1985). Similarities between surface and borehole samples (Snape 1993) also support the assumption that the respective sediments are contemporaneous and palaeoecologically comparable. The full range of diversity of acritarchs and other palynomorph groups present as well as their potential for high-resolution biostratigraphy are planned to be reported in a future publication.

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Article IV

Palynomorphs of the Fezouata Formation (Lower Ordovician, Morocco): age and environmental constraints of the Fezouata Biota

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Palynomorphs of the Fezouata Formation (Lower Ordovician, Morocco): age and environmental constraints of the Fezouata Biota

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Abstract

The present study documents new palynological investigations of the Fezouata Formation from the Anti-Atlas (Morocco). Palynomorphs were extracted from samples collected from both outcrop and drill cuttings. Outcrop samples were taken near Zagora, and including those collected during excavation of stratigraphic horizons where exceptionally well-preserved fossils of the Fezouata Lagerstätte occur. Subsurface samples were taken from the AZ-1 (Adrar Zouggar Mountain) borehole, which was extracted some 300 km to the south-east of Zagora. The palynological samples yielded acritarchs, chitinozoans, scolecodonts, conodonts and fragments of graptolites. The abundance and quality of preservation of palynomorphs varies greatly, but rich and diverse assemblages were recovered from several samples. The diversity and composition of the assemblages points to an open shelf environment. Generally mixed preservation states suggest resedimentation or differential transport histories. The acritarchs can be assigned to the diagnostic *messaoudensis-trifidum* acritarch assemblage, which is typical of the Tremadocian/Floian boundary interval of the Gondwanan margin in high southern palaeolatitudes. The acritarch taxa present in some of the lower parts of the

Fezouata Formation including levels of exceptional preservation can be attributed to sub-assemblages 1-2 of the *messaoudensis-trifidum* assemblage and thus point to a late Tremadocian age of the Fezouata Lagerstätte, confirming biostratigraphic data provided by graptolites of the *Araneograptus murrayi* graptolite biozone. Chitinozoans from the Fezouata Formation are from the *E. symmetrica* and *E. brevis* biozones and include various species that are well-known from several localities on the Gondwanan margin and from other palaeocontinents (Baltica, Laurentia, and South China), demarcating broad links between those regions. The coincidence between index fossils of these three groups, hitherto not all found in the same level, suggest that the age assignments of chitinozoan biozones may be in need of revision.

Keywords

Lower Ordovician, Morocco, Fezouata Formation, acritarchs, chitinozoans

1. Introduction

The Fezouata Formation (Tremadocian to Floian in age) in the Anti-Atlas of southeastern Morocco is renowned for its fossils. Macrofossils found in this formation include graptolites, trilobites, echinoderms, brachiopods, various arthropods, hyolithids, conularids, demosponges and cephalopods (Destombes et al., 1985, and references therein; Aceñolaza et al., 1996; Chatterton and Fortey, 2008; Chauvel and Regnault, 1986; Corbacho et al., 2013; Corbacho and López-Soriano, 2012; Corbacho and Vela, 2010, 2011; Donovan and Savill, 1988; Fortey, 2009, 2011, 2012; Henry et al., 1992; Horný, 1997; Kröger and Lefebvre, 2012; Lefebvre and Botting, 2007; Mergl, 1988; Noailles et al., 2010; Rábano, 1990; Sumrall and Zamora, 2011; Valent et al., 2013; Van Roy et al., 2015b; Van Roy and Briggs, 2011; Van Roy and Tetlie, 2006; Vela and Corbacho, 2007; Vidal, 1998a, 1998b; Vinther et al., 2008). Certain layers also contain soft-bodied fossil assemblages (Van Roy et al., 2010, 2015a, 2015b; Gaines et al., 2012; Martin et al., 2015). Deposits bearing exceptional preservation are usually termed 'Lagerstätte,' or more precisely 'Konservat-Lagerstätte' (Seilacher, 1970). The mode of preservation of the Fezouata Lagerstätte has not yet been precisely determined, owing to high degree of weathering of exposures in the Zagora area, but has been compared to Burgess Shale-type deposits characteristic of the Cambrian (Van Roy et al., 2010, 2015a). The Fezouata Lagerstätte is remarkable as the only Lower Ordovician Konservat-Lagerstätte known so far, and possibly the only post-Cambrian Lagerstätte that has been conserved via the Burgess Shale-type taphonomic pathway (Butterfield, 1995; Gaines et al., 2008; Gaines, 2014). Moreover, it contains a biota with elements typical of Cambrian Burgess Shale-type faunas, as well as more ‘modern’ groups typical of the Palaeozoic Evolutionary Fauna *sensu* Sepkoski (1981, 1984) (Van Roy et al., 2015a). Van Roy et al. (2010, p. 215) assumed that exceptional preservation occurred “from the top of the Lower Fezouata Formation through to the top of the Upper Fezouata Formation,” but Martin et al. (2015) determined that the exceptional preservation is limited to certain layers within a *ca.* 80 m thick interval, near the top of the lower (Tremadocian) part of the Formation.

Palynomorphs, i.e. organic-walled microfossils, have been described previously from the Fezouata Formation. These first reports primarily concerned acritarchs and chitinozoans. Acritarchs are by definition of unknown origin (Evitt, 1963), but commonly are interpreted as cysts of unicellular algae. Chitinozoans are probably eggs of an unknown animal (Paris and Nõlvak, 1999), which occupied the mixed layer of early Palaeozoic oceans (Vandenbroucke et al., 2010a).

Acritarchs from the Fezouata Formation were first studied by Deunff (1968a,b; Deunff *in* Destombes et al., 1985), who provided the first description of the now widely known genus *Arbusculidium*, and the first description of *Impluviculus milonii* (originally described as *Veryhachium miloni*) from Fezouata material. Subsequently, Elaouad-Debbaj (1984, 1988) studied acritarchs and chitinozoans from the lower part of the Fezouata Formation and chitinozoans from its upper part. She described the chitinozoan *Lagenochitina destombesi* (Elaouad-Debbaj, 1988), which was later used by Paris (1990) as the index species for his lowermost chitinozoan biozone. In an unpublished PhD thesis, Snape (1993) identified a large number of palynomorph species and several assemblages in the Fezouata Formation, albeit from a small number of samples and with poor stratigraphic constraints. He compared one of his acritarch assemblages to the ‘Watch Hill assemblage,’ which is now known as the *messaoudensis-trifidum* assemblage (Molyneux and Rushton, 1988; Servais and Molyneux, 1997). More recently, Nowak et al. (2015) provided a preliminary report on the *messaoudensis-trifidum* assemblage from borehole AZ-1 (Adrar Zouggar Mountain), in stratigraphic levels assigned to the Fezouata Formation.

The present study is part of a concerted effort to re-evaluate the Fezouata Formation in a new level of detail, using lithostratigraphy, biostratigraphy, chemostratigraphy, palaeoecology, and to constrain the stratigraphic position of intervals containing exceptional preservation (Martin et al., 2015). We here report on the palynology of the intervals bearing the Fezouata Lagerstätte, specifically acritarchs and chitinozoans, using material collected from outcrops of

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the Fezouata Formation from the part of the succession that has yielded exceptionally well-preserved fossils, as well as that collected from borehole AZ-1. Detailed logging and field observations allow us to integrate and constrain the palynological samples in a highly resolved, integrated stratigraphic framework.

2. Geological setting

During the Early Palaeozoic, Africa was a part of the supercontinent Gondwana, and Morocco was located close to the South Pole. Around the Cambrian/Ordovician boundary, the Rheic Ocean opened between Avalonia and Gondwana, and Avalonia began moving northwards (Cocks and Fortey, 2009). The Lower Ordovician (Tremadocian to Floian) Fezouata Formation was deposited in an epicontental sea on this newly rifted and subsiding margin of Gondwana. The formation is a succession of mudstones with quartz-rich siltstones and sandstones reaching a total thickness of about 900 m (Destombes et al. 1985, Martin et al. 2015; Vaucher et al. *this volume*). It has a wide distribution in the Anti-Atlas, with the most prominent outcrops in the Draa Valley around Zagora (Destombes et al., 1985). Historically, it has been divided into a lower (Tremadocian) and an upper (Floian) part, but the distinctive horizon that defines the boundary is often absent, as for example in the Zagora area (Destombes, 1962). The Fezouata Formation unconformably overlies sediments of the Tabanite Group (Guzhangian, Cambrian Series 3; Geyer and Landing, 2006) and is locally overlain by the sandstones of the Zini Formation (upper Floian). The Fezouata and Zini formations are both capped by an unconformity on which the Tachilla Formation (Darriwillian) was deposited. Together, the Fezouata, Zini, and Tachilla formations constitute the Outer Feijas Shale Group (Choubert, 1942). Both the Fezouata and the Zini formations were deposited under storm- and wave-dominance, but modulated by tidal action (Vaucher and Pittet, 2014; Vaucher et al. 2015, *this volume*).

3. Materials and methods

Outcrop samples were collected from various localities from the Ternata plain near Zagora (Fig. 1) during several field campaigns between 2012 and 2014. The respective sample levels were correlated using a detailed lithostratigraphical compound log, which was produced at the same time. The detailed log showing the position of the palynological samples (Fig. 2) corresponds to the interval spanning 240-330 m above the base of the Fezouata Formation in

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the compound log of the Lower Ordovician deposits (Vaucher et al. *this volume*, their fig. 2). This includes most of the two stratigraphic intervals yielding exceptionally preserved fossils (Martin et al., 2015). These two intervals are located below and above an easily recognizable, greyish blue, clay-dominated, *ca.* 20 m-thick interval (43 to 62 m in Fig. 2) that serves as a stratigraphic marker horizon to correlate the logs and position the various samples on the compound log. At Tizig Zaouine (30°31'04"N, 5°49'19"W), 26 samples (with prefix TZ-Paly) were taken that represent all but the topmost part of the stratigraphic interval bearing exceptionally preserved fossils. 17 samples (prefix FZ1) were taken during an excavation at Bou Izargane (30°29'59"N, 5°51'00"W). These samples are the product of a high-resolution sampling in three quarries, representing a total thickness of about four metres. Samples from each quarry are grouped together in Fig. 2. Another five samples were collected at Tamroute (30°29'47"N, 5°53'15"W) (samples TVDB 12-041 to -045), and one sample each at Oued Beni Zoli (30°28'54"N, 5°52'03"W) (sample TVDB 12-046) and Oued Ouaoufraou (30°31'15"N, 5°56'44"W) (sample HN-FF05).

Surface-collected samples from Tizig Zaouine, Tamroute, Oued Beni Zoli, and Oued Ouaoufraou are characterized by deep weathering to a buff yellow color, as is typical of near-surface Fezouata material (e.g. Van Roy et al., 2015a). By comparison, excavations at Bou Izargane reached less altered dark grey mudrocks from which the FZ1 samples were drawn. While samples from Bou Izargane have clearly been affected by weathering processes, as indicated by iron oxide staining along joints and cracks, the retention of some fraction of early diagenetic pyrite in most samples demonstrates that they were less affected by oxidative weathering than the other outcrop samples.

The borehole samples are cuttings from the AZ-1 borehole, which was drilled in 1963-64 at Adrar Zouggar Mountain, approximately 300 km southwest of Zagora. The drilling was executed by the petroleum company Petrofina for oil exploration, and attained a maximum depth of 3398.13 m. The interval between 624 m and 1134.8 m depth was assigned to the Fezouata Formation based on lithology. This interval is overlain by 144 m of the Zini Formation and subsequently by the Tachilla Formation, according to the drill log.

The samples were processed by both standard palynological techniques and by using a low-manipulation technique employing hydrofluoric acid (similar to the method described by Butterfield and Harvey, 2012) with the objective to recover ‘Small Carbonaceous Fossils’ (SCFs). These are fragile, uncommon palynomorphs that are normally destroyed during standard processing, used to recover acritarchs and chitinozoans. The standard palynological technique involved treatment by hydrofluoric and hot hydrochloric acids, followed by centrifugation. Samples from Tizig Zaouine and Bou Izargane were treated using only the low-manipulation approach. Residues from the acid treatment were filtered at 51 or 63 µm (63 in the case of low-manipulation treatment of samples from the borehole, 51 in all other cases) and subsequently at 15 µm.

Microfossils were hand-picked from the larger fraction (>51 or 63 µm), then gold-coated and studied by Scanning Electron Microscopy (SEM). Palynological slides were produced from the 15 to 51 or 63 µm fraction. Images of acritarchs in the slides were taken using a Zeiss AxioCam ERc5s mounted on a Zeiss Axio Imager A2 transmitted light-microscope. All processed samples, slides and SEM preparations are stored in the collections of the Evo-Eco-Paleo department of the University of Lille, France.

4. **Distribution of microfossils**

4.1. Microfossils in the outcrops

In the lower part of the outcrop section at Tizig Zaouine (see Fig. 2), acritarchs and chitinozoans are present in varying abundance and diversity, and with poor to moderate preservation. Sample 15 and all samples above number 16 are devoid of organic matter, including palynomorphs. In contrast, all but four samples of the TZ-Paly batch – which were processed with a low-manipulation technique – yielded conodonts. The conodonts from the outcrop (i.e., at Tizig Zaouine and Bou Izargane) and the borehole are the focus of a study by Lehnert et al. (*this volume*).

Samples from the excavation at Bou Izargane are rich in well-preserved acritarchs and chitinozoans, including taxa not otherwise recorded in this area. The composition of their respective assemblages varies mostly in relative quantities.

Of five samples from Tamroute (TVDB 12-041 to -045), three yielded acritarchs and chitinozoans (and graptolite fragments), but chitinozoans are abundant and identifiable in only one sample (TVDB 12-041). The other two samples are barren, despite their stratigraphic position, which is approximately equivalent to two of the fossiliferous samples.

The sample from Oued Beni Zoli (TVDB 12-046) is rich in acritarchs and chitinozoans, but diversity is limited. This sample corresponds to the palynomorph-barren upper part of the Tizig Zaouine section. It is stratigraphically the highest sample yielding palynomorphs in the studied interval.

A sample from Oued Ouaoufraou (HN-FF05) proved to be barren of palynomorphs. Most samples yielding acritarchs and chitinozoans also contained graptolite fragments. Despite the use of the low-manipulation technique to recover Small Carbonaceous Fossils, such microfossils have not been recorded from our samples.

4.2. Microfossils in borehole AZ-1

In borehole AZ-1, most organic matter takes the form of indistinct opaque organic matter. Abundant, identifiable acritarchs are limited to the lower part of the Fezouata Formation, i.e. between 965 and 1100.65 m depth (34.15-169.8 m above the base of the Fezouata Formation; Fig. 3). A few, degraded acritarchs were also found in other samples, but samples from the interval between 699 and 749 m are barren. Complete specimens of chitinozoans are present from the top down to 965 m. Fragments occur in all samples except the lowermost one. Additionally, a few samples yielded graptolite fragments, conodonts and scolecodonts. Preliminary information on acritarchs from borehole AZ-1 was provided by Nowak et al. (2015). For a discussion of the conodonts, see Lehnert et al. (*this volume*).

5. **Acritarchs**

The most common acritarch species in the studied outcrops (see Fig. 2) are *Stelliferidium trifidum* (Rasul 1974) Fensome et al. 1990 (Fig. 4N), *Caldariola glabra glabra* (Martin 1972) Molyneux *in* Molyneux and Rushton 1988 (Fig. 4B), *Cymatiogalea deunffii* Jardiné et al. 1974 (Fig. 4C), *C. messaoudensis* Jardinè et al. 1974 with its two varieties *C. messaoudensis* var. *messaoudensis* Jardinè et al. 1974 (Fig. 4F) and *C. messaoudensis* var. *inconnexa* Servais and Molyneux 1997 (Fig. 4E), and *Vogtlandia*? sp. (Fig. 4T). Frequently, when *C. deunffii* and *C. messaoudensis* are present, specimens that appear to represent a transitional state between the two are also observed (Fig. 4D), similar to specimens described by Servais and Molyneux (1997). Sphaeromorph acritarchs are omnipresent. Most of the latter would be assignable to the genus *Leiosphaeridia*, or defy identification because of poor preservation. They appear in all sizes (up to ~100 µm in diameter) and they are the most common type of acritarchs in the >51 µm size fraction. The following species are also fairly abundant where present: *Impluviculus milonii* (Deunff 1968a) Loeblich and Tappan 1969 (Fig. 4G), *Goniosphaeridium tuberatum* (Downie 1958) Welsch 1986 (Fig. 4H), *Multiplicisphaeridium* cf. *inconstans* Cramer and Diez 1977 (Fig. 4I), *Polygonium gracile* Vavrdová 1966 *emend.* Jacobson and Achab 1985 (Fig. 4K), *Tectitheca*? sp. (Fig. 4S), *Vavrdovella areniga* (Vavrdová 1973) Loeblich and Tappan 1976 (Fig. 4O), *Veryhachium lairdii* Deflandre 1946 *ex* Loeblich 1970 (Fig. 4P), unidentified *Stelliferidium* and at least one species of *Priscotheca* (Fig. 4Q).

Stellechinatum sicaforme Molyneux *in* Molyneux and Rushton 1988 (Fig. 4M) occurs frequently, but in low abundance. Rare constituents are *Acanthodiacrodium*? *dilatum* Molyneux *in* Molyneux and Rushton 1988 (Fig. 4A), *Cristallinium cambriense* (Slavíková 1968) Vanguestaine 1978, *Leiofusa simplex* (Combaz 1967) Martin 1975, *Pirea ornata* (Burmann 1970) Eisenack et al. 1976 (Fig. 4J), *Rhopaliophora palmata* (Combaz and Péniguel 1972) *emend.* Playford and Martin 1984 (Fig. 4L), *Stellechinatum uncinatum* (Downie 1958) Molyneux 1987, *Striatotheca* sp. (Fig. 4R), *Timofeevia* sp, and an unidentified species of *Peteinosphaeridium*?, resembling specimens previously reported from Argentina as "*Peteinosphaeridium* cf. *P. bergstroemii* Staplin, Jansonius and Pocock 1965" by Achab et al. (2006; pl. II, figs 12, 13). In addition, several unidentified species of *Acanthodiacrodium*, *Baltisphaeridium*, *Comasphaeridium*, *Goniosphaeridium*, *Lophosphaeridium*, *Polygonium* and *Micrhystridium* occur sporadically in the studied samples.

The assemblage of borehole AZ-1 is largely comparable (see Nowak et al., 2015). Apart from the rare species, *M.* cf. *inconstans* and *V. areniga* are not recorded from the borehole. *Stellechinatum sicaforme* is present in AZ-1, but was not reported by Nowak et al. (2015).

The acritarchs recovered from the Fezouata Formation include each of the typical elements of the *messaoudensis-trifidum* assemblage. This assemblage was originally described as the 'Watch Hill assemblage' by Molyneux and Rushton (1988) from the Lake District in northern England. It was named the '*trifidum* assemblage' by Fortey et al. (1991), the '*messaoudii-trifidum* assemblage' by Cooper et al. (1995) and subsequently corrected into the '*messaoudensis-trifidum* assemblage' by Servais and Molyneux (1997). The seven diagnostic species (or species groups) of the assemblage are *Acanthodiacrodium*? *dilatum*, *Caldariola glabra* s.l., *Cymatiogalea deunffii*, *C. messaoudensis*, *Stellechinatum sicaforme* s.l., *Stelliferidium trifidum* and *Vavrdovella areniga*. Each is present in the Fezouata Formation, although *A.*? *dilatum* is rare in the outcrop samples and is not observed in borehole samples. Similarly, *V. areniga* is not present in borehole samples.

5.1. Acritarch palaeobiogeography

After its original description from the English Lake District, the *messaoudensis-trifidum* assemblage was reported from other locations in England, Wales, Ireland, Belgium, Turkey, Argentina, Germany, the Czech Republic, Spain and Morocco (Snape, 1993; Molyneux et al., 2007 and references therein; Rubinstein et al., 2007; Aráoz, 2009; de la Puente and Rubinstein, 2009; Toro et al., 2010; Nowak et al., 2015). Aside from the Argentinean occurences, these localities correspond to positions at high southern latitudes during the Early

Ordovician according to current palaeogeographical reconstructions (Fig. 5A) (Torsvik and Cocks, 2013). Individual taxa of the *messaoudensis-trifidum* assemblage have also been reported from Baltica and South China (Molyneux et al., 2007 and references therein). Given that the reconstructed position of North Africa for the Early Ordovician is relatively close to other localities that yielded the *messaoudensis-trifidum* assemblage, its presence in Morocco is expected, but for a long time was overlooked. Vecoli and Le Herissé (2004) stated that the *messaoudensis-trifidum* assemblage had not been reported from North Africa and suggested the reason might be a lack of late Tremadocian sediments, unaware that Snape (1993) had in fact noted similarities between the ‘Watch Hill assemblage’ and one assemblage from the Fezouata Formation in an unpublished PhD thesis.

The *messaoudensis-trifidum* assemblage was regarded as a part of the ‘peri-Gondwana’ ‘Mediterranean’ or ‘cold-water’ province (see Servais et al., 2003 for a discussion), which was originally defined by the presence of *Arbusculidium filamentosum*, *Coryphidium* and *Striatotheca* by Li (1987) in the Floian, in contrast to the ‘warm-water’ province marked by the genera *Aryballomorpha*, *Athabascaella* and *Lua* (Volkova, 1997). It is now clear that provincialism is not simply related to cold and warm-water environments. Nevertheless, the *messaoudensis-trifidum* assemblage is typical of the margin of Gondwana at high southern latitudes. The reader is referred to Molyneux et al. (2013) for a detailed review of acritarch palaeobiogeography in the Early Ordovician.

5.2. Acritarch biostratigraphy

In general, the *messaoudensis-trifidum* assemblage ranges from the upper Tremadocian *Araneograptus murrayi* (British or Baltoscandic) to the lower Floian *Tetragraptus phyllograptoides* graptolite biozone (Molyneux et al., 2007). Higher biostratigraphic resolution is provided by the definition of five sub-assemblages by Cooper et al. (1995) (Fig. 6). The Tremadocian-Floian boundary presumably coincides with the boundary between sub-assemblages 4 and 5.

The assemblage recovered from the Fezouata Formation, both in the outcrop area near Zagora and in the borehole ~300 km southwest, contains none of the typical elements of assemblages above sub-assemblage 2, such as *Coryphidium* or triangular forms of *Veryhachium*. The presence of *Rhopaliophora palmata* in sample FZ1 13-16 provides an upper limit for the lower boundary of sub-assemblage 2. Because it is a rare species, its absence from lower strata is not diagnostic. The acritarchs of the Fezouata Formation therefore most probably represent sub-assemblage 2 and possibly sub-assemblage 1. The Fezouata assemblage as a whole is most comparable with the *messaoudensis-trifidum* assemblage from northern

Germany (Servais and Molyneux, 1997), also attributed to the upper Tremadocian. The sub-assemblages 1 and 2 of the *messaoudensis-trifidum* assemblage have been correlated with the *A. murrayi* and *Hunnegraptus copiosus* graptolite zones (Cooper et al., 1995), also indicating that the Moroccan assemblage corresponds to the upper Tremadocian. The acritarch data are, thus, fully consistent with that provided by graptolite collections from outcrop, which indicate the *A. murrayi* graptolite biozone for the studied strata, with an uncertain boundary to the following *H. copiosus* zone in the uppermost part (Martin et al., 2015).

6. **Chitinozoans**

The chitinozoan assemblages from both the outcrop (Figs. 2, 7) and borehole samples (Figs. 3, 8) are dominated by small species: *Eremochitina brevis* Benoît and Taugourdeau, 1961 (Figs. 8E,F), *Euconochitina* spp. and *Euconochitina*? sp. (Figs. 8D) in the borehole; *Euconochitina* spp., *Desmochitina minor* Eisenack, 1931 *s.l.* (Figs. 7A,E) and *Desmochitina* sp. (Fig. 7B) in outcrop. *Euconochitina* specimens show a range of morphological variation that encompasses *Eu. paschaensis* de la Puente and Rubinstein, 2009 (Figs. 7F, 8A,G) and *Eu. symmetrica* (Taugourdeau and de Jekhowsky, 1960) (Figs. 7G, 8B,C). The latter is distinguished from the former by a flaring collarette, a character that is not always preserved or easy to recognise. Because specimens in our material assignable to either of these two species seem to be end-members of a single population that also contains a morphological continuum of intermediary specimens, we here use a combined *Eu. paschaensis-symmetrica* group. *Euconochitina*? sp. in the present study closely resembles specimens from the Suri Formation in northwestern Argentina, figured by Achab et al. (2006; pl. V, figs 4, 9, 11, 12) as "*Conochitina* sp.".

Eremochitina aff. *baculata* Taugourdeau and de Jekhowsky, 1960 (Fig. 7K) dominates the assemblage in a single sample, FZ1 13-16, which yields one of the richest assemblages recovered in this study. This species is conspecific with specimens from the Leetse Formation at Tallinn, Estonia, figured by Nõlvak and Grahn (1993; pl. V, fig. E) as "*Eremochitina* sp." and by Hints and Nõlvak (2006; pl. IV, figs. 1-4, 10) as "*Eremochitina* sp. A, aff. *baculata*". *Lagenochitina esthonica* Eisenack, 1955 (Fig. 7Q) is very abundant in samples FZ1 341-345 and 349-350.
Er. brevis is represented in the outcrop by a few specimens in sample TVDB 12-046 (Fig. 7M), and perhaps by fragments in lower strata. *Euconochitina*? sp. has a limited occurrence in some of the richer samples from Bou Izargane (Fig. 7H), which also yielded *Cyathochitina*

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aff. *campanulaeformis* (Eisenack, 1931) Eisenack, 1955 (Fig. 7C), *Cyathochitina* sp. (Fig. 7D), *Lagenochitina* cf. *obeligis* Paris, 1981 (Fig. 7O) and *Rhabdochitina* cf. *magna* Eisenack, 1931 (the latter also occurs in borehole samples, see Fig. 8I). The outcrop samples furthermore produced *Eremochitina* cf. *mucronata* Taugourdeau and de Jekhowsky, 1960 (Fig. 7N), which is smaller than typical for the species, *Clavachitina*? sp. (Fig. 7I) and *Rhabdochitina gracilis* Eisenack, 1962 (Fig. 7J). *Desmochitina* is absent in the borehole samples. Both the borehole and the outcrop samples contained poorly preserved specimens of *Eremochitina* that might pertain to *Er. baculata* (Figs. 7L, 8H), unidentified species of *Lagenochitina* (Fig. 8J), and a few specimens resembling *L. destombesi* Elaouad-Debbaj, 1988, but differing in size or surface structure (Figs. 7P, 8K).

6.1. Chitinozoan palaeobiogeography

The chitinozoans identified in the Fezouata Formation show connections to assemblages from the subsurface of the neighbouring Algerian Sahara (Taugourdeau and de Jekhowsky, 1960; Benoît and Taugourdeau, 1961; Oulebsir and Paris, 1995), but also to the Lower Ordovician of other locations in peri-Gondwana (Czech Republic: Paris and Mergl, 1984; Fatka, 1993, 1999; Belgium: Martin, 1969; Samuelsson and Verniers, 2000; France: Rauscher, 1968; Paris, 1981; Holy Cross Mountains, Poland: Chlebowski and Szaniawski, 1974; Island of Rügen, Germany: Samuelsson, 1999, Samuelsson et al., 2000; Portugal: Paris, 1981) ‘western’ Gondwana (Argentina: Ottone et al., 1992; Achab et al., 2006; de la Puente, 2010; de la Puente and Rubinstein, 2009, 2013; Toro et al. 2010; Bolivia: Heuse et al., 1999), Baltica (Estonia: Grahn, 1984; Hints and Nõlvak, 2006; Norway: Owen et al., 1990; Sweden: Grahn, 1980; Grahn and Nõlvak, 2007), Laurentia (Quebec: Achab, 1980, 1986; Western Newfoundland: Batten, 2000; Spitsbergen: Bockelie, 1980) and South China (Hunan Province: Wang et al., 2013; Hubei Province: Chen et al., 2008, 2009; Yunnan Province: Gao, 1986) (Fig. 5B). In terms of numbers of common species, the greatest agreement is with the Estonian assemblage, South China and Western Newfoundland.

Vandenbroucke et al. (2010a, 2010b, 2013) showed that the palaeogeographic distribution of Late Ordovician chitinozoan assemblages reflects palaeoclimatic belts. Except for *Eremochitina brevis*, which is restricted to peri-Gondwana, and *Er.* aff. *baculata*, which until now was only known from Estonia, the chitinozoans present in the Fezouata Formation seem to be characterized by widespread distribution. Pending more complete documentation and analyses of full assemblages through discrete timeslices, the Early Ordovician chitinozoan assemblages do not appear to demonstrate latitudinal constraints.

6.2. Chitinozoan biostratigraphy

A chitinozoan biozonation for Gondwana has been proposed by Paris (1990) and was subsequently calibrated against the current chronostratigraphic stages (Webby et al., 2004). Therein, the total range of *Lagenochitina destombesi* defines the lowermost biozone, representing the upper lower to lower upper Tremadocian. This was based on the discovery of the species in the Fezouata Formation by Elaouad-Debbaj (1988). However, the lower and upper boundaries of its range have not been established. The *L. destombesi* zone was also adopted as the lowermost chitinozoan biozone in Baltoscandia (Nõlvak, 1999; Nõlvak et al., 2006) and South China (Chen et al., 2009). In Gondwana, it is followed in order by the *Lagenochitina conifundus* zone, the *Euconochitina symmetrica* zone, the *Eremochitina baculata* zone and the *Er. brevis* zone. The *symmetrica* to *brevis* zones were assigned to the Floian by Webby et al. (2004).

A major constituent of the chitinozoan assemblages in our study is the *Eu. paschaensis-symmetrica* group. According to de la Puente and Rubinstein (2009), *Eu. paschaensis* represents the *conifundus* zone in Argentina. In our samples, the range of specimens assignable to *Eu. paschaensis* overlaps with that of *L.* cf. *destombesi*. Furthermore, *Eu. paschaensis* shows seamless transitions within populations to *Eu. symmetrica*, the index species of the biozone that follows the *conifundus* zone in ‘northern’ Gondwana. In the same samples, *Eremochitina* aff. *baculata*, a species which is close to *Er. baculata* is abundantly present, although no unambiguous examples of actual *Er. baculata* were recovered. A few specimens from the uppermost outcrop sample bearing palynomorphs are assignable to *Er. brevis*, which traditionally is taken to indicate a (late) Floian age, but still coincides with acritarchs of the *messaoudensis-trifidum* assemblage and the graptolite *A. murrayi*. In the borehole, *Er. brevis* also coincides with essentially the same acritarch assemblage, although not at its first downhole appearance, which would be more explicit. It is also interesting to note that in the borehole, the intervals with abundant acritarchs and chitinozoans respectively are hardly overlapping (and are most likely extended downwards due to mixing with cuttings from overlying strata in the drilling fluid), suggesting that, if the acritarch assemblages are coeval, the chitinozoans from the surface are probably for the most part older than those from the borehole.

Our data indicate an overlap between the ranges of *Eu. symmetrica* (as part of the *paschaensis-symmetrica* group) and *Er. brevis* in the upper part of the sections investigated (in the borehole, and in sample TVDB 12-046). In addition, if the tentative identifications of *Er. brevis* in the lower part of the outcrop section (TZ-Paly 10) can be confirmed, this overlap

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would span an even larger portion of the stratigraphic section. The overlapping ranges of these index fossils necessitate a redefinition of their respective biozones from total-range zones to partial-range zones (i.e., biozones defined to span the interval from the FAD of the index fossil to the FAD of the index fossil of the overlying biozone), which has become the standard way of defining chitinozoan biozones (Vandenbroucke, 2008; Verniers et al., 1995). Awaiting a formal redefinition of these biozones, we have here established a local biozonation using the partial range zones for the *Eu. paschaensis-symmetrica* group and *Er. brevis*.

If we follow the calibrations in Webby et al. (2004), the chitinozoan ranges and biozones would point to a Floian age of the Fezouata Lagerstätte. However, this would be at odds with acritarch and graptolite biostratigraphy, which both clearly suggest a Tremadocian age (Martin et al., 2015). This example suggests that the chronostratigraphy and age assignments of chitinozoan biozones are in need of revision (following a global survey of the co-occurrence of the index taxa and those of other fossil groups).

7. **Preservation, taphonomy and palaeoenvironment**

The acritarchs and chitinozoans of the Fezouata Formation show a mixture of preservational states with well-preserved and badly degraded specimens in the same samples. This pattern may point to exhumation and resedimentation or differential transport histories of individual fossils within single samples. This is consistent with regular disturbance by storms, an observation consistent with sedimentologic interpretations of the Fezouata (Martin et al., 2015; Vaucher et al. *this volume*). The preservation also usually shows a variation between flattened and three-dimensional individuals within individual samples. In chitinozoans, the chamber often remains partially inflated, while the neck is compressed (e.g. Figs. 7D,O, 8F). In acritarchs, three-dimensionality is mostly retained in vesicles with a thick wall, and in larger (>50 µm) sphaeromorphs. Three-dimensional specimens are not equally distributed and are most common in samples from Bou Izargane and in borehole samples corresponding to 734, 905 and 940 m depths. This suggests temporal changes in the taphonomic histories of at least a part of the organic-walled microfossils, which might be related to the exceptional preservation of macrofossils in the same layers at Bou Izargane.

The surface and eventual ornamentation of chitinozoans is often abraded, although the taxon *Desmochitina minor* represents a notable exception in that it usually retains a granular surface to some degree. Some specimens of *Lagenochitina* also show a structured surface. The abrasion can be attributed to transport before burial and possibly, in some cases, resedimentation.

Chitinozoan vesicle walls are often perforated by microborings (Fig. 7D), sometimes heavily. Such microborings have been attributed to bacteria and fungi (Eisenack, 1973; Grahn, 1981). They might represent parasites on the living organism or digestion of shed shells (Wrona, 1980; Grahn, 1981). Vesicles with a high density of microborings are typically poorly preserved (abraded and fragmented), implying an extended period of exposure. Acritarchs rarely show microborings.

The chitinozoan assemblages are dominated by small species, while larger forms are rare except for samples FZ1 13-16 and TZ-Paly 1, 2 and 13. The sample FZ1 13-16 is particularly interesting, as it is directly adjacent to FZ1 19-20. Both samples yielded extremely abundant and well-preserved chitinozoans of mostly the same species (a few more in the latter case), but while the lower sample is dominated by the particularly large *Er.* aff. *baculata* and *Rhabdochitina gracilis*, these are rare in the overlying sample, and mostly represented by fragments. Such fragments of large tubular chitinozoans are relatively common in other samples too, while complete specimens are overall rare. This points to size sorting and possibly a higher tendency of long and narrow forms to break during transport (although the breaking of large vesicles can also partly be explained by a size dependant higher probability of fragmentation by the formation of cracks in the host rock and during the maceration process). The fact that chains of *D. minor* and *Eu. paschaensis* are observed (Figs. 7G, 8E), but none that include more than two individuals, is consistent with this pattern.

The best preserved acritarch assemblages from both outcrop and borehole samples are dominated by galeate and polygonomorph species, and generally show a rather high diversity of spiny forms. According to studies on the distribution of acritarch groups in relation to the distance from the shoreline, this indicates an open shelf environment, a fair distance away from the shore and not shallow (e.g. Li et al., 2004; Lei et al., 2012). This is in agreement with an offshore environmental setting close to storm wave-base interpreted by Martin et al. (2015) for the same stratigraphic interval of the Fezouata Formation. Nearshore assemblages are typically less diverse and dominated by smooth-walled forms and species of *Micrhystridium* with short spines (e.g. Stricanne et al., 2004).

Comparison of assemblages from Bou Izargane (FZ1) with those from approximately coeval horizons at Tizig Zaouine (TZ-Paly 5-7; see Fig. 2) suggests a pronounced effect of oxidative weathering on the organic palynomorph remains. The dark grey FZ1 samples yield the most diverse and abundant assemblages recovered from surface materials, and include the best states of preservation (Fig. 4, 7), while more intensely weathered samples from coeval strata at Tizig Zaouine yield primarily fragmented material with substantially reduced diversity of identifiable forms. These findings underscore the susceptibility of thin organic remains to degradation during oxidative weathering. They also support previous observations that the taphonomic expression of the soft-bodied macrofossils of the Fezouata has been profoundly affected by oxidative weathering (Van Roy et al., 2010, 2015a), as also observed in the early Cambrian Chengjiang biota (Forchielli et al., 2014).

While the presence/absence patterns of palynomorphs in the outcrop samples can mostly be attributed to surface weathering, the absence of palynomorphs at certain levels in the borehole cannot be explained as such, but the presence of opaque organic matter suggests the influence of alteration. The unequal distribution of acritarchs and chitinozoans means that either alteration affected the two groups differently, or that this pattern reflects original ecological and/or taphonomic effects. The differences in preservation are not related to conspicuous variations in lithology. Furthermore, the pattern is different between the Zagora and Adrar Zouggar areas, as the palynomorph assemblages in the borehole appear to be more stratigraphically restricted than those from the studied outcrops. Specifically, no acritarchs that are evidently younger and no chitinozoans that are evidently older than the studied outcrop interval were found in the borehole, but younger acritarch assemblages have been reported from the upper Fezouata Formation (Deunff, 1968b; Snape, 1993), and older chitinozoans from the lower (Elaouad-Debbaj, 1988).

8. Conclusions

The present palynological study focuses on the Fezouata Lagerstätte, i.e. the part of the Fezouata Formation bearing exceptionally preserved fossils. Two palynological techniques were used (a standard and a low-manipulation technique) which have yielded abundant and diverse acritarchs and chitinozoans, but no ‘Small Carbonaceous Fossils.’

The presence of the *messaoudensis-trifidum* acritarch assemblage in this interval is confirmed. Acritarch assemblages from the outcrop and the borehole AZ-1 are overall comparable. They correspond to sub-assemblages 1?/2 of the *messaoudensis-trifidum* assemblage, indicating a late Tremadocian age, which is in accordance with a previous assignment of the *A. murrayi* graptolite biozone to this interval. The occurrence of the *messaoudensis-trifidum* assemblage in the Early Ordovician of Morocco provides further evidence for its biogeographical distribution on the margin of Gondwana at high latitudes (peri-Gondwana).

The chitinozoans of the Fezouata Formation show connections to other sites in peri-Gondwana, but also to western Gondwana, Baltica, Laurentia and South China. The chitinozoans from the levels attributed clearly to the late Tremadocian include the index species of the *Euconochitina symmetrica* and *Eremochitina brevis* biozones, which are so far considered to be indicative of the early and late Floian. These results indicate that the calibration between the chronostratigraphic stages and the chitinozoan biozonation for the Gondwanan margin may require revision.

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Figures

Fig. 1. Map of sampling sites. Modified from supplementary information S1 of Van Roy et al. (2010). A) Ordovician outcrop areas around Zagora with marked sampled localities. B) section of the map of Morocco and adjacent areas showing the distribution of Ordovician outcrops and positions of Zagora and the Adrar Zouggar Mountain.

Fig. 2. Lithostratigraphy of the Fezouata Lagerstätte, positions of palynological samples, and ranges of selected acritarch and chitinozoan taxa. Lithostratigraphy of the Tizig Zaouine section, north of Zagora (see also Fig. 1). Graptolite biozonation according to Martin et al. (2015). *H. c.* = *Hunnegraptus copiosus*. Stage slice according to Bergström et al. (2009).

Fig. 3. Ranges of chitinozoan taxa in borehole AZ-1. Position of the *messaoudensis-trifidum* assemblage according to Nowak et al. (2015). *p.-s.* = *paschaensis-symmetrica*. The actual boundary between the *paschaensis-symmetrica* and *brevis* zones may lie higher, since the First Appearance Datum of *Eremochitina brevis* cannot be determined with certainty from the well cuttings due to probable mixing with overlying strata.

Fig. 4. Selected acritarchs from the Fezouata Formation near Zagora. Scale bar = 20 µm. Sample numbers are followed by slide numbers (in parentheses; s = standard maceration, lm = low-manipulation treatment) and England Finder Graticule coordinates. A) *Acanthodiacrodium*? *dilatum* Molyneux *in* Molyneux and Rushton, 1988; FZ1 3-4 (lm1), T51/3. B) *Caldariola glabra glabra* (Martin, 1972) Molyneux *in* Molyneux and Rushton, 1988; FZ1 4-5 (lm1), T37. C) *Cymatiogalea deunffii* Jardiné et al., 1974; FZ1 4-5 (lm1), N31/2. D) transient between *Cymatiogalea deunffii* (Downie, 1958) Martin, 1969 and *Cymatiogalea messaoudensis* Jardiné et al., 1974; TVDB 12-044 (s2), X33/2. E) *Cymatiogalea messaoudensis* Jardiné et al., 1974 var. *inconnexa* Servais and Molyneux, 1997; FZ1 13-16 (lm1), F51/3. F) *Cymatiogalea messaoudensis* var. *messaoudensis* Jardiné et al., 1974; FZ1 66-67 (lm1), G39/4. G) *Impluviculus milonii* (Deunff 1968a) Loeblich and Tappan 1969; TZ-Paly 1 (lm1), H42. H) *Goniosphaeridium tuberatum* (Downie 1958) Welsch 1986; FZ1 4-5 (lm1), V42/3. I) *Multiplicisphaeridium* cf. *inconstans* Cramer and Diez 1977; FZ1 66-67 (lm1), G43. J) *Pirea ornata* (Burmann 1970) Eisenack et al. 1976; FZ1 31-32 (lm1), P49/4. K) *Polygonium gracile* Vavrdová, 1966; FZ1 66-67 (1), P46. L) *Rhopaliophora palmata* (Combaz and Peniguel, 1972) emend. Playford and Martin, 1984; TVDB 12-044 (s1), L34. M) *Stellechinatum sicaforme* Molyneux *in* Molyneux and Rushton, 1988 var. *contextum* Servais and Molyneux, 1997; FZ1 3-4 (lm1), T51/2. N) *Stelliferidium trifidum*

(Rasul, 1974) Fensome et al., 1990; TZ-Paly 4 (lm1), L48. O) *Vavrdovella areniga* (Vavrdová, 1973) Loeblich and Tappan, 1976; TZ-Paly 1 (lm1), H49. P) *Veryhachium lairdii* group Deflandre, 1946 ex Loeblich, 1970 *sensu* Servais et al. 2007; FZ1 76-80 (lm1), P34. Q) *Priscotheca* sp.; TZ-Paly 12 (lm1), D27. R) *Striatotheca* sp. TZ-Paly 1 (lm1), H34/4. S) *Tectitheca*? sp.; FZ1 3-4 (lm1), R39/2-R40/1. T) *Vogtlandia*? sp.; TZ-Paly 12 (lm1), P34/2.

Fig. 5. Palaeogeographical reconstruction of the Lower Ordovician (ca. 480 Ma). The base map was derived from BugPlates (see Torsvik, 2009). Red circle = Zagora. A) Distribution of the *messaoudensis-trifidum* assemblage. (1) Dingle Peninsula, Ireland (Connery and Higgs, 1999; Todd et al., 2000). (2) England, Wales and Isle of Man (Molyneux *in* Chadwick et al., 2001; Cooper and Molyneux, 1990; Molyneux, 1999; Molyneux and Dorning, 1989). (3) Ardennes, Belgium (Breuer and Vanguestaine, 2004; Vanguestaine and Servais, 2002). (4) Rügen, Germany (Servais and Katzung, 1993; Servais and Molyneux, 1997). (5) Sierra Morena, Spain (Mette, 1989, Servais and Mette, 2000). (6) Bohemia, Czech Republic (Fatka, 1993). (7) Southeastern Turkey (Dean and Martin, 1992; Martin, 1996). (8) Northwestern Argentina (de la Puente and Rubinstein, 2009; Rubinstein et al., 2007; Toro et al., 2010). B) Distribution of chitinozoan species found in the Fezouata Formation during the Lower Ordovician. (1) Belgium (Martin, 1969; Samuelsson and Verniers, 2000). (2) Rügen, Germany (Samuelsson, 1999, Samuelsson et al., 2000). (3) Serra do Buçaco, Portugal (Paris, 1981). (4) Mayenne and Orne areas, France (Paris, 1981). (5) Montagne Noire, France (Rauscher, 1968). (6) Bohemia, Czech Republic (Paris and Mergl, 1984; Fatka, 1993, 1999). (7) Algerian Sahara (Taugourdeau and de Jekhowsky, 1960; Benoît and Taugourdeau, 1961; Oulebsir and Paris, 1995). (8) Holy Cross Mountains, Poland (Chlebowski and Szaniawski, 1974). (9) Eastern Cordillera, Bolivia (Heuse et al., 1999). (10) Northwestern Argentina (Ottone et al., 1992; Achab et al., 2006; de la Puente, 2010; de la Puente and Rubinstein, 2009, 2013; Toro et al. 2010). (11) Hubei Province, China (Chen et al., 2008, 2009). (12) Hunan Province, China (Wang et al., 2013). (13) Yunnan Province, China (Gao, 1986). (14) Skåne, Sweden (Grahn, 1980; Grahn and Nõlvak, 2007). (15) Tallinn, Estonia (Grahn, 1984; Hints and Nõlvak, 2006). (16) Oslo region, Norway (Owen et al., 1990). (17) Québec, Canada (Achab, 1980, 1986). (18) Western Newfoundland, Canada (Batten, 2000). (19) Spitsbergen, Norway (Bockelie, 1980).

Fig. 6. Distribution of *messaoudensis-trifidum* sub-assemblages. Modified after Molyneux et al. (2007). Sub-assemblages following Cooper et al. (1995), Time Slices following Webby et al. (2004), Stage Slices following Bergström et al. (2009). Data on Argentina was taken from

Rubinstein et al. (2007). *T. ph.* = *Tetragraptus phyllograptoides*.

Fig. 7. Selected chitinozoans from the Fezouata Formation near Zagora. Scale bars = 100 µm. A) *Desmochitina minor* s.l. Eisenack, 1931; FZ1 356-360. B) *Desmochitina* sp.; TZ-Paly 1. C) *Cyathochitina* aff. *campanulaeformis* (Eisenack, 1931) Eisenack, 1955; FZ1 349-350. D) *Cyathochitina* sp., vesicle wall showing multiple microborings; FZ1 82-89. E) two chained individuals of *Desmochitina minor* Eisenack, 1931; FZ1 356-360. F-G) *Euconochitina paschaensis-symmetrica* group; F: specimen assignable to *Eu. paschaensis* de la Puente and Rubinstein, 2009; FZ1 13-16. G: specimen assignable to *Eu. symmetrica* (Taugourdeau and de Jekhowsky, 1960); FZ1 31-32. H) *Euconochitina*? sp.; TVDB 12-046. I) *Clavachitina*? sp.; TZ-Paly 1. J) *Rhabdochitina gracilis* Eisenack, 1962; FZ1 13-16. K) *Eremochitina* aff. *baculata* Taugourdeau and de Jekhowsky, 1960; FZ1 13-16. L) *Eremochitina* cf. *baculata* Taugourdeau and de Jekhowsky, 1960; TZ-Paly 10. M) *Eremochitina brevis* (Benoit and Taugourdeau, 1961); TVDB 12-046. N) *Eremochitina* cf. *mucronata* Taugourdeau and de Jekhowsky, 1960; TZ-Paly 2. O) *Lagenochitina* cf. *obeligis* Paris, 1981; FZ1 66-67. P) *Lagenochitina* cf. *destombesi* Elaouad-Debbaj, 1988; FZ1 4-5. Q) *Lagenochitina esthonica* Eisenack, 1955; FZ1 356-360.

Fig. 8. Selected chitinozoans from the Fezouata Formation in the AZ-1 borehole. Scale bars = 100 µm. A-C,G) *Euconochitina paschaensis-symmetrica* group; A: specimen assignable to *Eu. paschaensis* de la Puente and Rubinstein, 2009; 965 m. B-C: specimen assignable to *Eu. symmetrica* (Taugourdeau and de Jekhowsky, 1960); 965 m. G: two chained individuals assignable to *Eu. paschaensis*; 930 m. D) *Euconochitina*? sp.; 749 m. E-F) *Eremochitina brevis* (Benoit and Taugourdeau, 1961); E: flattened specimen; 874 m, F: specimen with inflated chamber; 905 m. H) *Eremochitina* cf. *baculata* Taugourdeau and de Jekhowsky, 1960; 749 m. I) *Rhabdochitina* cf. *magna* Eisenack 1931; 699 m. J) *Lagenochitina* sp., 1981; 930 m. K) *Lagenochitina* cf. *destombesi* Elaouad-Debbaj, 1988; 930 m.

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Figure 1

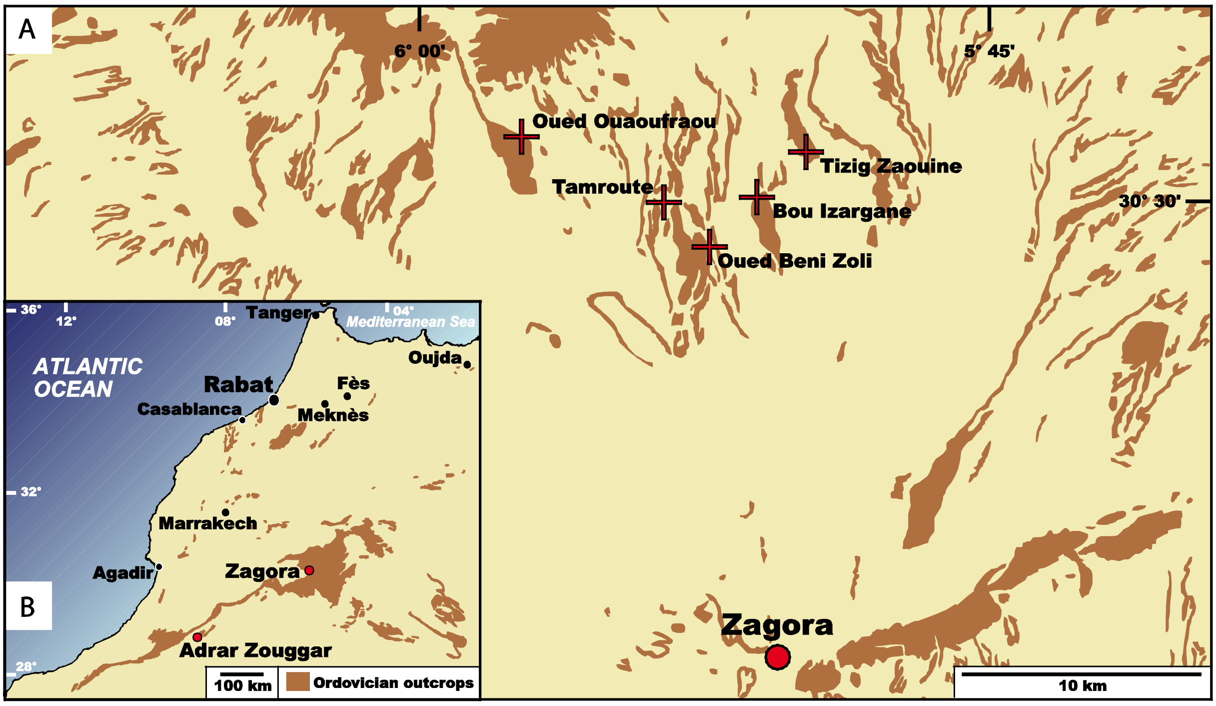

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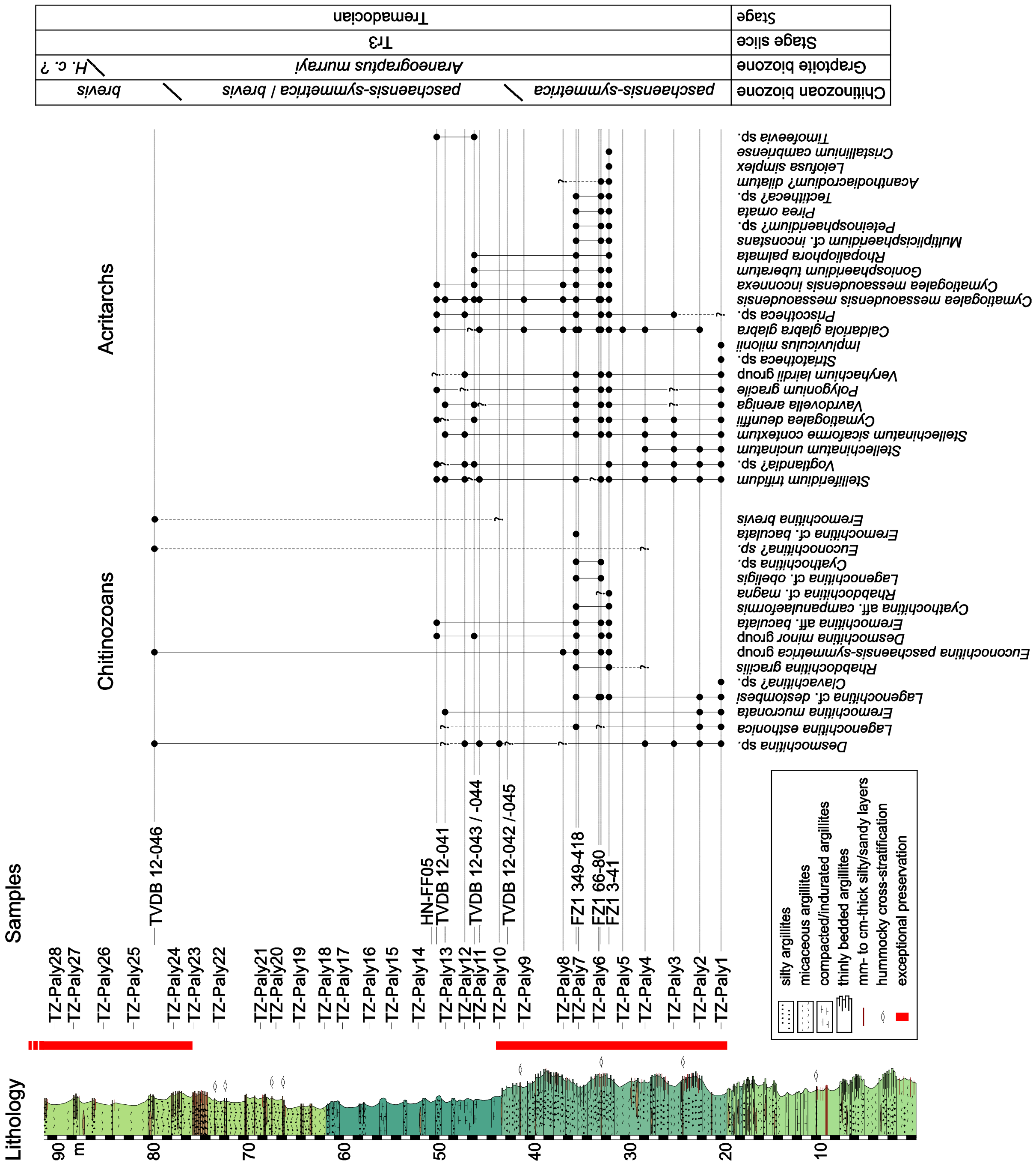
Figure 2


Stage
Tremadocian
Stage slice
Tr3
Graptolite biozone
Araneograptus murrayi
H. c. ?
Chitinozoan biozone
paschaensis-symmetrica
paschaensis-symmetrica / brevis
brevis
Acritarchs
Timofeevia sp.
Cristallinium cambriense
Leiofusa simplex
Acanthodiacrodium? dilatum
Tectitheca? sp.
Pirea ornata
Peteinosphaeridium? sp.
Multiplicisphaeridium cf. inconstans
Rhopaliophora palmata
Goniosphaeridium tuberatum
Cymatiogalea messaoudensis inconnexa
Cymatiogalea messaoudensis messaoudensis
Priscotheca sp.
Caldariola glabra glabra
Impluviculus milonii
Stratotheca sp.
Veryhachium lairdii group
Polygonium gracile
Vavrdovella areniga
Cymatiogalea deunffii
Stelliechinatum sicaforme contextum
Stelliechinatum uncinatum
Vogtlandia? sp.
Stelliferidium trifidum
Chitinozoans
Eremochitina brevis
Eremochitina cf. baculata
Euconochitina? sp.
Cyathochitina sp.
Lagenochitina cf. obeligis
Rhabdochitina cf. magna
Cyathochitina aff. campanulaeformis
Eremochitina aff. baculata
Desmochitina minor group
Euconochitina paschaensis-symmetrica group
Rhabdochitina gracilis
Clavachitina? sp.
Lagenochitina cf. destombesi
Eremochitina mucronata
Lagenochitina esthonica
Desmochitina sp.
Samples
TVDB 12-046
HN-FF05
TVDB 12-041
TVDB 12-043 / -044
TVDB 12-042 /-045
FZ1 349-418
FZ1 66-80
FZ1 3-41
TZ-Paly28
TZ-Paly27
TZ-Paly26
TZ-Paly25
TZ-Paly24
TZ-Paly23
TZ-Paly22
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TZ-Paly2
TZ-Paly1
Lithology
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m
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20
10
silty argillites
micaceous argillites
compacted/indurated argillites
thinly bedded argillites
mm- to cm-thick silty/sandy layers
hummocky cross-stratification
exceptional preservation

Figure 3

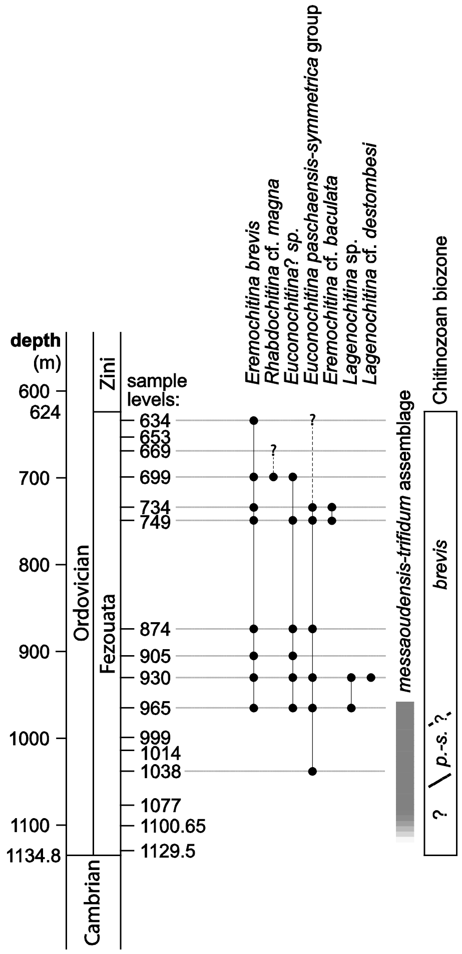
depth
(m)
600
624
700
800
900
1000
1100
1134.8
Zini
Ordovician
Fezouata
Cambrian
sample levels:
634
653
669
699
734
749
874
905
930
965
999
1014
1038
1077
1100.65
1129.5
Eremochitina brevis
Rhabdochitina cf. *magna*
Euconochitina? sp.
Euconochitina paschaensis-symmetrica group
Eremochitina cf. *baculata*
Lagenochitina sp.
Lagenochitina cf. *destombesi*
?
?
messaoudensis-trifidum assemblage
Chitinozoan biozone
brevis
p.-s.
?
?

Figure 4

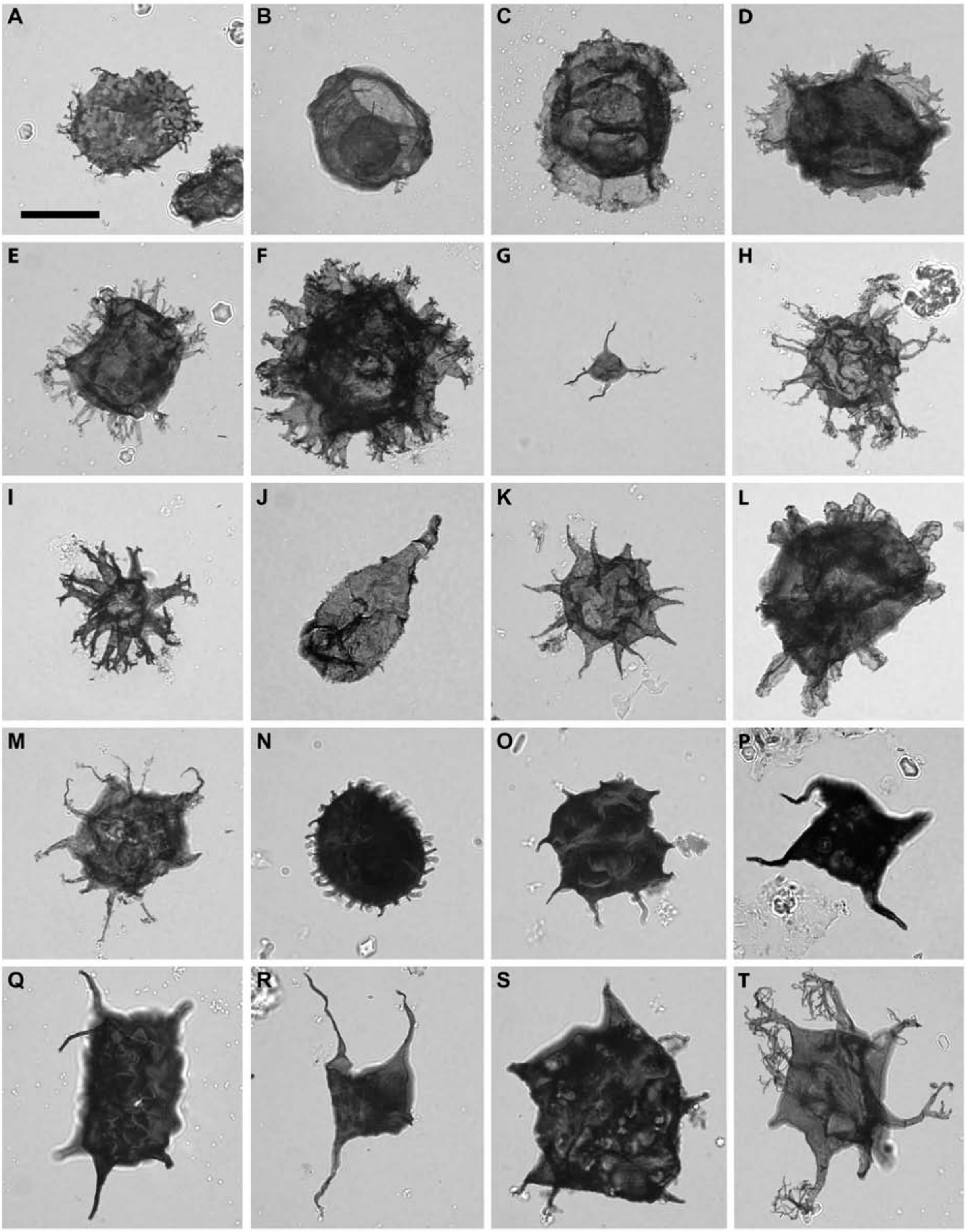

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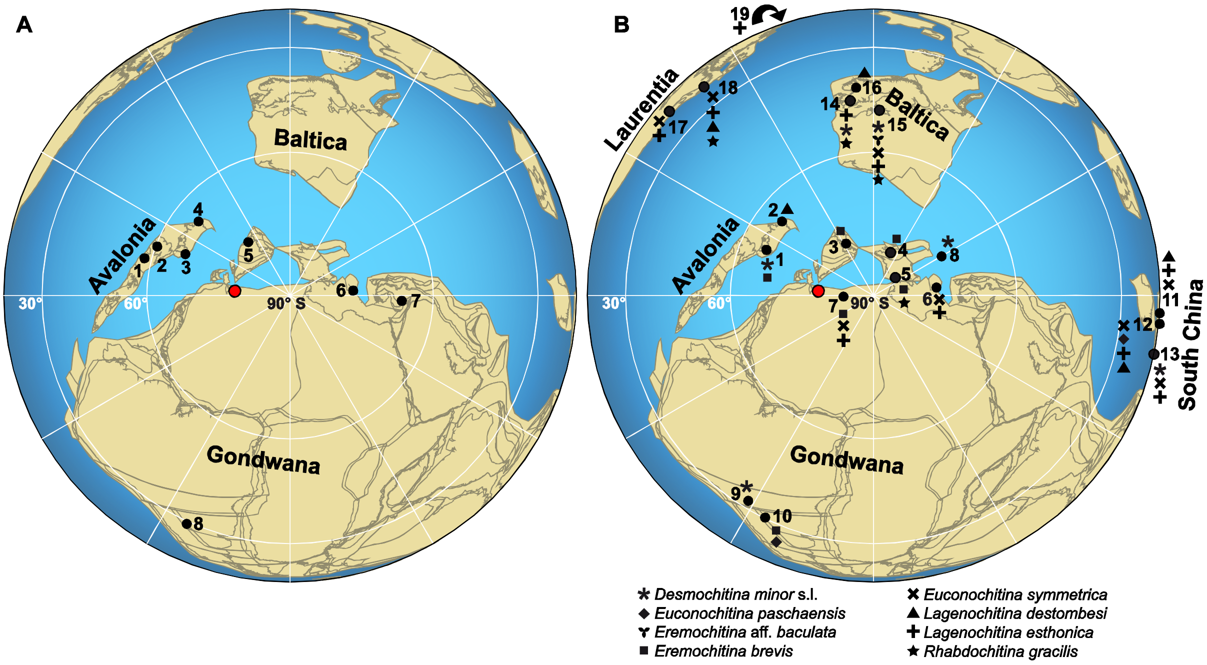
Figure 5


A
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1
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7
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30°
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Gondwana
B
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South China
30°
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90° S
Gondwana
✱ Desmochitina minor s.l.
◆ Euconochitina paschaensis
Y Eremochitina aff. baculata
■ Eremochitina brevis
✖ Euconochitina symmetrica
▲ Lagenochitina destombesi
✚ Lagenochitina esthonica
★ Rhabdochitina gracilis

Figure 6

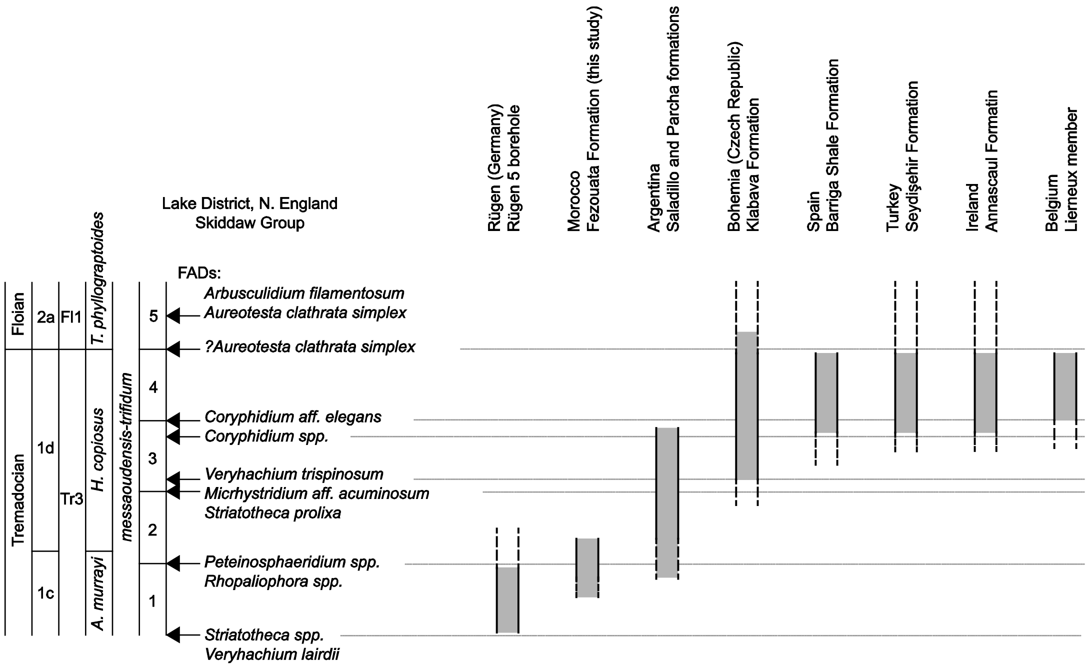

Lake District, N. England
Skiddaw Group
Rügen (Germany)
Rügen 5 borehole
Morocco
Fezouata Formation (this study)
Argentina
Saladillo and Parcha formations
Bohemia (Czech Republic)
Klabava Formation
Spain
Barriga Shale Formation
Turkey
Seydişehir Formation
Ireland
Annascaul Formatin
Belgium
Lierneux member
Floian
Tremadocian
2a
1d
1c
Fl1
Tr3
T. phyllograptoides
H. copiosus
A. murrayi
messaoudensis-trifidum
5
4
3
2
1
FADs:
Arbusculidium filamentosum
Aureotesta clathrata simplex
?Aureotesta clathrata simplex
Coryphidium aff. elegans
Coryphidium spp.
Veryhachium trispinosum
Micrhystridium aff. acuminosum
Striatotheca prolixa
Peteinosphaeridium spp.
Rhopaliophora spp.
Striatotheca spp.
Veryhachium lairdii

Figure 7

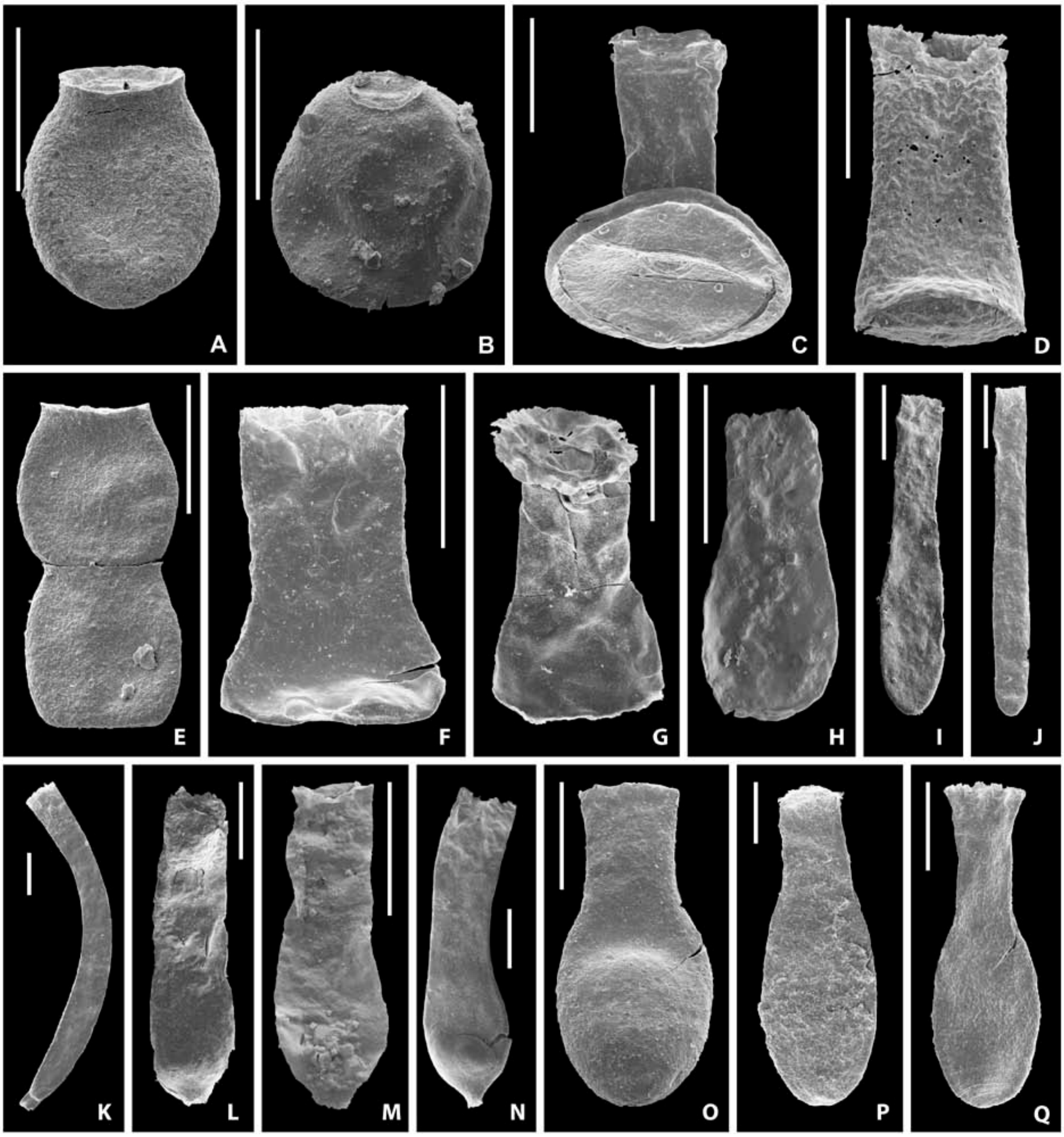
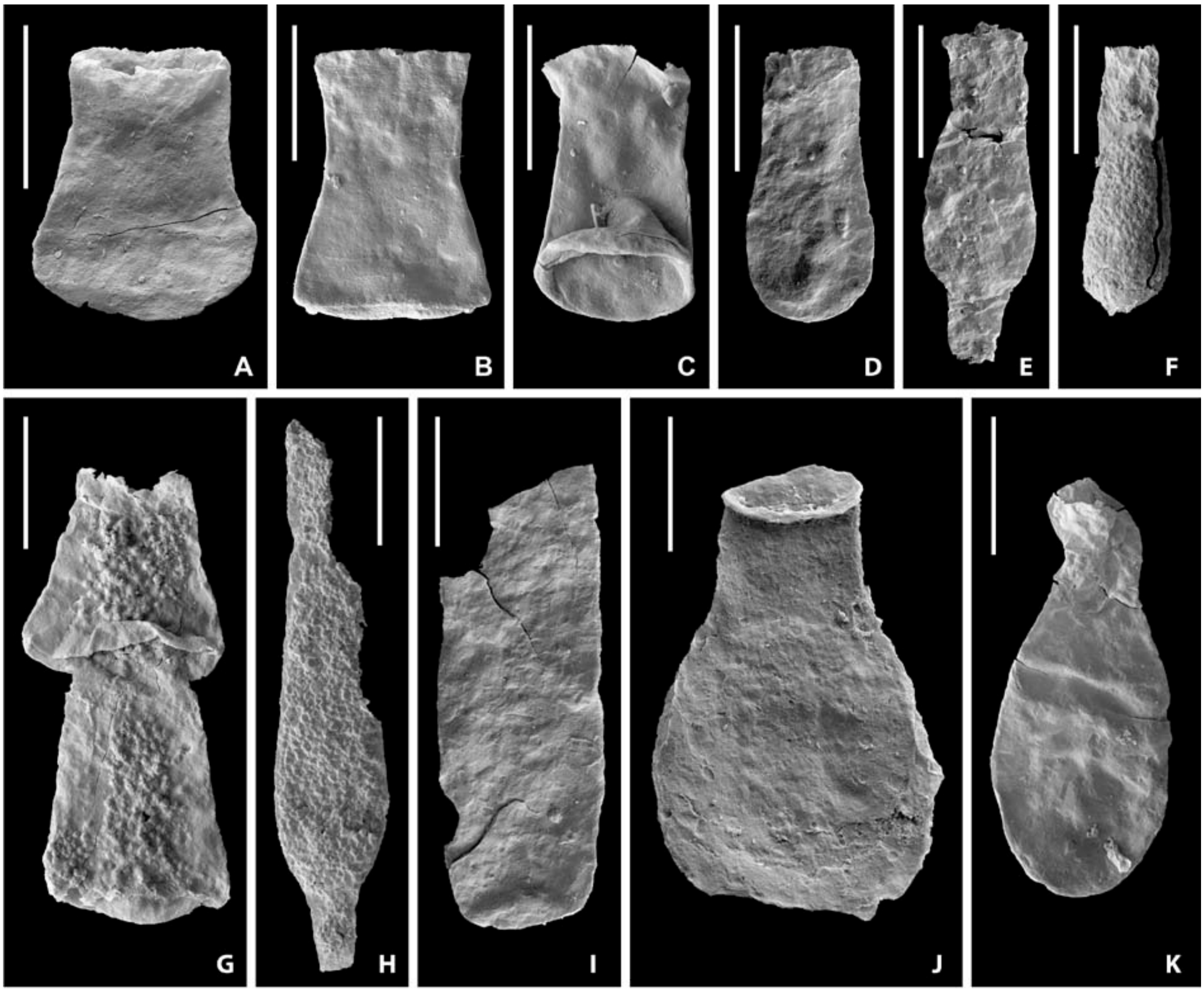


Figure 8



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Article V

Conodonts from the Lower Ordovician of Morocco – a contribution to age and faunal diversity of the famous Fezouata Lagerstätte

Lehnert, O., Nowak, H., Sarmiento, G., Servais, T., Gutiérrez-Marco, J.-C. & Akodad, M.

in preparation for *Palaeogeography, Palaeoclimatology, Palaeoecology*

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Conodonts from the Lower Ordovician of Morocco – a contribution to age and faunal diversity of the Fezouata Lagerstätte

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Abstract

This study documents unusually preserved conodonts of the Fezouata Formation, recovered from the AZ-1 borehole at Adrar Zouggar Mountain and from outcrops near Zagora in south-eastern Morocco. The Fezouata Formation was deposited on the peri-Gondwanan shelf near the South Pole during Early Ordovian times. It is composed of mostly fine-grained siliciclastics and it is well known for including some intervals displaying the exceptionally well preserved Fezouata Biota. Studies on different microfossil groups, including conodonts, increase the diversity recorded from this exceptional ecosystem. Strongly recrystallised conodont elements were extracted from the fine-grained siliciclastic sediments by diluted hydrofluoric acid (HF), which was used for isolating palynomorphs. The material is dominated by simple cone taxa such as *Parapaltodus*, *Semiacontiodus*, *Scolopodus*, *Scalpellodus*, *Drepanoistodus*, *Acodus*, *Paltodus*, and *Cornuodus*. In addition, a few elements of early *Prioniodus* are recovered. This composition allows an estimation of uppermost Tremadocian? through basal Floian ages for the fragmented elements because characteristic elements of younger assemblages, including ramiform (e.g. *Oepikodus*, *Baltoniodus*) or coniform (e.g. *Tropodus*, *Protopanderodus*) apparatuses, have not been recorded. The association is devoid of any warm/tropical and temperate water taxa and is typical for faunas

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in the cold water environments of the subpolar siliciclastic shelves during Early Ordovician times. The new term of 'subpolar faunal domaine' is proposed for these conodont associations of low diversity that occur at high southern latitudes during the Early Ordovician. Ecological implications and palaeobiogeographical relationships of the conodont faunas are discussed

Keywords: Morocco, Gondwana, Fezouata Formation, conodonts, Lower Ordovician.

1. Introduction

The Lower Ordovician Fezouata Formation of southeastern Morocco is famous for its records of Tremadocian to Floian faunas. The macrofossil record includes different groups such as cephalopods, echinoderms, brachiopods, trilobites and various other arthropods, graptolites, sponges, hyolithids and conularids (e.g. Martin et al., 2015; Van Roy et al., 2015a, and references therein). The presence of exceptionally well preserved fossils with possibly a Burgess Shale-like mode of preservation marks a 'Konservat-Lagerstätte' (*sensu* Seilacher, 1970), which may be the only post-Cambrian Lagerstätte of this type (Gaines et al., 2012; Gaines, 2014; Martin et al., 2015; Van Roy et al., 2010, 2015a, 2015b).

In the Fezouata Lagerstätte, soft-bodied biota typical of Cambrian Burgess Shale-type faunas co-occur with fossil groups typical for Sepkoski's (1984) Palaeozoic Evolutionary Fauna (Van Roy et al., 2015a), which started to flourish during the Great Ordovician Biodiversification Event (GOBE; e.g. Servais et al. 2010, with references therein). After five decades of documenting different faunal groups, exceptionally well-preserved fossils were not documented before 2006 when the paper by Van Roy and Tetlie (2006) on spinose arthropod appendages was published.

Martin et al. (2015) show that the exceptional faunal preservation in the thick siliciclastic Fezouata Formation is limited to a number of horizons in an approximately 80 m thick interval in the upper Lower Fezouata Formation (uppermost Tremadocian to basal Floian?).

Despite of all faunal lists and abundant palaeontological literature (e.g. Van Roy et al., 2015a, with references therein), the timing of the formation of the Fezouata Konservat-Lagerstätte is not very well dated. Graptolites and palynomorphs are important to constrain the age of the Lagerstätte.

Palynomorphs, specifically acritarchs, have been described from the Fezouata Formation for the first time by Deunff (1968a,b), and the literature on this group is summarized in Nowak et al. (2015, this volume). *Lagenochitina destombesi*, described by Elaouad-Debbaj (1988) from this formation, is the index taxon of the lowermost, and unfortunately long-lasting, chitinozoan biozone in the Ordovician (Paris, 1990). Most important for time constraints of the Fezouata Lagerstätte are the associated acritarchs belonging to the *messaoudensis-trifidum* assemblage (e.g. Servais and Molyneux, 1997, with references therein), which recently was documented by Nowak et al. (2015, this volume) from the Fezouata Formation in the Adrar Zouggar Mountain (borehole AZ-1). This acritarch assemblage is indicative of the upper Tremadocian through lower Floian in many peri-Gondwanan successions in high southern latitudes (Servais et al., 2003; Molyneux et al., 2013).

Based on graptolites, the part of the Fezouata Biota including exceptional preservation has been attributed by Martin et al. (2015) to the upper *Araneograpthus murrayi* through basal *Hunnegraptus copiosus* zones (upper Tremadocian). The graptolite faunas in this critical interval are revised by Gutiérrez-Marco and Martin (this volume), indicating that exceptional preservation extends into the Floian.

So far, Ordovician conodonts from Morocco have only been described by Bultynck and Sarmiento (2003) as reworked material (early Middle Ordovician) from a Siluro-Devonian succession in the Meseta (Khemis-n'Ga) and by El Bourkhissi and Sarmiento (1997) from the Middle Ordovician Taddrist and Izegguirene formations in the Anti-Atlas. The present study focusses on much older conodont material from an interval overlapping stratigraphically with the Lower Ordovician Fezouata Lagerstätte, with the goal to gain new biostratigraphic and palaoebiogeographic data based on collections from different areas.

2. Geological setting

During Early Ordovician times, Africa was an integral part of the Gondwana supercontinent, which occupied palaeolatitudes from the South Pole to the equator (e.g. Torsvik and Cocks, 2013a, 2013b). The shelf sequence studied in Morocco was deposited in cold water environments at extremely high latitudes close to the palaeo-south pole (Torsvik and Cocks, 2011, 2013a, 2013b). Plate-tectonic processes triggered rifting and subsidence in the latest Cambrian and earliest Ordovician, when the Rheic Ocean started to open up between Gondwana and Avalonia, with Avalonia being considered a well-constrained microcontinent (Servais and Sintubin, 2009, with references therein) that drifted north towards Baltica during the Ordovician (e.g. Cocks and Fortey, 2009), causing the subsequent closure of the Tornquist Sea and finally collided with Baltica during Late Ordovician times (e.g. Torsvik and Rhenström, 2003). At that point the study area in the Moroccan Anti-Atlas was covered by the large ice cap of the Hirnantian Gondwana glaciation (e.g. Le Heron et al., 2007; Le Heron and Craig, 2008)

The Lower Ordovician (Tremadocian to Floian) Fezouata Formation, widely distributed in the Anti-Atlas, was deposited after the rifting processes that separated Avalonia. The sedimentation of the thick succession of fine-grained siliciclastics (mud- and quartz-rich siltstones and sandstones) of about 900 m in maximum thickness took place in a vast but shallow epicontinental basin along the Gondwana margin (Destombes et al., 1985; Martin et al., 2015; Vaucher et al., this volume). This siliciclastic succession, which in the past has been subdivided into a Lower (Tremadocian) and Upper (Floian) Fezouata Formation, has its most important outcrops in the Draa Valley around Zagora (Destombes et al., 1985). However, the lithologic separation of its lower and upper part by a distinct horizon is not possible in certain regions such as the Zagora area (Destombes, 1962).

The Fezouata Formation is resting unconformably on the Guzhangian Tabanite Group (Geyer and Landing, 2006) and is in places covered by sandstones of the upper Floian Zini Formation. For the Fezouata and Zini formations, Vaucher et al. (this volume) present a first depositional model showing wave-dominated and tide-modulated deposition of sediments formed in foreshore to proximal offshore, with the deposition of sandstone lenses in lower shoreface environments under storm activity.

Both formations are separated by an unconformity from the overlying Darriwilian deposits of the Tachilla Formation. The three formations, the Fezouata, Zini, and Tachilla formations, constitute together the Lower through Middle Ordovician Outer Feijas Shale Group of Choubert (1942).

3. Materials and methods

Various localities in the Ternata plain near Zagora (Fig. 1) have been sampled in detail during several field campaigns, also for gaining biostratigraphic data based on palynomorphs (Nowak et al., this volume). A part of the compiled stratigraphic log of the Lower Ordovician strata by Vaucher et al. (this volume), has partly been used to produce a detailed stratigraphic log for showing the position of palynomorphs (Nowak et al., this volume, their fig. 2) and of conodont samples (Fig. 2). This detailed sketch displays the interval spanning 240-330 m above the base of the Fezouata Formation (Vaucher et al., this volume, their fig. 2) which includes the majority of the stratigraphic intervals of the Fezouata Lagerstätte with the exceptionally preserved faunal assemblages (Martin et al., 2015). Between the two principal Lagerstätten bearing intervals, a conspicuous approx. 20 m thick greyish blue and clayey interval is intercalated (43 to 62 m in Fig. 2). It serves as a local stratigraphic marker to correlate the different sections and also the sample positions in the compiled section (Fig. 2). 26 samples (prefix TZ-Paly) were taken at Tizig Zaouine (30°31'04''N, 5°49'19''W, Fig. 1) for palynomorph studies. The sample levels include beds from the lower stratigraphic interval bearing exceptionally preserved faunas and from the lower part of the upper interval (Fig. 2).

17 densely-spaced samples (prefix FZ1) were taken from the excavations of a ca. 4 m thick interval in three quarries at Bou Izargane (30°29'59''N, 5°51'00''W; Fig. 1). Samples from each quarry are compiled in the composite section shown on Fig. 2. The sample material collected from the Bou Izargane excavations represents dark grey mudrocks that are much less altered than those exposed in other outcrop locations clearly affected by weathering processes (Nowak et al., this volume).

In addition, the subsurface material from the AZ-1 borehole (drilled in 1963 and 1964 at Adrar Zouggar Mountain, ca 300 km southwest of Zagora, by the petroleum company Petrofina for oil exploration) originates from cuttings sampled in the drill core deposit of the ONHYM (Office National des Hydrocarbures et des Mines) at Rabat. The drilling stopped at a maximum depth of 3398.13 m. The interval between 624 m and 1134.8 m depth was assigned in the logging to the Fezouata Formation, based on lithological comparison with outcrop areas. This interval is overlain by 144 m of sediments assigned to the Zini Formation and subsequently by the Tachilla Formation (unpublished drill log).

The conodont material studied in the present paper is derived from the siliciclastic palynomorph samples and was processed in the microfossil laboratory at the University of Lille following a non-standard, low-manipulation palynomorph preparation technique involving hydrofluoric acid treatment (see Nowak et al, this volume). This procedure caused acid etching and recrystallisation of most of the recovered conodonts and made them extremely fragile. The sample residues were filtered at mesh sizes of 51 or 63 µm for larger fractions, and subsequently at 15 µm for small palynomorphs. Larger microfossils such as conodonts were hand-picked from the fraction of >51 or 63 µm and put on stubs for SEM studies. The studied material is stored on the stubs in the collections of the Evo-Eco-Paleo department at Lille.

4. Conodont faunas and biostratigraphy

Stratigraphic information from the cuttings in the AZ-1 borehole based on palynomorphs is provided by Nowak et al. (2015, this volume) and the succession was indirectly correlated to the graptolite zonation in the Fezouata Formation (see Martin et al., 2015). With respect to continuous outcrop sections, our new stratigraphic data on conodonts show some discrepancy to the correlation of the whole Fezouata Lagerstätte by Martin et al. (2015) with the upper part of the late Tremadocian stage slice Tr 3 of Bergström et al. (2009; *A. murrayi* and *H. copiosus* graptolite zones), because some parts of the succession sampled for palynomorphs and conodonts (Fig. 2) appear to be early Floian in age. We recovered taxa typical for the upper part of the Tremadocian *P. proteus* zone and the lower part of the subsequent Floian *Prioniodus elegans* zone from the studied succession. The determination of taxa is impossible or difficult in a large portion of the fragmented and etched material (surface ornamentations are mostly not preserved, elements are recrystallised), and only a small percentage of the determinable material provides information for the stratigraphic interpretation and discussion presented herein. Most probably some fragmentation of the material already occurred during the depositional processes in the siliciclastic shelf environments. Therefore, it must be pointed out that the record used for our stratigraphical interpretations is strongly biased by the destruction of the more fragile elements in the recovered conodont assemblages. In several cases, when only single and not well preserved specimens were recovered, taxa are rather termed with 'cf.' In the case of specimens showing some similarity to a taxon, but being out of range and having similar elements in different species of the genus, the species is indicated by 'aff.'.

For the comparison and the correlation of the studied Lower Ordovician material to the Baltoscandian zonation and its faunal sucessions, the basic papers by van Wamel (1974), Lindström, 1971, Löfgren (1978, 1985), Stouge and Bagnoli (1988) and more specific papers on upper Tremadocian through lower Floian conodonts (Bagnoli et al., 1988; Bergström 1988; Löfgren, 1994, 1997a, 1997b, 1999; Tolmacheva et al., 2001) are relevant. Larger monographs and publications relevant for the biozonations on Laurentia include papers dealing with faunas in deeper settings by Ethington and Clark (1971, 1982), Stouge and Bagnoli (1988), and Ross et al. (1997).

Löfgren (1994) subdivided the *P. proteus* zone in the Siljan district of central Sweden into four subzones which cannot be recognized in the Moroccan section studied here, where the conodont record starts in the uppermost subzone of the *P. proteus* zone called after *A. deltatus*. The base of the *A. deltatus* subzone may be at level FZ1 37-41 (Fig. 2) where the FAD of *A. deltatus* (Fig. 4B) is observed together with specimens of *P. proteus* (Fig. 4J). Below this level only fragmented material was found and some specimens which can be attributed to *Parapaltodus* sp. Therefore, it cannot be excluded that the subzone would start slightly further down. *Tripodus* sp. is also present (Fig. 4AA) looking somewhat similar to the basal Middle Ordovician *T. laevis*. The record of *Tripodus* starts earlier in the Tremadocian. The second subzone of the *P. proteus* zone is named after this genus (Löfgren, 1994). *P. proteus* and *A. deltatus* co-occur with *Parapaltodus* aff. *P. flexuosus* (Fig. 4D), *Semiacontiodus* cf. *cornuformis*. (Fig. 4T,U) and *Protopanderodus* cf. *P. leonardii* (Fig. 4P; sample TZ-Paly 7).

Cornuodus elements with very deep basal cavities (well seen in splitted elements) have been attributed to *Cornuodus longisbasis* (Fig. 4N) which unfortunately is one of the most long-ranging and not time-specific taxon (Tremadocian *P. deltifer* through Hirnantian *A. ordovicicus* zone; Löfgren, 1999).

The occurrence of *Scolopodus* aff. *S. krummi* displays a position of the material in the Tremadocian-Floian transition. Tolmacheva (2006) showed that the typical costate elements of *Scolopodus* are recorded in the upper *P. proteus* zone for the first time and have some wide stratigraphic range afterwards. Early *Scolopodus* sometimes also show some shorter costae and not all costae are continuously running from the basal part of the element towards the top (like in *S. rex*, which was referred to *S. striatus* by Tolmachaeva, 2006). The fragmented specimens from Morocco resemble *S. krummi*, which has its FAD in the *P. proteus* zone of the Argentine Precordillera (Albanesi, 1998) and is common in levels in the *P. elegans* zone (Lehnert, 1995). However, the Moroccan specimens (*Scolopodus* aff. *S. krummi*, Fig. 4S,X), are not sufficiently well preserved to confidently place them into this species.

Unfortunately, several of the taxa common in the *P. proteus* zone, including *A. deltatus*, *P. proteus*, *Drepanodus arcuatus* (Fig. 4K) and *Drepanoistodus forceps* (Fig. 4L) are ranging higher up into the Floian, well into *P. elegans* zone, in many other areas. This is obvious for *A. deltatus*, *D. arcuatus* and *D. forceps* from their ranges in the stratotype section for the base of the Floian at Diabasbrottet in south-central Sweden (Maletz et al., 1996). *Tropodus* cf. *T. comptus* and *T.* cf. *T. sweeti* (Fig. 4V,Z) bear the same problem. *T. comptus* and *T. sweeti* range from the *P. proteus* zone well into the Floian and through the *P. elegans* zone, *T. sweeti* ranges even into the upper *O. evae* zone (e.g. Stouge and Bagnoli, 1988; Albanesi, 1998). In addition, *Paltodus* cf. *P. inaequalis* (Fig. 4H) is present in this part of the section. The fragmentary material of *Semiacontiodus* sp. and *Tropodus* sp. is also not age indicative. *P. selenopsis* (Fig. 4M) has its FAD within the *P. elegans* zone (e.g. Stouge and Bagnoli, 1988), which may allow us to put a stippled line just below its occurrence in TZ-Paly 19.

Based on the recorded conodont succession, the 'Fezouata Lagerstätte' with its exceptionally preserved biota formed during the Tremadocian/Floian transition in the interval spanning the upper *P. proteus* through *P. elegans* zone in Baltic terms. Unfortunately, the conodont material from a number of samples is poorly preserved, so that the conodont biostratigraphy in the Fezouata Formation may be regarded as just preliminary. Additional processing of samples dedicated to conodont research and the discovery of stratigraphically useful bedding plane assemblages may eventually provide a tool for a more precise stratigraphy and for better age constraints of the 'Fezouata Lagerstätte'.

Conodonts from the AZ-1 borehole

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Stratigraphic information on the drill cuttings is limited, because of a possible mixing of the material in the borehole. Nevertheless, it is worth to show the succession based on material sampled from this drilling, that presumably ranges up into the Floian *O. evae* zone. There is no conodont information about the basal part of the Ordovician siliciclastics in the core, as the record starts with *Semiacontiodus* sp. at a depth of 1077 m (Fig. 3). It could be that some of the older strata on top of the Cambrian are stratigraphically as old as the *P. deltifer* zone, but the whole lower part of the Ordovician succession could also fall into the upper Tremadocian *P. proteus* zone. The record of material indicating the uppermost subzone of this youngest Tremadocian conodont zone starts at a depth of 1038 m with the presence of *A. deltatus* (Fig. 3; Fig. 4A,C,I). Within its range it is accompagnied by *P. proteus* (Fig. 4G) and stratigraphically not useful species such as *C. longibasis*, *Parapaltodus* aff. *P. simplicissimus* (similar to the much younger late Floian/Dapingian *P. simplicissimus*), and elements of *Parapaltodus* sp.

However, fragmented material of *Prioniodus* including an S element and fragments of processes with a strong denticulation (*Prioniodus* sp.; Fig. 4Q,W) has been found. Such pronounced denticles are not yet present on the processes of *P. gilberti* elements, the *Prioniodus* species indicative of the *P. proteus* zone. Such stronger denticulation starts later in the early Floian taxa *P. oepiki*, *P. adami*, and *P. elegans*. In Newfoundland, Stouge and Bagnoli (1998) established three local zones based on these species and showed that the lowermost of these zones (*P. oepiki* zone) falls into the lower *Tetragraptus approximatus* graptolite zone defining the base of the Floian. The occurrence of *P.* cf. *P. oepiki* (Fig. 4R) together with *Paltodus* cf. *P. inaequalis* suggests that the base of the Floian is located at a depth of 965 m or below, or even at 999 m with the first *Prioniodus* sp. showing a pronounced denticulation.

The assemblages between 749 m and 905 m depth are indicative of the *P. elegans* and *O. evae* zones. In other areas, *S. stola* is present in the *P. elegans* zone, but more common in the *evae* Zone (e.g. Lehnert, 1995; Albanesi, 1998). *Periodon selenopsis* is also typical for this interval (e.g. Stouge and Bagnoli, 1988). The recrystallised *Scalpellodus* aff. *S. gracilis* (Fig. 4O) is similar to *S. gracilis*, but the Baltoscandian *Scalpellodus* taxa *S. latus* and *S. gracilis* are typical Middle Ordovician forms.

These aspects show that the material from this part of the section, including elements of *Tropodus* sp., *Periodon* cf. *selenopsis* (Fig. 4F), *Stolodus* cf. *S. stola* (Fig. 4Y) and *Tripodus* aff *T. laevis* (Fig. 4AB), falls in the frame of the *P. elegans* and *O. evae* zones, but there is no indication and/or stratigraphic index taxon to show where to place the boundary between both zones. The occurrence of *Paroistodus* cf. *P. parallelus* (Fig. 4E) at 749 m depth may display that this level in AZ-1 is not younger than upper *O. evae* zone, where usually *P. parallelus* has its last occurrence (e.g. Löfgren 1997b).

5. Conodont palaeogeography of higher latitude peri-Gondwana faunas

For the focus of this paper, our stratigraphical frame for palaeobiogeographic comparison is the Lower Ordovician in the cold-water environments on peri-Gondwana shelf areas in subpolar and high latitudes regions. In contrast to limited reports on assemblages from these siliciclastic successions, a large number of monographs and scientific publications exist about highly diverse Lower Ordovician conodont assemblages from tropical and subtropical Gondwana and peri-Gondwana (e.g. Australia, North China, South China), Laurentia and Baltica, located in equatorial to mid latitudes during this interval. In the last few decades, there was a constant increase in studies from tropical areas with carbonate environments, such as Siberia and Gondwana areas located close to the palaeoequator at this time, especially from the Chinese palaeoplates. Since the first paper by An (1981), a flood of Ordovician conodont papers has been published from South China, North China and Tarim, and evaluated biostratigraphically, biogeographically, as well as with respect to biodiversifications (Wu et al., 2012, 2014a, 2014b, with references therein).

In tropical and subtropical ‘eastern’ and ‘northeastern’ Gondwana (e.g. Australia, South China, Korea and Malaysia; Zhen and Nicoll, 2009), representing the northernmost part of the supercontinent (cf. Servais and Sintubin, 2009), a separate faunal province, the ‘Australasian Province’ with typical *Serratognathus* faunas, is developed during this time (Zhen and Nicoll, 2009, with references therein). This province is now termed ‘Australian Province’ in the latest model of Zhen and Percival (2003).

In this paper, however, we only refer in our reference list to basic papers on lower to mid latitude faunas relevant for correlations and subsequent zonations in higher latitude peri-Gondwana areas. For more information on the well known faunal provinces, the reader is referred to general palaeogeographical discussions in many previous publications (see Bergström, 1990; Rasmussen, 1998, with references therein). Although it is evident that Ordovician conodont faunas are not only of biostratigraphic importance, but also represent a pronounced provincialism useful for palaeogeographic reconstructions (e.g. Bergström, 1990), it is clear that Ordovician faunas in wide parts of high latitude peri-Gondwana are relatively unknown, except in some stratigraphic intervals with carbonate sedimentation. For that reason, the recovery of material from the siliciclastic sediments of Morocco provides very significant new insights.

In contrast to the highly diverse conodont associations in lower latitudes, Lindström (1976) and Bergström (1990) suggested a separated 'Mediterranean Province' for the low diverse Lower Ordovician faunas in Germany (Frankenwald area; Sannemann 1955) and those from the Armorican Massif (Lindström et al., 1974). According to Vanguestaine et al. (2004), the material from the Salm Group in Belgium, and probably also faunal assemblages from Turkey, France (Montagne Noire) and the Czech Republic, should be part of this cold water province.

In this context, it is useful to compare the faunal diversity in the Fezouata material with other high-latitude conodont associations. The peri-Gondwana shelf areas facing the Tornquist Sea and the Iapetus Ocean are characterized by faunal assemblages adapted to cold water environments (Bagnoli and Stouge, 1991). Based on faunal evidence and plate-tectonic reconstructions, Christiansen and Stouge (1999) established a palaeo-oceanic circulation model for the Lower Ordovician, including in their concept not just palaeomagnetic data, but also the palaeobiogeographic record. They showed the circulation patterns along the Gondwana margins based on provincialism in different faunal groups. Based on the palaeogeographical reconstruction by Torsvik and Cocks (2013a), Servais et al. (2014) postulated cold surface water currents along the Gondwana margins located in middle to high latitudes.

The Lower Ordovician peri-Gondwana conodont faunas adapted to cold water conditions include mainly pandemic taxa in low diverse assemblages. The latter aspect seems to be most characteristic. The associations are apparently dominated by just a few coniform taxa. The occurrences of such low diverse high latitude faunas are marked in Figure 5 and are briefly mentioned and discussed below.

Iran

In the Eastern Alborz Mountains of Iran (Fig. 5-1), abundant material has been recovered from upper Tremadocian sediments (*Paltodus deltifer* zone) yielding a mix of coniform 'cold water' taxa, including Baltoscandian 'cold water' species of *Paltodus* and *Paroistodus*, together with some elements of Laurentian 'warm water' species of *Rossodus* and *Variabiloconus* (Ghopadi Pour et al., 2011). A small and low diverse fauna was reported from the Damghan area of northern Iran and recovered in the frame of a trilobite study from the Lashkarak Formation (Ghopadi Pour et al., 2007). It is a typical cold water association of coniform taxa from the upper *P. proteus* zone and includes *A. deltatus*, *Drepanodus arcuatus, P.* cf. *P. subaequalis, Drepanoistodus* aff. *amoenus*, and *Semiacontiodus* sp.

Turkey

Data from Turkey presented by Gedik (1977, with references therein) concern conodonts from the Soboda Formation, a thin carbonate unit in the Ordovician siliciclastic succession of the Taurides (Fig. 5-2), that provides information on a low diverse upper Floian fauna composed of exclusively Baltoscandian ‘cold water’ taxa. It is the only documentation of these subpolar Floian faunas mentioned for the first time by Barnes in Dean (1973) and showing no ‘visits’ of any Laurentian type warm water elements like in Iran to the east.

Czech Republic

There are a few reports on Ordovician conodonts faunas from the Prague Basin (Fig. 5-3), but only one is documenting the low diverse Lower Ordovician faunas from the Floian Klabava Formation (Zusková, 1993). The lower part of the formation (Olesna Member) bears a lot of fragmented conodonts and phosphatic brachiopods on the bedding planes, but this lower Floian subpolar material is dominated by only some robust drepanodiform elements of some *Drepanodus* or *Drepanoistodus* apparatus, while no other taxa are observed. This association displays an extremely low diversity in the clastic cold water succession deposited close to the Floian palaeo-south pole.

France and Germany

The data about Lower Ordovician faunas from the Montagne Noire in southern France (Küppers and Pohler, 1992; Fig 5-4), the Frankenwald area in Germany (Sannemann, 1955; Fig 5-5) and the Armorican Massif in northern France (Lindström, 1976; Fig. 5-6) have been discussed by Vanguestaine et al. (2004) with respect to their ‘cold water’ aspects. Previously, the faunas from the Frankenwald area and the Armorican Massif have been discussed by Lindström (1976), who suggested the establishment of a separate faunal province for these associations of ‘cold water’ taxa. This view was supported by Bergström (1990), who formally called it the ‘Mediterranean Province’, but also pointed out that more detailed knowledge about these poorly preserved faunas would be necessary for quantitative comparisons with other areas.

It should be mentioned that Serpagli et al. (2007) described two species of a new genus (*Hammanodus*) from the Montagne Noire, which so far has been found only in peri-Gondwana (Spain, Eastern Cordillera of NW Argentina, Voldman et al., 2013) and may be restricted to the mid to high latitudes of the Gondwana shelf areas. In this context, they mention that in the frame of resampling the limestone beds in this area, a diverse Tremadocian conodont fauna was recovered (altogether 14 species; Serpagli et al., 2007, p. 1447). Unfortunately, only the occurrence of the two subzonal indices and subspecies of *P.*

deltifer – P. deltifer pristinus and P. deltifer deltifer – are mentioned and figured, but there is no list of the remaining taxa provided.

Spain (Iberia)

Sarmiento et al. (2011) compiled all available Ordovician conodont information from the Iberian Peninsula (Fig. 5-7). Lower and Middle Ordovician conodont assemblages are known from clasts in a Missippian mass flow deposit (Sarmiento and Gutiérrez-Marco, 1999), which provide important information about Ordovician carbonate units reworked into these olistostromes. The Lower Ordovician material includes a number of Baltoscandian taxa together with *Hammanodus*, a taxon that was described by Serpagli et al. (2007) from the uppermost Tremadocian of the Montagne Noire and is possibly restricted to the peri-Gondwana margin.Just one Floian assemblage from the Cantabrian Zone of northern Spain has preliminarily been reported by Gutiérrez-Marco and Bernárdez (2003) from the uppermost Barrios Formation, indicating only the presence of Baltoscandian-type coniform genera such as *Drepanodus*, *Drepanoistodus*, and *Protopanderodus*.

Belgium (eastern Avalonia)

It has been pointed out by Vanguestaine et al. (2004) that the majority of the fragmented material from the Salm Group in Belgium (Fig. 5-8) is difficult to determine and belongs mainly to apparatuses of *Drepanodus* species and *D. arcuatus*. There are also strongly recurved coniform elements present, which might represent rare taxa of the so-called '*franconicus* fauna' known from the Frankenwald area in Germany (Sannemann, 1955). This subpolar association is extremely low diverse and devoid of any 'warm water' taxa.

Mexico

The upper Tremadocian cold water faunas from Oaxaca in Mexico (Fig. 5-9) described by Landing et al. (2007) are composed mainly of typical Baltoscandian coniform taxa (species of *Paltodus*, *Drepanodus*, *Cornuodus*, *Paroistodus*), but some 'warm water' elements such as *Acanthodus uncinnatus* and species of *Variabiloconus* (*V. transiapetus* and *V. variabilis*) are also present, presumably showing some influence of warmer surface water currents.

Colombia

Faunas decribed from the El Hídago Formation in Colombia (Borrero et al., 2007; Fig. 5-10) are dominated by widespread coniform taxa such as *Paltodus deltifer*?, *Paroistodus numarcuatus*, *Acodus deltatus*, and *Cordylodus* sp. This low diverse fauna is older than the latest Tremadocian to earliest Floian Fezouata assemblages. However, in addition to this record, Gutiérrez-Marco et al. (2007) documented elements from this formation such as *Parapaltodus simplicissimus*, *Drepanodus robustus*, *Drepanoistodus* cf. *tablepointesis, Semicacontiodus* cf. *cornuformis*, *Costiconus*? cf. *ethingtoni*, showing that even the Middle Ordovician faunas in Colombia are still partly composed of a few widespread simple cone taxa.

Peru

There are some reports on low to moderately diverse Lower Ordovician faunas from Peru (Sarmiento et al., 2001; Gutiérrez-Marco et al., 2006, 2008; Fig. 5-11). The late Floian faunas from the San José Formation in the Eastern Cordillera are composed mainly of widespread Baltoscandian taxa such as *Protopanderodus rectus, Drepanoistodus basiovalis, Drepanoistodus forceps*, *Drepanodus arcuatus*, *Ansella* cf. *jemtlandica*, together with *Trapezognathus diprion* and *Gothodus costulatus.* The latter taxon is known from Baltica, but common in NW Argentina, specifically in the Famatina range. *Trapezognathus* species are abundant in coeval strata of Iran showing that the genus is common in mid-latitude peri-Gondwana. *Erraticodon patu*, also present in this fauna, is common in low latitude Australia, but has also been reported from NW Argentina (Voldman et al., 2013).

Northwestern Argentina

In an intermediate position and possibly influenced by some warmer current along the western Gondwana margin, South American faunas from northwestern Argentina (Fig. 5-11) display some higher degree in biodiversity. In clear contrast to the Fezouata material from Morocco, the mid latitude faunas from northwestern Argentina exhibit mixed assemblages of higher diversity including typical Baltoscandian and Laurentian elements (Zeballo et al., 2008, with references therein). As pointed out by Zeballo et al. (2008), the “Early Ordovician basin of northwestern Argentina may correspond to the Shallow-Sea Realm and Cold Domain and probably records the development of a differentiated conodont province in the southern South American margin of Gondwana”. These authors claim that the higher diverse faunas in this part of Gondwana are dominated by some endemic species, taxa known from Baltoscandia serve as correlation tools and there are also Laurentian-type ‘visitors’. This is reflected by the record in various publications (e.g. Albanesi et al., 2011; Zeballo and Albanesi 2013a, 2013b; Zeballo et al. 2013, with references therein). For this reason, Zeballo and Albanesi (2013b) established a separate ‘Southwestern Gondwana Province’ for the ‘Cold Domain’ in the ‘Shallow-Sea Realm’, based on the palaeogeographic concepts by Zhen and Percival (2003).

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Even when material from Morocco is mainly recrystallised and quite fragmented, we can suggest a low diversity for the fauna which is composed of ‘Baltoscandian’ elements adapted to colder temperatures. We can observe a pattern of low diversity in the southernmost circumpolar areas during Lower Ordovician times. Therefore, we propose a low diverse ‘subpolar faunal domain’ devoid of any influence by warmer current systems bringing ‘Laurentian-type’ taxa to the southern Gondwana margin like in mid latitude of eastern (cf. Servais and Sintubin, 2009; traditionally ‘western’ Gondwana: NW Argentina, Peru, Colombia, Mexico) and western Gondwana (e.g. Iran; traditionally ‘eastern’ Gondwana). At this southern polar margin of the supercontinent, the faunas are composed of few widespread ‘cold water’ taxa that are not indicators of any faunal province, but represent ‘cold water’ taxa, well-known from the ‘Balto-Scandian Province’ in the ‘Cold Domain’ of the ‘Shallow Sea Realm’ of Zhen and Percival (2003). However, even when this concept is taking into account the older literature on conodont provincialism, there is still no province or domain that represents the shallow sea realm at circumpolar latitudes.

Zhen and Percival (2003) show the ‘Balto-Scandian Province’ as the only province of the ‘Cold Domain’ in the ‘Shallow Sea Realm’ characterized by low diversity. However, in contrast to high latitude peri-Gondwana areas, conodont diversity flourished on Baltica. For the Lower Ordovician ‘mixed’ faunas of NW Argentina, which are dominated by endemic taxa, but include Baltoscandian and Laurentian type elements, Zeballo and Albanesi (2013a) established a separate faunal province. Following the terminology of Servais and Sintubin (2009, their fig. 1), their new ‘Southwestern Gondwana Province’ for the ‘Cold Domain’ in the ‘Shallow-Sea Realm’ (Zeballo and Albanesi 2013a) should be recognized as a ‘Southeastern Gondwana Province’, if we look to the configuration of plates amalgamated in the Gondwana supercontinent relative to their latitudinal position and the South Pole (compare Servais and Sintubin, 2009, fig. 1).

This overview on previous models of conodont biogeography indicates that for the real low diverse faunas in the ‘Shallow Sea Realm’, a separate ‘subpolar domain’ is needed for the “really cold” siliciclastic peri-Gondwana shelves close to the South Pole. The creation of such a domain should fill the biogeographic gap existing so far and it should include the low divese subpolar ‘cold water’ faunas described from Morocco, Belgium, Germany, the Czech Republic, Turkey and France. A subpolar province in the ‘Cold Domain’ cannot be an alternative, because the widespread taxa representative of it are not indicative for any separate faunal province, and as discussed by Rasmussen (1998, p. 76), “it is necessary to exclude pandemic, deeper water conodont faunas from a data-set, before paleobiogeographic models can be tested". In other words, such widespread open marine taxa are useless for any provincial discrimination.

6. Conclusions

The discovery of conodont material in the Lower Ordovician Fezouata Shale of the Zagora area represents the first conodont record from the siliciclastic beds bearing the exceptionally well preserved Fezouata Biota and contributes to the biodiversity in these cold and shallow water deposits.

The horizons of the 'Fezouata Lagerstätte' with soft-tissue preservation include conodonts correlated with the interval spanning the uppermost Tremadocian *Acodus deltatus* subzone of the *Paroistodus proteus* zone through the lower Floian *Prioniodus elegans* zone.

The Early Ordovician faunal association is comparable in its low diversity to other coeval conodont faunas composed of widespread taxa from the cold water environments on the subpolar siliciclastic peri-Gondwana shelves. In this, the Moroccan faunas differ from higher latitude peri-Gondwana areas exhibiting a mix with 'warm water' taxa known from tropical and subtropical environments (e.g. the 'Southwestern Gondwana Province' of Northern Argentina) due to the influence of warmer currents. We therefore propose a 'subpolar faunal domaine' characterized by low diverse assemblages of widespread 'cold water' conodont taxa.

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Figure captions

Fig. 1. Location map of sample sites (modified from Van Roy et al., 2010). A) Outcrops of Ordovician successions in the Zagora area with marked sample locations. B) Distribution of Ordovician outcrops on a map of Morocco and adjacent areas showing the positions of Zagora and Adrar Zouggar Mountain.

Fig. 2. Lithostratigraphy of the Fezouata Lagerstätte, sample positions and ranges of selected conodont taxa. Lithostratigraphy of the Tizig Zaouine section, north of Zagora (see also Fig. 1). Stage slices according to Bergström et al. (2009).

Fig. 3. Conodont sample levels in borehole AZ-1. Position of the *messaoudensis-trifidum* assemblage according to Nowak et al. (2015, this volume). *p.-s.* = *Euconochitina paschaensis-symmetrica*. As pointed out by Nowak et al. (this volume), the boundary between the *paschaensis-symmetrica* and *Eremochitina brevis* zones may be higher up, because of the uncertainty using material from well cuttings.

Fig. 4. Conodonts recovered from the Fezouata Formation; TZ-Paly and FZ1 numbers refer to outcrop material recovered from the study region north of Zagora (Tizig Zaouine section and Bou Izargane area; see Figs. 1, 2). AZ1 numbers refer to sample levels in borehole AZ-1 indicated in fig. 3. Scale bars = 50 µm. A) *Acodus deltatus*; Sd element; AZ1-07. B) *Acodus deltatus*; FZ1 31-32. C) *Acodus deltatus*; AZ1-07. D) *Parapaltodus* aff. *P. flexuosus*; TZ-Paly 20. E) *Paroistodus* cf. *parallellus*; AZ1-11 F) *Periodon* cf. *selenopsis*; M element; AZ1-07. G) *Paroistodus proteus*; AZ1-07. H) *Paltodus* cf. *inaequalis*; TZ-Paly 27. I) *Acodus deltatus*; Sc element; AZ1-04. J) *Paroistodus proteus*; FZ1 3-4. K) *Drepanodus arcuatus*; TZ-Paly 23. L) *Drepanoistodus forceps*; TZ-Paly 24. M) *Periodon selenopsis*; TZ Paly 20. N) *Cornuodus longibasis*; TZ-Paly 17. O) *Scalpellodus* aff. *S. gracilis*; AZ1-09. P) *Protopanderodus* cf. *P. leonardii*; TZ-Paly 7. Q) *Prioniodus* sp.; AZ1-09. R) *Prioniodus* cf. *oepiki*; M element; AZ1-07. S) *Scolopodus* aff. *S. krummi*; TZ-Paly 17. T) *Semiacontiodus* cf. *cornuformis*; FZ1 37-41. U) *Semiacontiodus* cf. *cornuformis*; FZ1 37-41. V) *Tropodus* cf. *T. sweeti*; TZ Paly 28. W) *Prioniodus* sp.; Sc element; AZ1-07. X) *Scolopodus* aff. *S. krummi*; FZ1 395-396. Y) *Stolodus* cf. *S. stola*; AZ1-09. Z) *Tropodus* cf. *T. sweeti*; TZ-Paly 22. AA) *Tripodus* sp.; FZ1 37-41. AB) *Tripodus* aff *T. laevis*; AZ1-07.

Fig. 5. Distribution of the low diverse cold water conodont assemblages composed of cosmopolitan taxa in the Lower Ordovician. Plate tectonic reconstruction (ca. 480 Ma;

Tremadocian palaeogeography) derived from BugPlates (see Torsvik, 2009). Red circle = Zagora. (1) Iran (Alborz Mountains; Ghodabi Pour et al., 2011). (2) Turkey (Taurides; Gedik, 1977). (3) Czech Republic (Prague Basin; Zusková, 1993). (4) Montagne Noire, France (Küppers and Pohler, 1992; Serpagli et al., 2007). (5) Germany (Frankenwald area; Sannemann, 1955). (6) Armorican Massif, France (Lindström, 1976). (7) Spain (Iberia; Sarmiento et al., 2011, with references therein). (8) Belgium (eastern Avalonia; Vanguestaine et al., 2004). (9) Mexico (Oaxaca, Mixteca–Oaxaquia terrane of Torsvik and Cocks 2013a; Landing et al., 2007). (10) Colombia (Borrero et al., 2007; Gutiérrez-Marco et al., 2007). (11) Peru (e.g. Gutiérrez-Marco et al., 2008). (12) Northwestern Argentina (Eastern Cordillera; Albanesi et al. 2011; Zeballo and Albanesi, 2013a, 2013b; Zeballo et al., 2008, 2013, with references therein).

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Figure 1

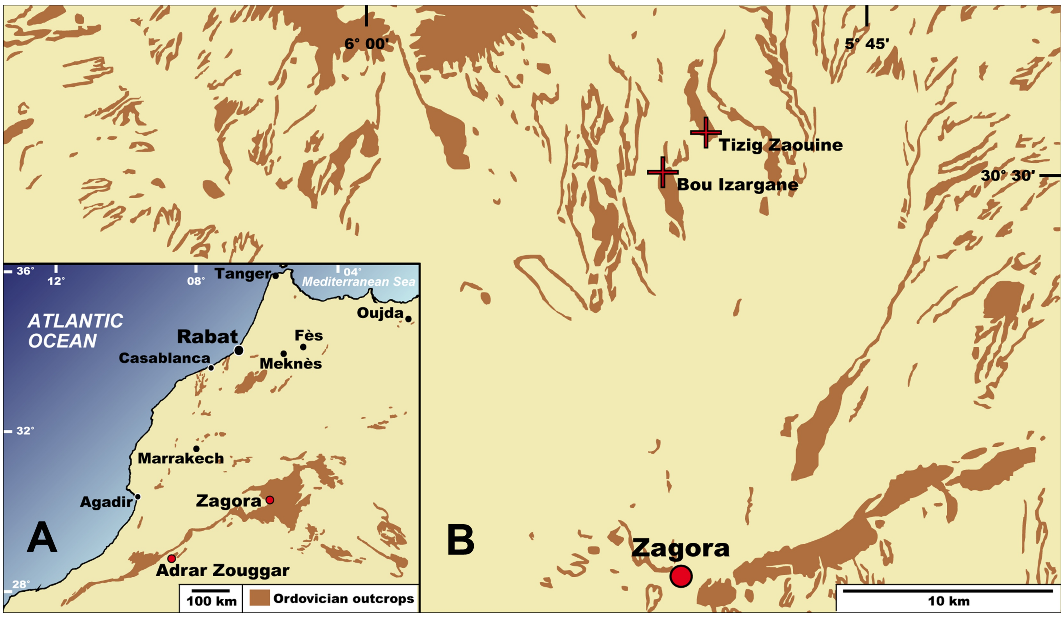

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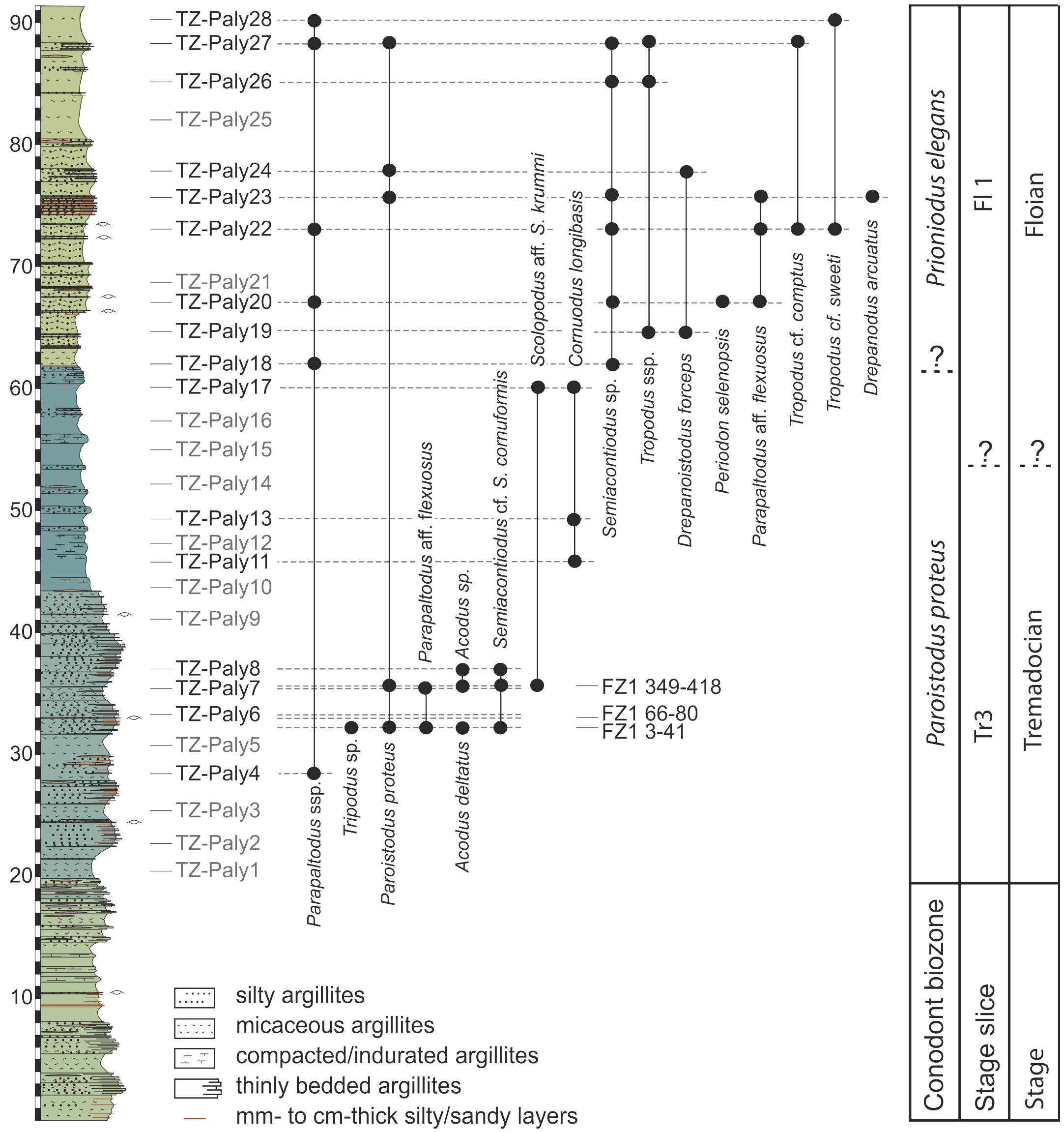
Figure 2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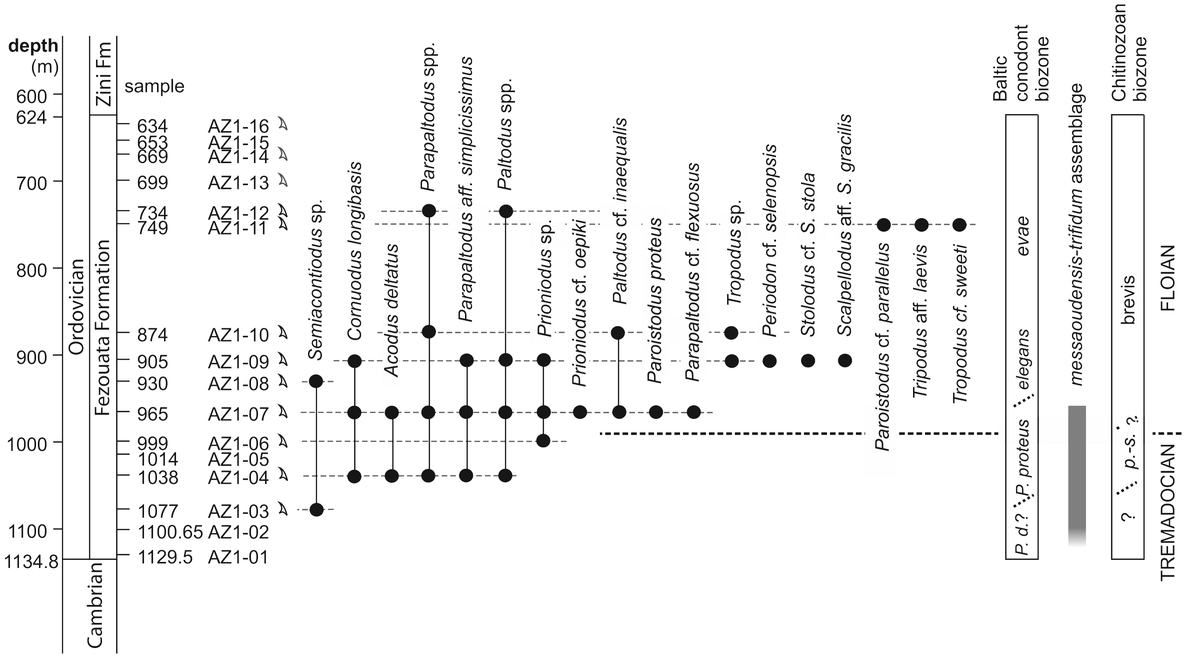
TZ-Paly6
TZ-Paly5
TZ-Paly4
TZ-Paly3
TZ-Paly2
TZ-Paly1
FZ1 349-418
FZ1 66-80
FZ1 3-41
Parapaltodus ssp.
Tripodus sp.
Paroistodus proteus
Parapaltodus aff. flexuosus
Acodus sp.
Acodus deltatus
Semiacontiodus cf. S. cornuformis
Scolopodus aff. S. krummi
Cornuodus longibasis
Semiacontiodus sp.
Tropodus ssp.
Drepanoistodus forceps
Periodon selenopsis
Parapaltodus aff. flexuosus
Tropodus cf. comptus
Tropodus cf. sweeti
Drepanodus arcuatus
silty argillites
micaceous argillites
compacted/indurated argillites
thinly bedded argillites
mm- to cm-thick silty/sandy layers
Conodont biozone
Stage slice
Stage
Prioniodus elegans
Paroistodus proteus
?
Fl 1
Tr3
?
Floian
Tremadocian
?

Figure 3


depth
(m)
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624
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Ordovician
Cambrian
Zini Fm
Fezouata Formation
sample
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653 AZ1-15
669 AZ1-14
699 AZ1-13
734 AZ1-12
749 AZ1-11
874 AZ1-10
905 AZ1-09
930 AZ1-08
965 AZ1-07
999 AZ1-06
1014 AZ1-05
1038 AZ1-04
1077 AZ1-03
1100.65 AZ1-02
1129.5 AZ1-01
Semiacontiodus sp.
Cornuodus longibasis
Acodus deltatus
Parapaltodus spp.
Parapaltodus aff. simplicissimus
Paltodus spp.
Prioniodus sp.
Prioniodus cf. oepiki
Paltodus cf. inaequalis
Paroistodus proteus
Parapaltodus cf. flexuosus
Tropodus sp.
Periodon cf. selenopsis
Stolodus cf. S. stola
Scalpellodus aff. S. gracilis
Paroistodus cf. parallelus
Tripodus aff. laevis
Tropodus cf. sweeti
Baltic conodont biozone
evae
elegans
P. proteus
P. d.?
messaoudensis-trifidum assemblage
Chitinozoan biozone
brevis
p.-s.
?
FLOIAN
TREMADOCIAN

Figure 4

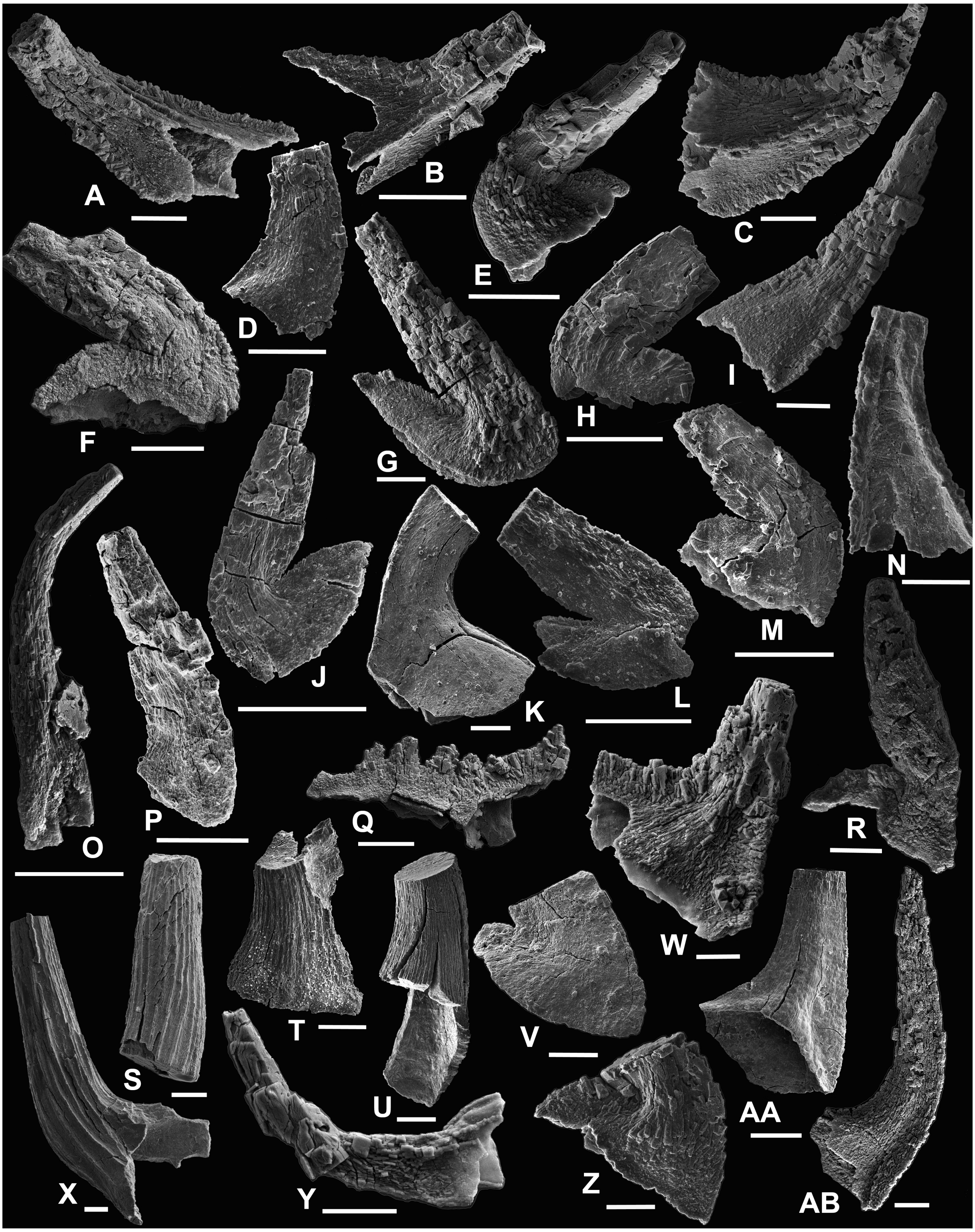

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Figure 5

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Article VI

The Lower Ordovician Fezouata Konservat-Lagerstätte from Morocco: Age, environment and evolutionary perspectives

Martin, E.L.O., Pittet, B., Gutiérrez-Marco, J.-C., Vannier, J., El Hariri, K., Lerosey-Aubril, R., Masrour, M., Nowak, H., Servais, T., Vandenbroucke, T.R.A., Van Roy, P., Vaucher, R. & Lefebvre, B.

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ABSTRACT

The Lower Ordovician Fezouata Konservat-Lagerstätte from southern Morocco has been one of the major palaeontological discoveries of the last decade. It provides a unique insight into one of the most critical periods in the evolution of marine life: the Cambrian–Ordovician transition. However, its potential for deciphering key trends in animal diversification was hitherto largely limited by major uncertainties concerning its stratigraphic position, age and environmental setting. Based on extensive fieldwork, fossil evidence, and facies recognition, our study provides clarification on these three crucial issues. Exceptional preservation is limited to two intervals within the Fezouata Shale. Graptolites indicate a late Tremadocian age for the Fezouata Konservat-Lagerstätte as a whole, which is supported by biostratigraphical evidence provided by acritarchs. Sedimentological features and reconstructed patterns of relative sea-level changes indicate relatively shallow-water environmental conditions, under distal storm influence, in an offshore to lower shoreface siliciclastic ramp setting. The Fezouata Biota represents a unique and exceptional window into the palaeobiodiversity in open-marine conditions, thus contrasting with the other Ordovician Konservat-Lagerstätten presently known. In our analyses of this new set of data, we pave the way for accurate temporal, faunal and environmental comparisons with other Lower Palaeozoic Konservat-Lagerstätten, and unlock the full potential of the Fezouata Biota to better understand the processes and scenarios of early animal radiations.

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1. Introduction

The Cambrian–Ordovician time interval (c. 541–443 Ma) is characterised by the evolution and radiation of animals that led to irreversible changes in marine ecosystems (Bambach et al., 2007; Vannier et al., 2007; Butterfield, 2011; Erwin and Valentine, 2013). Triggered by complex interacting factors (Smith and Harper, 2013; Maruyama et al., 2014; Santosh et al., 2014; Zhang et al., 2014), the Cambrian Explosion is the initial visible phase of animal diversification and is defined by the appearance in the fossil record of a wide spectrum of new anatomies and functionalities, and by complex ecological systems that have no counterparts in the Precambrian (Erwin et al., 2011; Shu et al., 2014). This evolutionary and ecological revolution is evidenced by several early to middle Cambrian Konservat-Lagerstätten (*sensu* Seilacher, 1970; termed "Lagerstätten" below; Fig. 1), which have yielded abundant and diverse remains of both shelly and non-biomineralised organisms such as those of Chengjiang (Hou et al., 2004; Zhao et al., 2009), Sirius Passet (Peel and Ineson, 2011), Emu Bay (Paterson et al., 2015), or the Burgess Shale (Caron and Jackson, 2008). They provide detailed information on the anatomy, lifestyles, and behaviours of early animals and also on their interactions within the evolving trophic web (Dunne et al., 2008; Vannier, 2011). Postdating the Cambrian Explosion, the Great Ordovician Biodiversification Event (GOBE) represents the second major burst in marine biodiversity. During most of the Ordovician Period, a sustained exponential diversification took place within almost all animal phyla (Harper, 2006; Servais et al., 2008, 2010). Unlike the Cambrian Explosion, the GOBE is primarily recognised from diversity

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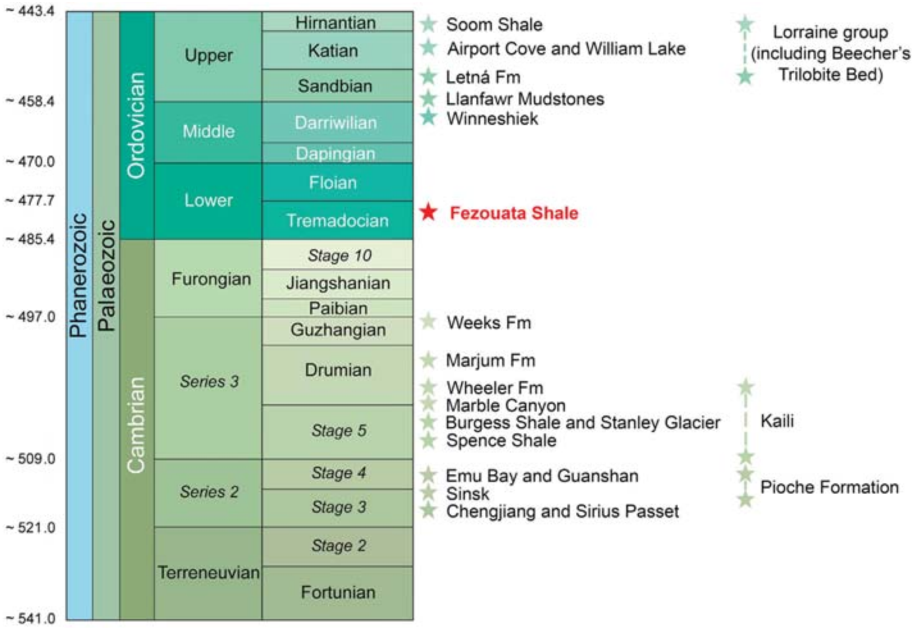

Fig. 1. Stratigraphic distribution of the main diverse exceptionally preserved faunas from the Cambrian and the Ordovician. Numerical ages in Ma.

analyses based on the fossil record of shelly faunas and microfossils. Indeed, Ordovician Lagerstätten are rare and most of them occur in the Upper Ordovician, long after the initial stages of the GOBE (Fig. 1). Moreover, they typically contain low diversity faunas that lived in restricted marine environments (e.g. Beecher's Trilobite Bed from the Lorraine Group, Farrell et al., 2013; Soom Shale, Gabbott, 1998; William Lake Biota of Manitoba, Young et al., 2007).

The recent discovery of a Burgess Shale-type Lagerstätte in the Lower Ordovician of Morocco (Zagora area, Central Anti-Atlas, Fig. 2A; Van Roy et al., 2010) provided unexpected and unprecedented

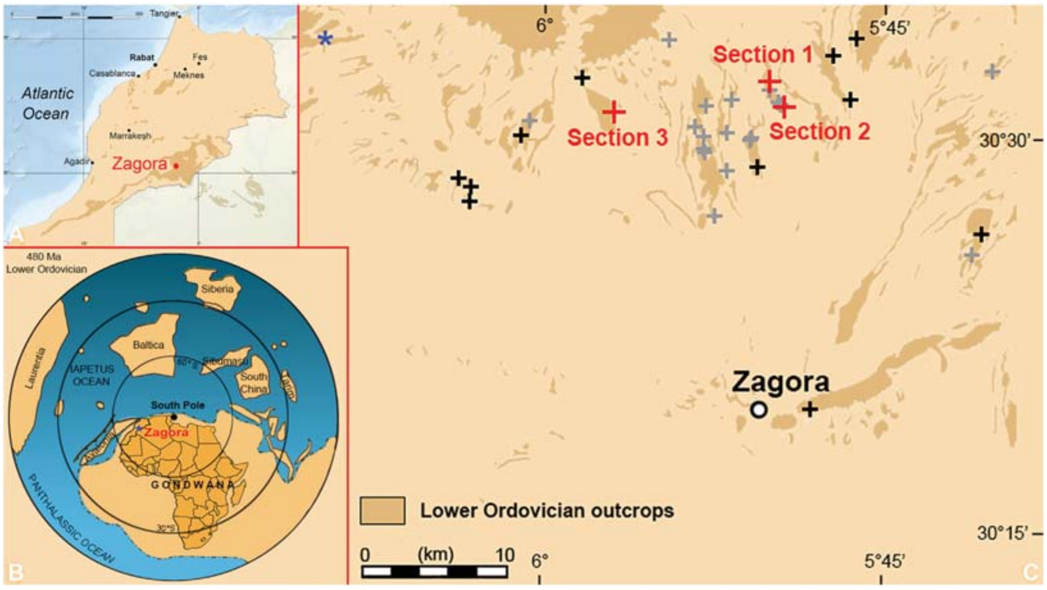

Fig. 2. A, Lower Ordovician outcrops of northern Morocco and location of Zagora; B, Palaeogeography of Africa (blue star represents Zagora) in the Early Ordovician (modified from Cocks and Torsvik, 2004; Torsvik and Cocks, 2011); and C, Lower Ordovician outcrops in the Zagora area. Small black crosses indicate logged sections and red crosses the three key sections used to build the composite stratigraphic column (Fig. 4). Small grey crosses and blue asterisk indicate the inspected and non-inspected localities that yielded EPF respectively (Van Roy et al., 2010; modified). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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possibilities to obtain high-resolution information on both the aftermath of the Cambrian Explosion and the very beginning of the Ordovician radiation event. Although still largely undescribed, the diverse fossil assemblages of the Fezouata Biota (Fig. 3) are characterised by the co-occurrence of organisms typical of Cambrian Burgess Shale-type biotas (Van Roy et al., 2010), such as anomalocaridids (Van Roy and Briggs, 2011; Gaines et al., 2012a; Van Roy et al., 2015) and some demosponges (Botting, 2007) with classical Ordovician faunal elements. The biomineralised component of the Fezouata Biota is dominated by trilobites (e.g. Destombes, 1972; Rábano, 1990; Henry et al., 1992; Vidal, 1998a,b; Chatterton and Fortey, 2008; Fortey, 2009, 2011a,b) and echinoderms (Ubaghs, 1963; Chauvel, 1966, 1969, 1971a,b, 1978; Chauvel and Régnault, 1986; Donovan and Savill, 1988; Lefebvre and Botting, 2007; Noailles et al., 2010; Sumrall and Zamora, 2011). The fauna also contains a great abundance of xiphosurid arthropods (Van Roy et al., 2010), palaeoscolecidan worms, annelids (machaeridians, Vinther et al., 2008), molluscs (Babin and Destombes, 1990; Horný, 1997; Kröger and Lefebvre, 2012), hyolithids (Marek, 1983; Valent et al., 2013), brachiopods (Havliček, 1971; Mergl, 1981, 1988), and conularids (Destombes et al., 1985). Graptolites are also abundant but have not been studied in detail so far (Destombes and Willefert, 1959; Willefert in Destombes et al., 1985; Aceñolaza et al., 1996). Despite this remarkable diversity, two main obstacles have so far limited the impact of the Fezouata Lagerstätte. First, most fossils were collected from isolated excavations lacking an accurate positioning within the lithological succession. This led Van Roy et al. (2010) to hypothesise that the Fezouata Lagerstätte could span a time period of almost 10 Myr (late Tremadocian to late Floian). Second, major uncertainties remained concerning the environmental setting of the Fezouata Biota, especially in terms of bathymetry, energy and oxygenation. The Lower Ordovician succession in the Zagora area has remained virtually unstudied since the pioneering work of Destombes et al. (1985). Based on extensive fieldwork in the Zagora area, new fossil studies, and facies recognition, we here provide clarification on these two crucial chronological and environmental issues, making it possible for the first time 1) to establish precise comparisons with other Lower Palaeozoic Lagerstätten and 2) to test the potential of the Fezouata Lagerstätte in resolving the pace and amplitude of the animal diversification in the Early Palaeozoic.

2. Geological setting

In the Anti-Atlas of south-eastern Morocco, the Cambrian–Ordovician transition is exposed in the Ternata plain, 30 km north of Zagora. The Guzhangian (Cambrian series 3) sandstones of the Tabanite Group are unconformably overlain by the Tremadocian to Floian (Lower Ordovician) deposits of the Lower Fezouata, the Upper Fezouata, and the Zini formations, which, together with the Tachilla Formation (Middle Ordovician), form the Outer Feijas Group (Destombes et al., 1985; Geyer and Landing, 2006). The Lower and Upper Fezouata formations constitute a thick (up to 1200 m) and rather monotonous sequence dominated by silty and micaceous argillites. A glauconitic and ferruginous horizon has often been used as a possible lithological marker for the boundary between the two formations, which have been regarded as Tremadocian and Floian in age respectively (Destombes et al., 1985). However, this horizon is missing in the Zagora area, where the Fezouata Lagerstätte is located. Consequently, the Lower and Upper Fezouata formations are here considered together as a single lithological unit: the Fezouata Shale, which is topped by the sandstone-dominated Zini Formation (Destombes, 1962; Destombes et al., 1985).

During the Early Ordovician, the Anti-Atlas was located on the southern margin of Gondwana and situated in the southern hemisphere at high latitudes (c. 65°S), relatively close to the South Pole (Fig. 2B, Cocks and Torsvik, 2004; Torsvik and Cocks, 2011, 2013). The Lower Ordovician sediments were deposited in a rifting context associated with the northward drift of Avalonia away from the Gondwanan palaeocontinent (Cocks and Torsvik, 2004).

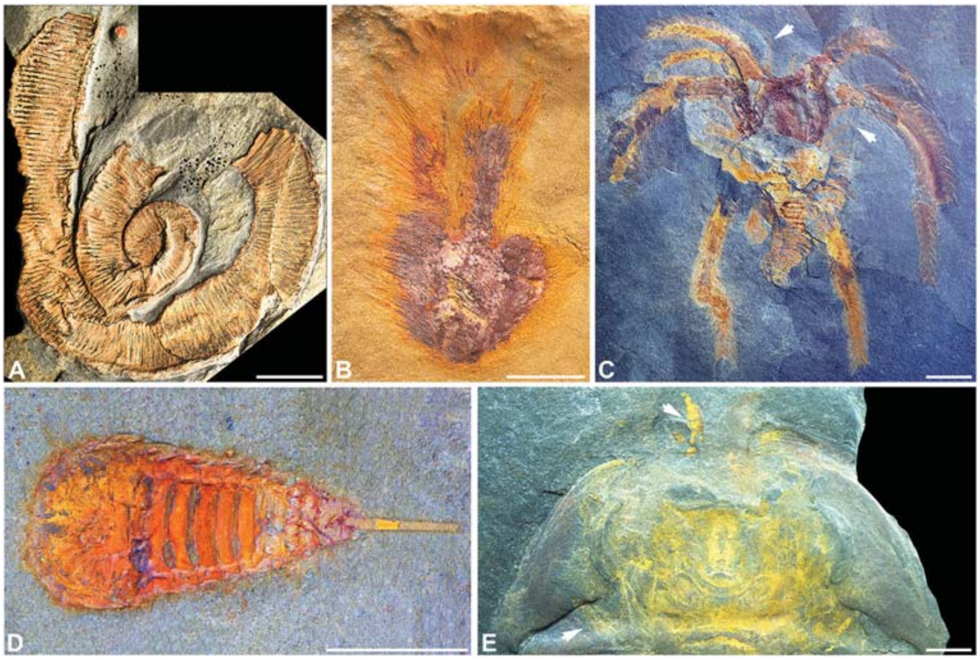

Fig. 3. Examples of exceptionally preserved fossils from the Fezouata Biota (latest Tremadocian; Zagora area, Morocco). A, undetermined palaeoscolecid worm, AA-BGF2-OI-1; B, *Pirania auraeum* Botting, 2007, demosponge, AA-JBZ-OI-115; C–E, arthropods with preserved appendages (arrows); C, *Furca* sp. (Marrellomorpha), AA-BIZ31-OI-39; D, Xiphosuran (Chelicerata) with fully segmented opisthosoma, FSL 712 411; E, *Bavarilla* sp. (Trilobita), AA-BIZ15-OI-16. All specimens were photographed under alcohol. Scale bars: A–C, 5 mm; D–E, 2 mm.

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3. Material and methods

3.1. Exceptional preservation

The Fezouata Lagerstätte is a Konservat-Lagerstätte that is by definition characterised by the occurrence of exceptionally well-preserved fossils (EPF). In the Fezouata Lagerstätte, EPF were soft-bodied and lightly sclerotised organisms (e.g. worms, sponges, arthropods) that are usually preserved via pyritisation and subsequent weathering to iron oxides, giving the fossils a reddish colour. EPF typically display more or less complete anatomical (e.g. digestive structures) and exoskeletal features (e.g. arthropod appendages).

3.2. Fieldwork

The whole Lower Ordovician succession exposed in the Zagora area (Central Anti-Atlas, Morocco; Fig. 2C) was logged at a decimetre scale from fourteen different sections (black and red crosses on Fig. 2C). Data were compiled in a single, synthetic c. one thousand-metre-thick stratigraphic column. All localities yielding EPF mentioned in the original contribution of Van Roy et al. (2010) were included in this study, except one located c. 15 km west of the main outcrop area (blue asterisk on Fig. 2C). EPF localities were carefully located and positioned along the stratigraphic column based on their lithological characteristics (colour, composition, marker beds) and faunal elements (mostly graptolites, trilobites, and to a lesser extent echinoderms). Graptolites were collected throughout the succession, but particular attention was paid to horizons yielding EPF. Changes in lithology and sedimentary structures were observed throughout the succession and were used to reconstruct short-term and long-term relative sea-level changes. EPF and graptolites were photographed using a Nikon D3X camera (with a Micro-Nikkor AF 60 mm f/2.8D macrolens) and a Leica MZ12.5 microscope, equipped with a Leica integrated digital camera. When necessary, fossils were immersed under dilute ethanol in order to enhance contrast and avoid reflective spots. All fossil specimens are deposited in the collections of the Cadi Ayyad University, Marrakesh (Faculté des Sciences et Techniques, Guéliz; sample number prefix AA), except for one, which is deposited in the palaeontological collections of Lyon 1 University, Villeurbanne (sample number prefix FSL).

4. Results and interpretations

4.1. Stratigraphic distribution and age of the Fezouata Biota

The lithology of the Fezouata Shale Formation is fairly homogeneous and largely dominated by fine-grained siliciclastic deposits, except in its lowermost and uppermost parts. The lower part of the Fezouata Shale is characterised by a transgression from a foreshore environment, whereas its upper part records a regressive trend. The distribution of EPF throughout the thousand-metre-thick Fezouata Shale shows that exceptional preservation occurs within a restricted interval in the lower part of the succession. Fig. 4 summarises the stratigraphic distribution of graptolites across this interval and its facial characteristics (colour, lithology, sedimentary structures). About three hundred well-preserved graptolite specimens were collected, identified, and used for dating the lower part of the Fezouata Shale. Graptolites also occur locally as monospecific mass-occurrences of *Araneograptus murrayi* (Hall) and “*Tetragraptus*” *bulmani* Thomas. The facies evolution within the entire succession and the structural context of the Lower Ordovician in the area of Zagora are beyond the scope of this contribution and will be the subjects of a separate study.

The studied succession is rather homogeneous, being composed of mainly thinly-bedded argillites with frequent intercalations of silts and millimetre- to centimetre-thick silty to sandy beds. Facies variations consist of slight differences in argillite composition (e.g. presence of silts or micas), or in diagenesis (e.g. induration, bedding). EPF are restricted to a 70-metre-thick interval developed between 260 and 330 m above the basal contact with the Guzhangian Tabanite Group and are usually found in relatively fine facies, the beds overlying them being coarser. They occur within two distinct intervals of c. 25 (interval 1) and 15 (interval 2) metres in thickness respectively, separated by a c. 30-metre-thick interval where only biomineralised remains are found (e.g. brachiopod shells, echinoderm skeletons, trilobite carapaces).

Eleven graptolite species have been recognised through the studied succession (Fig. 5). These include the index species of the *A. murrayi* and *Hunnegraptus copiosus* graptolite biozones, which are the uppermost graptolite zones of the Tremadocian (Loydell, 2012). *A. murrayi* occurs in great abundance from 240 to 295 m above the base of the Fezouata Shale. EPF-bearing Interval 1 falls within the *A. murrayi* Biozone. EPF-bearing Interval 2 mainly belongs to the upper part of the *A. murrayi* Biozone. Only the uppermost part of this interval corresponds to the following *H. copiosus* Biozone, as indicated by the first occurrence of *H. copiosus*. EPF-bearing intervals 1 and 2 are thus both of late Tremadocian age and correlate with the Tr3 substage of Bergström et al. (2009).

4.2. Environmental setting of the Fezouata Biota

Ripple marks, hummocky cross-stratification (HCS), and normally-graded tempestites are repeatedly found throughout the section, including in the two intervals with EPF (Fig. 6A–D). These sedimentary structures are interpreted as being induced by storm wave action on the sea floor (Harms et al., 1975; Duke, 1985; Duke et al., 1991; Gupta, 1998) and suggest a depositional environment at or above storm wave-base. However, HCS observed in the studied succession are only at a millimetre- to centimetre-scale, whereas they can reach several decimetres elsewhere in the succession (e.g., near the contact with the Zini Formation). These small-scale HCS suggest a relatively shallow depositional environment, most probably located within the offshore to lower shoreface (as defined by McLane, 1995; Fig. 6E).

Three long-term cycles of relative sea-level fluctuations are recognised in the entire Fezouata Shale, but only the first and the second of them are documented in the presented section (Fig. 4). All are composed of a transgressive phase marked by an evolution from silt-dominated to clay-dominated intervals and a regressive phase marked by the opposite trend. Exceptional preservation occurs at the end of the regressive phase of the first cycle and at the beginning of the transgressive phase of the second cycle (Fig. 4). Additionally, facies changes towards more argillaceous sedimentary deposits and fewer silty tempestites, or towards more silty argillites interrupted by more frequent silty or fine-sandy tempestites are interpreted as transgressive and regressive phases of short-term cycles respectively. Two of them are associated with the preservation of EPF.

5. Discussion

5.1. Exceptional preservation: stratigraphic distribution and environmental factors

The distribution of EPF within the Fezouata Shale is restricted to two narrow stratigraphic intervals, which contradicts earlier assessments (Van Roy et al., 2010) that exceptional preservation occurs throughout the Fezouata Shale. This is a common point shared with most major Cambrian and Ordovician Lagerstätten in which exceptional preservation is limited to a relatively narrow stratigraphic interval, ranging from a few metres – e.g. Sinsk (Russia; Ivantsov et al., 2005), Emu Bay (Australia; Gehling et al., 2011), the Spence Shale (USA; Liddell et al., 1997), the Burgess Shale (Canada; Collom et al., 2009), or the Llanfawr Mudstones (UK; Botting et al., 2011) – to a few tens of metres, as in Chengjiang (China; Babcock and Zhang, 2001), the Pioche Shale (USA; Moore and Lieberman, 2009), Wheeler Formation (USA; Brett et al.,

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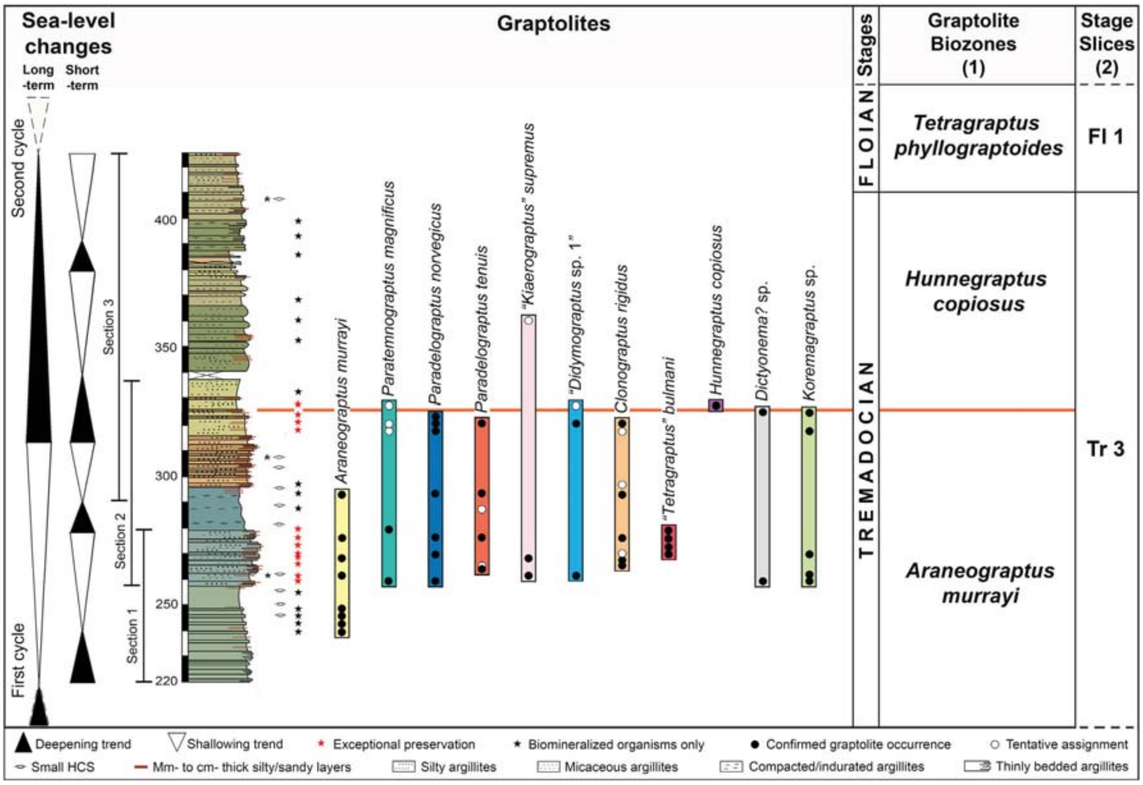

Fig. 4. Partial composite section of the Fezouata Shale (Lower Ordovician, Zagora area) showing the distribution of Exceptionally Preserved Fossils (EPF; red stars) and the vertical range of diagnostic graptolites. Right columns modified from (1) Loydell (2012) and (2) Bergström et al. (2009). The colours in the logged section roughly correspond to the colours of outcropping rocks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2009), or the Soom Shale (South Africa; Aldridge et al., 1994). An exception is the Guanshan Biota (China; Hu et al., 2010), which seems to occur throughout the entire Wulongqing Formation, which can reach up to 60 m in thickness. Environmental conditions maintained over a relatively short timespan may account for the preservation of EPF within a narrow stratigraphic interval (Hagadorn, 2002). Exceptional preservation is often associated with the rapid burial of organisms, which is supposed to promote oxygen restriction and to favour the preservation of soft tissues and lightly sclerotised features (Gaines et al., 2012b). Different mechanisms of entombment have been proposed. For example, a mostly turbiditic origin is often suggested for the mudrock–siltstones of the Burgess Shale (Gabbott et al., 2008), with probably a rhythmic deposition from waxing and waning density currents (Gabbott and Zalasiewicz, 2009). Recent studies of the Burgess Shale communities (Caron and Jackson, 2008; Caron, 2009) show that the fauna was mostly preserved *in situ* and only moderately disturbed by the event of burial. Most organisms were buried *in situ* by distal mudflow events. In Chengjiang, a typical sedimentary succession is recognised (Hu, 2005). It consists of background layers dominated by hemipelagic mud, which are interrupted by event layers that contain soft-bodied fossils. These event layers are generated by bottom-flowing density currents, which are responsible for the burial of the fauna.

Although storms played an important role in the overall depositional mode of the Fezouata Shale (as indicated by the presence of numerous HCS and tempestites), the storm waves seem to have had a limited influence on the relatively distal deposits that contain EPF. Indeed, storm currents were weak in this area, as attested by the relatively small scale of the HCS found, resulting from a mainly oscillatory movement at the seafloor. The animal communities of the Fezouata Shale were probably buried *in situ* during storm events, which mobilised more proximally a large amount of coarser sediments. Between two storm events, the background sedimentation resulted from the decantation of mud suspended by wave action. It is not associated with any sedimentological structures, such as HCS and tempestites. This depositional scenario would be comparable to the one invoked for the Chengjiang and other Burgess Shale-type Lagerstätten (Gaines et al., 2012b).

The geochemical context of the Fezouata Shale has not yet been explored and will be investigated on fresh rocks obtained from drill cores (in progress). No detailed information is available on the redox conditions that prevailed at the water–sediment interface and within the sediment. However, the presence of iron oxides in the majority of the weathered EPF suggests that an early mineralisation of pyrite took place on both soft and sclerotised tissues and was induced by microbial activity under anaerobic conditions (Gabbott et al., 2004; Vinther et al., 2008; Van Roy et al., 2010). The exceptional preservation of giant anomalocaridids in silica-chlorite concretions is unusual among Burgess Shale-type Lagerstätten and possibly involved the dissolution of volcanic ashes in the sediment (Gaines et al., 2012a). Field observations indicate that bioturbation associated with EPF-bearing intervals was limited to mostly narrow horizontal burrows, very close to the water–sediment interface. This supports a low infaunal activity, possibly related to dysoxic/anoxic conditions within the sediment.

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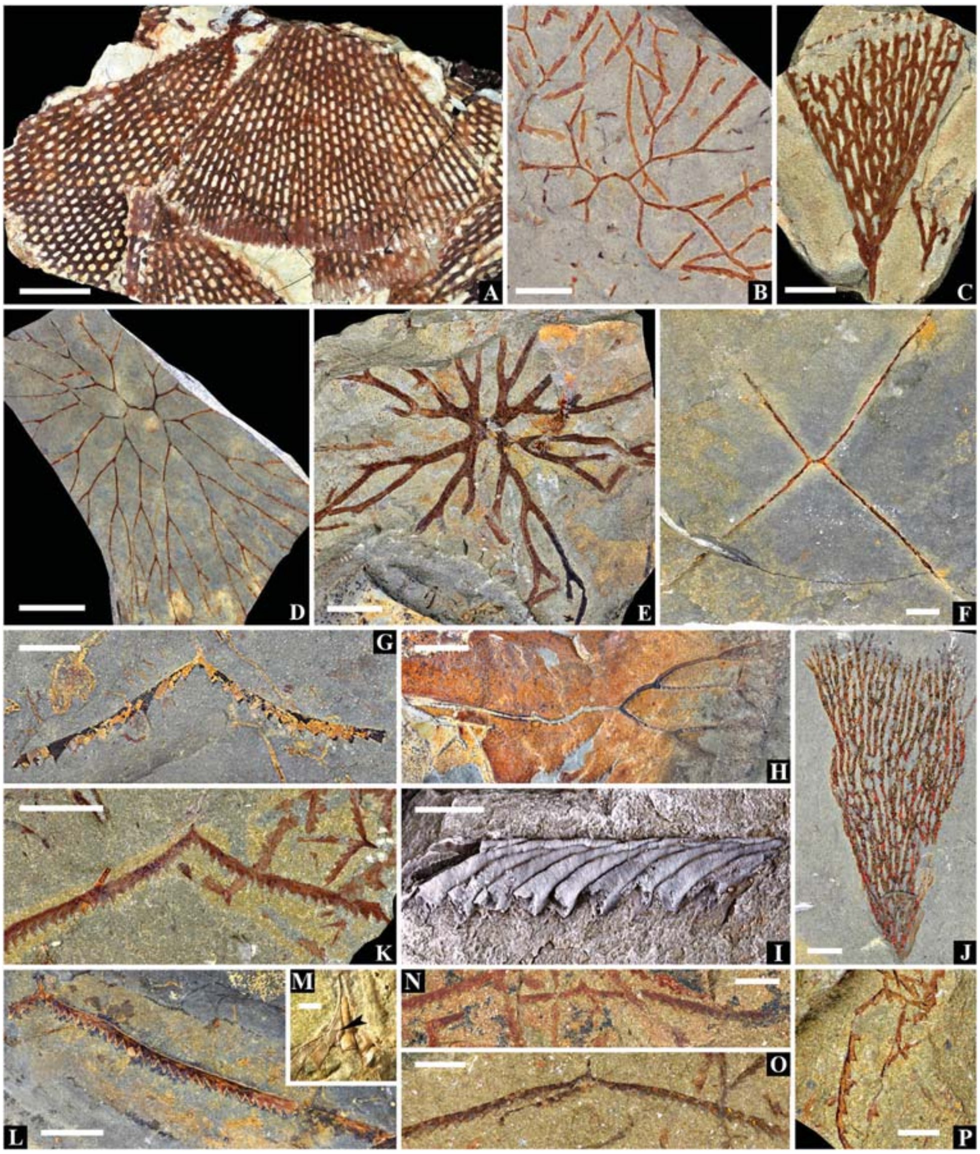

Fig. 5. Graptolites of the Fezouata Biota (late Tremadocian; Zagora area, Morocco). A, *Araneograptus murrayi* (Hall, 1865), AA-BIZ3-OI-35 showing nematularium (upper left) and distal end on another young colony (centre-right); B, *Paradelograptus tenuis* Lindholm, 1991, AA-OFTa-OI-23; C, *Koremagraptus* sp., AA-FETi-OI-1; D, *Clonograptus rigidus* (Hall, 1858), AA-JTZb-OI-19; E, *Paradelograptus norvegicus* (Monsen, 1937), AA-JTZ-OI-10; F, "*Tetragraptus*" *bulmani* Thomas, 1973, AA-BIZ13-OI-9; G, "*Didymograptus* sp. 1" (cf. Lindholm, 1991), AA-BIZ31-OI-40; H–I, *Paratemnograptus magnificus* (Pritchard, 1892), fragment of a large rhabdosome (F, AA-BZG-OI-13) and detail of a stipe showing plaited thecal structure (triad budding without bithecae), AA-BIZ13-OI-10; J, *Dictyonema*? sp., AA-BZG-OI-14; K–M, "*Kiaerograptus*" *supremus* Lindholm, 1991, K = AA-BGF2-OI-7; L = AA-BGF2-OI-6, with detail of the proximal end (M) showing sicular bitheca (arrow); N–O, *Hunnegraptus copiosus* Lindholm, 1991, N = AA-JBZ-OI-117; O = AA-JBZ-OI-116; and P, *Paradelograptus* sp., AA-JTZ-OI-9. All specimens, except A, H, I and M, were photographed under alcohol. Scale bars: A, D, and H, 20 mm; E, 10 mm; C, F, K, L, and J, 5 mm; B, G, N, and O, 3 mm; I, and P, 2 mm; and M, 0.5 mm.

5.2. Dating the Fezouata Lagerstätte

Graptolites (*A. murrayi* and *H. copiosus* biozones) indicate a late Tremadocian age for the EPF-bearing intervals of the Fezouata Shale. Therefore, the Fezouata Lagerstätte does not extend to the Floian as suggested previously (Van Roy et al., 2010). It cannot be entirely ruled out that *H. copiosus* occurs lower in the stratigraphy. As the base of the *H. copiosus* Biozone is defined by the First Appearance Datum of this biozonal marker graptolite (Egenhoff et al., 2004), a larger portion of the interval 2 may belong to the *H. copiosus* Biozone. However, the resulting changes would be of little significance regarding the age of the Fezouata Biota, which would remain late Tremadocian (Tr3 of Bergström et al., 2009).

The only excavation that was not re-studied in detail (blue asterisk in Fig. 2C) yielded the graptolite *Clonograptus* along with the trilobite *Dikelokephalina brenchleyi*. Both would suggest a late Tremadocian age (Fortey, 2009, 2011b).

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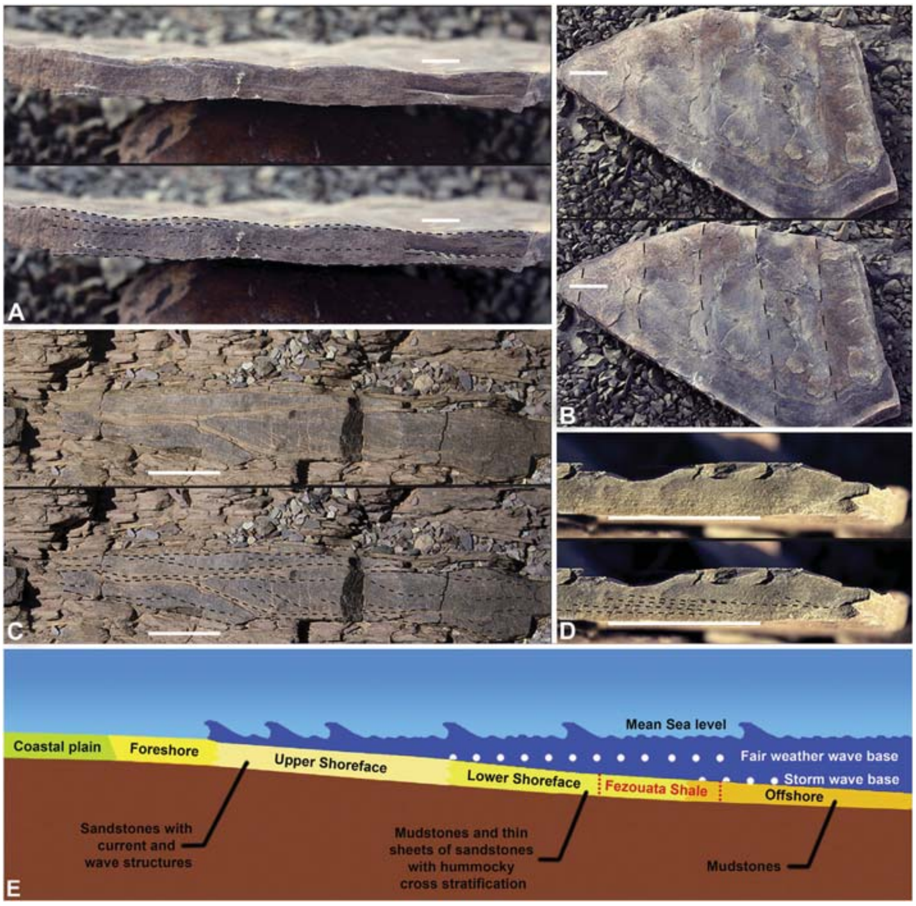

Fig. 6. Typical sedimentary structures used to characterise the palaeoenvironment of the Fezouata Shale. A–B, 2D-wave ripples in a distal tempestite, in section and slab surface, respectively. C, small, centimetre-scale hummocky cross stratifications (HCS) from the top of the section. D, thin, possibly wave-induced cross-laminated structures in a distal silty tempestite. E, general palaeoenvironmental reconstruction for the Fezouata Shale deposition. Terminology of depth zones follows the definition of McLane (1995). Scale bars: A–B, 1 cm; and C–D, 3 cm.

Graptolites are both abundant and well preserved throughout the Fezouata Shale (Fig. 5). They are reliable markers for dating and correlations, especially in the Ordovician (Webby et al., 2004; Sadler et al., 2009). The graptolite assemblages of the Fezouata Shale are dominated by planktonic forms that are assumed to have lived in epipelagic niches (Cooper et al., 1991, 2012a), with a small percentage of rooted benthic dendroids (Fig. 5C and J). The planktonic ones have a cosmopolitan distribution and have been widely used for global correlations. They occur in Scandinavia (Lindholm, 1991), North America (Williams and Stevens, 1991; Maletz, 1997; Jackson and Lenz, 2003), South America (Maletz and Egenhoff, 2001; Ortega and Albanesi, 2005), China (Feng et al., 2009) and southwestern Europe (Aceñolaza et al., 1996; Pillola et al., 2008).

Microfossils, such as acritarchs, chitinozoans, and conodonts, are also accurate biostratigraphic markers, but their study requires fresh material (e.g. from well drillings or boreholes; Elaouad-Debbaj, 1988) for high-resolution dating. Acritarchs typical of the late Tremadocian to lower Floian *messaoudensis–trifidum* assemblage occur in the lower part of the Fezouata Shale below and within EPF-bearing interval 1. This particular acritarch assemblage indicates a late Tremadocian age, correlating to the top of the *A. murrayi* and the base *H. copiosus* graptolite biozones (Molyneux et al., 2007). Cuttings from a drill, which presumably crosses the Fezouata Shale, about 300 km southwest of Zagora, yielded comparable acritarch assemblages equally pointing to a late Tremadocian age (Nowak et al., 2015).

5.3. Environmental setting: implications

Sedimentological features indicate that the Fezouata Shale was deposited above storm wave-base, in a relatively shallow, open-marine environment (offshore to lower shoreface, Fig. 6e). Based on comparisons with the depth of storm influence in modern oceans (Immenhauser, 2009), a palaeodepth ranging from 50 to 150 m is proposed for the depositional area of the Fezouata Shale. The Fezouata Biota also delivers interesting indications of water depths. Based on the characteristics of the mitrate (Echinodermata, Stylophora) *Peltocystis cornuta* from the Fezouata Formation, Lefebvre and Botting (2007) concluded that the environment was shallow and of moderately high energy. In addition, non-calcareous algae are present in the fauna (Van Roy et al., 2010), but they might also have been transported in from shallower waters. Thus, their presence should be considered with caution and is not a reliable depth indicator. In this respect, the visual systems of the articulated benthic trilobites are probably more useful. All trilobites of this stratigraphic interval seem to have eyes (except *Ampyx* cf. *priscus*; Vidal, 1998a,b). This would suggest that there must have been at least some visible light, but not necessarily enough for

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photosynthesis. As a consequence, a maximum depth of 150 m might be overestimated, given the low insolation received in high latitudes (Kirk, 2011). The weak contrasts in lithology and facies throughout the cycles of short- and long-term sea-level changes indicates relatively low-amplitude sea-level fluctuations and thus, a relatively stable sea level close to storm wave-base over a relatively long time span (at least from the *A. murrayi* to the *H. copiosus* biochrons that represent a duration of about 2 Myr; Cooper et al., 2012b).

The palaeoenvironmental setting (open shelf close to the limit between the lower shoreface and the offshore) of the Fezouata Biota differs markedly from that of all Ordovician Lagerstätten presently known (Fig. 1), which are associated with particular marine environments. Indeed, the Winneshiek Biota (USA) lived in a possible estuarine embayment (Liu et al., 2006), the Beecher's Trilobite Bed (USA) was deposited under dysoxic conditions in an environment of deposition of distal turbidites (Farrell et al., 2013), the Llanfawr mudstones (UK) represented deep-water or abyssal environments (Botting et al., 2011), the Letná Formation (Czech Republic; Fatka et al., 2013), the Airport Cove and William Lake (Canada; Young et al., 2007) were located in shallow peritidal settings and the Soom Shale (South Africa) was close to a retreating ice front (Aldridge et al., 2001).

Therefore, the Fezouata Lagerstätte opens a unique and exceptional window into the marine biodiversity within open-marine environments during the Early Ordovician and makes it possible for the first time to establish accurate comparisons with the older well-documented open-marine exceptional biotas from the Cambrian. Among them, the Burgess Shale (Canada; Collom et al., 2009), Kaili (China; Zhao et al., 2005), Sinsk (Russia; Ivantsov et al., 2005), and Sirius Passet (Greenland; Ineson et al., 2011) Lagerstätten are associated with distal offshore environments, whereas the Emu Bay Shale Lagerstätte (Australia; Gehling et al., 2011) is characterised by a relative nearshore setting affected by the tectonics of an active margin. In terms of environmental setting, the Fezouata Lagerstätte may best compare with the Guanshan and Chengjiang Lagerstätten (Hu, 2005; Hu et al., 2010; MacKenzie et al., 2015), although the environmental conditions that prevailed at Chengjiang are still debated (see Zhao et al., 2012). A lower shoreface/offshore depositional environment has been inferred for these three localities, in which early diagenetic pyritization represents the dominant mode of soft-tissue preservation (Gabbott et al., 2004; Van Roy et al., 2010; Vinther et al., 2008).

Another important characteristic of the Fezouata Lagerstätte is its high latitudinal position (c. 65°S) compared with that of other Ordovician and Cambrian Lagerstätten (Fig. 2B, Cocks and Torsvik, 2004; Torsvik and Cocks, 2011). The Hirnantian Soom Shale Lagerstätte (South Africa) was previously thought to be located at 60°S, but more recent palaeogeographic reconstructions suggest a much lower latitude (i.e. 35°S; Whittle et al., 2007; Torsvik and Cocks, 2013). Unlike the Soom Shale (Gabbott, 1998), no glaciogenic sediments are associated with the Fezouata Biota. This raises the important question of the climatic conditions and seawater temperature that prevailed and may have influenced the diversity and composition of the Fezouata Biota. Nevertheless, the very nature of the global climate state during the Early and Middle Ordovician is under discussion (Trotter et al., 2008; Vandenbroucke et al., 2009; Nardin et al., 2011; Turner et al., 2011).

5.4. A Late Tremadocian Lagerstätte : evolutionary perspectives

The Fezouata Biota is a key source of information for understanding the biotic turnover that took place during the Cambrian–Ordovician transition, i.e. after the Cambrian Explosion and before the GOBE. The co-existence of Burgess Shale-type faunal elements (such as marrellomorphs and anomalocaridids) with remarkably derived, typical post-Cambrian organisms (such as crinoids, ostracods and xiphosurids) indicates that the transition between the Cambrian and Palaeozoic Evolutionary Faunas (Sepkoski, 1979) was more complex and extended than hitherto realised. Moreover, the presence of several surprisingly advanced forms in the biota, such as xiphosurid arthropods, machaeridians, or cheloniellids (Van Roy et al., 2010), suggests that at least in some non-biomineralised groups, the GOBE started earlier than previously thought. This supports the idea that, rather than being two distinct events, the Cambrian Explosion and the GOBE might in fact represent different phases of the same dynamic of diversification (Droser and Finnegan, 2003; Van Roy et al., 2010).

6. Conclusions

Exceptional preservation in the Fezouata Shale is restricted to two relatively narrow intervals that belong to the upper Tremadocian (*A. murrayi* to basalmost *H. copiosus* graptolite biozones). The animal communities of the Fezouata biota lived in an open-marine environment, in a relatively shallow setting (offshore to lower shoreface transition) close to the storm wave-base. Organisms were very likely buried *in situ* during storm events, with a background sedimentation resulting from the decantation of mud suspended by wave action. By offering better chronological and environmental constraints, our results reveal the potential of the Fezouata Biota for understanding the early steps of animal life. Future investigations will concentrate on the identification of the taphonomic and/or abiotic factors controlling the restricted stratigraphic distribution of EPF within the thousand-metre-thick Fezouata Shale.

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Article VII

Exceptionally preserved arthropodan microfossils of possible crustacean origin from the Middle Ordovician Winneshiek Lagerstätte, Iowa, USA

Nowak, H., Harvey, T.H.P., Liu, H., McKay, R.M. & Servais, T.

in preparation for *Lethaia*

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Exceptionally preserved arthropodan microfossils of possible crustacean origin from the Middle Ordovician Winneshiek Lagerstätte, Iowa, USA

Hendrik Nowak, Thomas H. P. Harvey, Paul Liu Huaibao, Robert M. KcKay and Thomas Servais

The Middle Ordovician Winneshiek Shale (Darriwilian; Winneshiek County, Iowa, USA), hosts a Konservat-Lagerstätte that has yielded a diverse fauna including soft-bodied fossils. The shale is rich in organic content, in particular fragmentary cuticular remains. Palynological acid treatment enables the extraction of these "small carbonaceous fossils" (SCFs) from the matrix, allowing a more detailed view of their morphology. This method has yielded exceptionally well-preserved crustacean-type setae and a population of distinctive microfossils that we tentatively identify as the mandibles of a small-bodied crustacean. The Winneshiek mandibles share some important features with those of branchiopod crustaceans, including the apparent lack of a mandibular palp, but they are unusual in having a curved gnathal edge with no division into incisor and molar processes. The abundance of the mandibles points to a previously cryptic organism of importance in the Winneshiek biota or a nearby ecosystem. By comparison to previously described crustacean SCFs from the Cambrian of Canada, the Winneshiek fossils both extend the range of this taphonomic window, and imply an ecological expansion of small-bodied crustaceans into restricted, marginal marine environments by the Middle Ordovician.

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Introduction

The fossil record of crustaceans in the Ordovician is largely limited to the easily preserved ostracods and phyllocarids (Perrier *et al*., 2015; Racheboeuf *et al*., 2009; Sepkoski Jr, 2000; Vannier *et al*., 2003). Exceptionally preserved specimens from Konservat-Lagerstätten (sensu Seilacher, 1970) can contribute enormously to fill the gaps. Liu *et al*. (2006) reported phyllocarids with preserved appendages and trunks from the Winneshiek Shale in Iowa, USA. This Lagerstätte has also yielded eurypterids, ostracods and other arthropods, vermiform organisms in three-dimensional preservation and other soft-bodied fossils, unusually large conodonts (elements up to 16 mm in length), possible jawless fishes, linguloid brachiopods and molluscs, among others (Liu *et al*., 2006). The eurypterids are currently the oldest known (Lamsdell *et al*., 2015). This site is one of few Konservat-Lagerstätten in the Ordovician (Van Roy *et al*., 2015), the only other Konservat-Lagerstätte known so far from the Middle Ordovician (also Darriwilian) being the Llanfallteg Formation in south-west Wales (Legg & Hearing, 2015; Whittington, 1993). The Winneshiek Lagerstätte is still barely studied. Since preliminary reports mentioned the preservation of eurypterid cuticules and the presence of other arthropods, the prospects for the search for arthropod remains in palynological assemblages were excellent. Such non-standard palynomorphs have been termed “small carbonaceous fossils” (SCFs) by (Butterfield & Harvey, 2012). SCFs reported from the Cambrian include crustacean remains such as branchiopod-like mandibles and filter plates (Butterfield & Harvey, 2012; Harvey & Butterfield, 2008; Harvey *et al*., 2012b) and copepod mandibles (Harvey & Pedder, 2013; Harvey *et al*., 2012b), providing valuable insight into the evolution and ecology of early crustaceans. An attempt to search for organic microfossils in the Winneshiek Shale has now yielded, *inter alia*, numerous objects that we tentatively identify as mandibles of diminutive crustaceans, as well as possible crustacean filter plates, which are described herein.

Geological context

The Winneshiek Shale (Darriwilian, Middle Ordovician) is found around the city of Decorah, Winneshiek County, Iowa, USA. It is a well laminated, greenish brown to medium or dark grey, sandy shale (Liu *et al*., 2006; Wolter *et al*., 2011). It is restricted to a circular area with a diameter of about 5.6 km (25 km²), with a thickness of 18 to 27 m (Lamsdell *et al*., 2015; Liu *et al*., 2009; McKay *et al*., 2011). Preliminary studies have interpreted this structure as an

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impact crater, the “Decorah impact structure” (Kass *et al.*, 2013a; 2013b; Liu *et al.*, 2009; McKay *et al.*, 2010; 2011). The environment is thought to have been restricted, brackish, shallow marine (Liu et al., 2006; 2013).

Only one small outcrop is known, which is mostly submerged under the Upper Iowa River. At this site, the Iowa Geological Survey (IGS) excavated the upper four metres of the Winneshiek Shale in 2010 by damming the river temporarily. Two drill cores are available that penetrated the entire shale succession (McKay *et al.*, 2011). The shale overlies an impact breccia/conglomerate and is overlain by the widely distributed sandstones of the St. Peter Formation (Calvin, 1906; Liu *et al.*, 2006).

Materials and methods

Nineteen samples were taken during an excavation in 2010 from the drained bed of the Upper Iowa River. These represent the uppermost 3.8 m of the Winneshiek Shale and its discordant upper boundary with the St. Peter Formation (Fig. 1).

A few tens of grams of rock per sample were treated each with a standard palynological maceration technique, employing hydroflouric and hydrochloric acid. The residue was filtered with mesh-sizes of 51 and 15 µm. Extracts of the size fraction between 15 and 51 µm were then mounted in resin on permanent palynological slides. These were studied and photographed under a ZEISS Axio Imager.A2 transmitted light microscope with a mounted AxioCam ERc5s.

All samples are housed at the Geological Survey Iowa (accession numbers forthcoming).

Results

Mandibles

Of nineteen samples representing the uppermost 3.8 m of the Winneshiek Shale, fourteen yielded the carbonaceous microfossils that we tentatively identify as crustacean mandibles (Fig. 2A-H). They were not recovered from the uppermost four and the sixth uppermost sample (see Fig. 1). The number of specimens recorded from each sample varies between one and nine. In total, 66 specimens were identified, including fragments.

The possible crustacean mandibles are light to dark brown. Their total length has a range of 55-130 µm (measured from 25 complete specimens). It should be noted that smaller specimens would be slim enough to not be retained by the 15 μm filter mesh. The mandibles are divided by a constriction into a boat-shaped posterior part and an anterior part bearing the ventrally leaning gnathal edge (Fig. 3, g). They show a pattern of longitudinal wrinkles, most strongly near the gnathal edge. This part is also darker or less translucent. The gnathal edge lies more or less parallel to the long axis of the posterior part. It is convexly curved, carrying 7-11 (commonly 8-10) backwards-arched, partially overlapping teeth. The teeth are of unequal length, with those near the anterior end being larger, except for a smaller, rudimentary, anteriormost tooth that is not always developed (Fig. 1D-G, black chevrons; Fig. 3, r). The tips of the teeth are usually broken off, but lengths of up to 11 μm were measured. There is a strong and statistically significant linear correlation between the total length of the mandibles and the length of the gnathal edge ($r^2 = 0.91$; $p = 0.003$; n = 25; Fig. 4A), but no correlation between total length and number of cusps ($r^2 = 0.14$; $p = 0.523$; n = 22; Fig. 4B). The posterior part of the mandibles has an opening along the inner side to the cavity where muscles were attached (Fig. 3, c). The basal (or dorsal) articulation on the posterior end is marked by conspicuous rims (Fig. 3, a). A possible secondary articulation is represented by a more or less prominent knob or edge on the outer margin, just below the aforementioned constriction (Fig. 3, s).

There is no clear morphological distinction between left and right mandibles.

Other organic microfossils

The mandibles are accompanied by a rich organic fossil content including arthropod cuticles of various kinds, mostly attributable to eurypterids (J. Lamsdell, 2015, personal communication), cyanobacterial sheaths, algae and acritarchs, that have also been recovered during a separate earlier study (unpublished report, P. Zippi, 2015, personal communication). Arthropod remains also include rare isolated or arrays of setae. They are unbranched or plumose. In two cases, plumose setae with interlocking setules form a tight net (Fig. 2I-J). This structure is very similar to SCFs from the middle Cambrian Deadwood Formation figured and identified as branchiopod filter plates by Harvey *et al*. (2012b). However, our specimens are far less complete.

Discussion

Mandibles of Mandibulata are commonly divided into a molar (*pars molaris*) and an incisor (*pars incisivus*), or derivatives thereof (Edgecombe *et al*., 2003). In branchiopods, the molar part can constitute the entire gnathal edge (Richter, 2004). The lack of a distinct incisor and

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the apparent lack of a mandibular palp both are indicative of a branchiopod affinity. The curvature of the gnathal edge, however, is an unusual feature.

Branchiopod-like SCFs were found in marine sediments from the Cambrian in Canada (Harvey *et al*., 2012b). Extant branchiopods inhabit mostly freshwater habitats, with only a minor part of the order Cladocera living under marine or brackish conditions (Bowman & Abele, 1982). Our material documents that by the Middle Ordovician, small-bodied crustaceans, possibly cladoceran branchiopods, had spread to restricted, marginal marine environments. The small size of the Winneshiek mandibles also fits in the size range of Cladocera. The pre-Pleistocene fossil record of cladocerans is extremely patchy (Womack *et al*., 2012, and references therein). Their oldest known occurrence is in the Early Devonian Rhynie Chert of Scotland (Anderson *et al*., 2003). If the Winneshiek mandibles are in fact derived from cladocerans, this would be their oldest record so far, but the mandibles alone are insufficient for a confident identification. The possible filter plates may also pertain to crustaceans, and in particular branchiopods. There is, however, no evidence linking the mandibles and branched setae besides rare co-occurrences.

A secondary articulation is developed in several crustacean groups (Snodgrass, 1950). If the knob on our specimens (Fig. 3, s) has a similar function, it would indicate a rotation of the mandibles nearly around the long axis, specifically around an axis connecting the two articulations (Fig. 3, h). This would be consistent with the orientation of the gnathal edge and its eccentric position. The presence of prominent pointed teeth suitable for biting and the presumed grasping mechanics suggest a predatory feeding habit.

Compared with other animal remains in the studied samples and considering the small sample sizes, the mandibles are recurring with unusual regularity, if not (at this point) in high absolute numbers. No other specific type of animal fossil was recorded from as many samples. We would therefore expect the original animal to be fairly abundant and an important part of the crater ecosystem or an adjacent fauna. However, until now, no complete specimen has been identified. Clearly, they represent the most recalcitrant part of an otherwise hardly preservable organism. Harvey & Pedder (2013) made a similar observation about mandibles in Cambrian SCF assemblages. The taphonomic history of the Winneshiek mandibles that allowed their preservation with finest details may have been similar to that of specimens from the Cambrian of Canada reported from the Mount Cap Formation (early Cambrian), the Deadwood Formation (middle-late Cambrian), the Earlie Formation (middle Cambrian) and the Nolichucky Shale (middle-late Cambrian) (Butterfield & Harvey, 2012; Harvey & Butterfield, 2008; Harvey & Pedder, 2013; Harvey *et al*., 2012a; 2012b).

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Figures

Fig. 1: Stratigraphic position relative to the St. Peter Formation and yield of samples from the Winneshiek Shale.

Fig. 2: Possible crustacean mandibles and setae from the Winneshiek Shale. Sample numbers are followed by slide number in parentheses and England Finder Graticule coordinates. A-H, Mandibles. A, WS-18(1), E26. B, WS-18(1), V29/1. C, WS-6(1), P39. D, WS-10(1), M45/4. E, WS-12(2), W53/2. F, WS-14(1), G49. G, WS-15(1), O45/4. H, mirrored, WS-11(1), G24. I-J, Setal plates. I, WS-9(1), O41/4. J, WS-6(1), Y27/3. Black chevrons indicate rudimentary anteriormost teeth.

Fig. 3: Line drawing of the mandible in fig. 1D with main morphological features marked. a = posterior articulation; s = possible secondary articulation; c = cavity opening; h = presumed hinge axis; g = gnathal edge; r = rudimentary anteriormost tooth.

Fig. 4: Scatterplots of morphometric values. A, total length versus length of gnathal edge (n = 25). B, total length versus number of teeth ($r^2 = 0.14$; $p = 0.523$; n=22).

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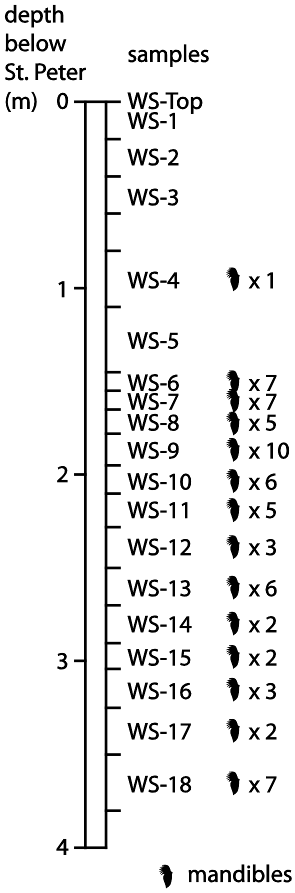
Figure 1


depth below St. Peter (m)
0
1
2
3
4
samples
WS-Top
WS-1
WS-2
WS-3
WS-4 x 1
WS-5
WS-6 x 7
WS-7 x 7
WS-8 x 5
WS-9 x 10
WS-10 x 6
WS-11 x 5
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WS-16 x 3
WS-17 x 2
WS-18 x 7
mandibles

Figure 2

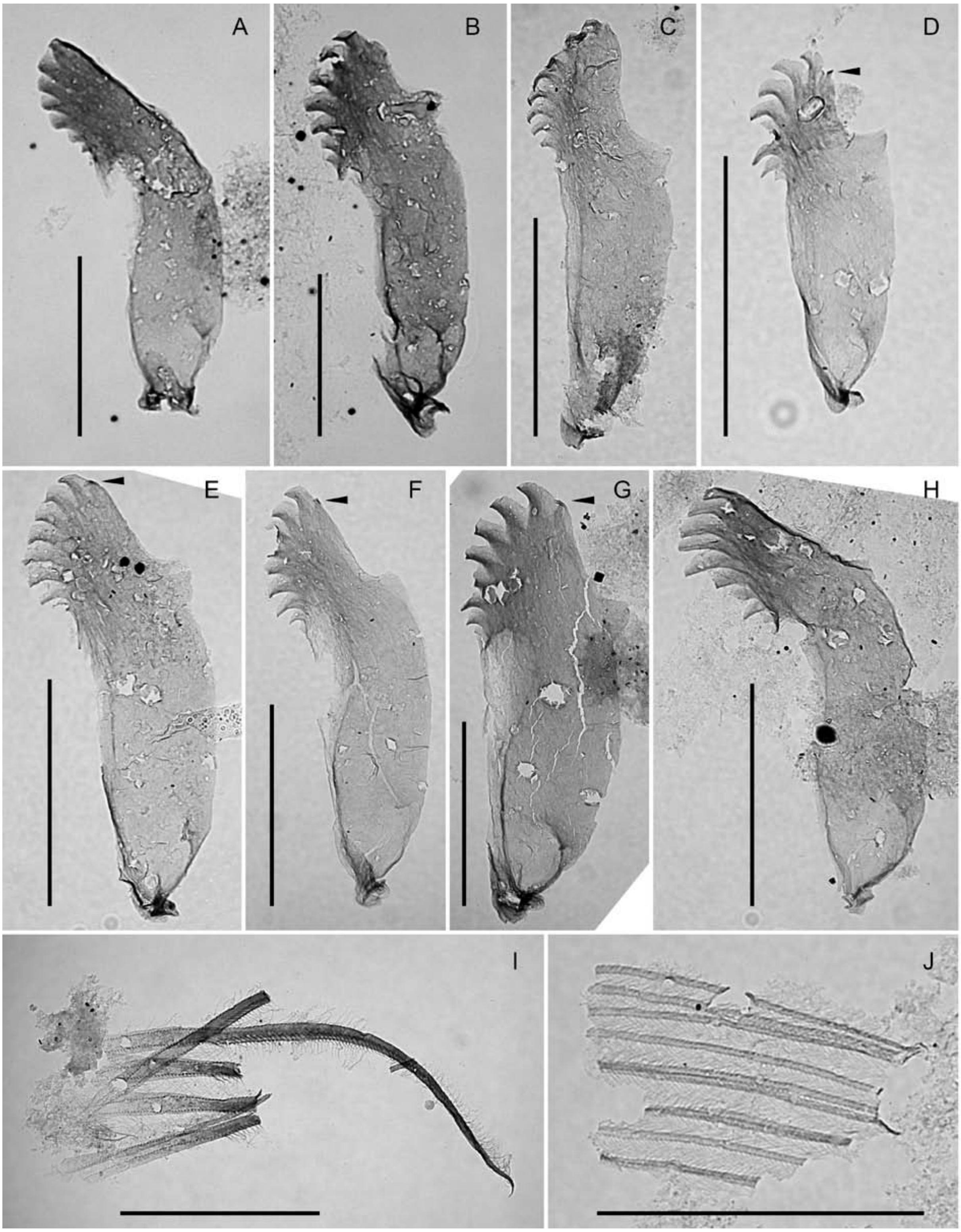

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Figure 3

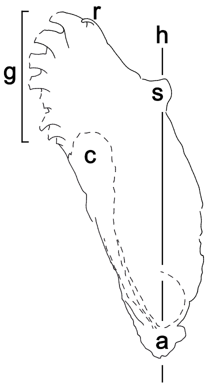

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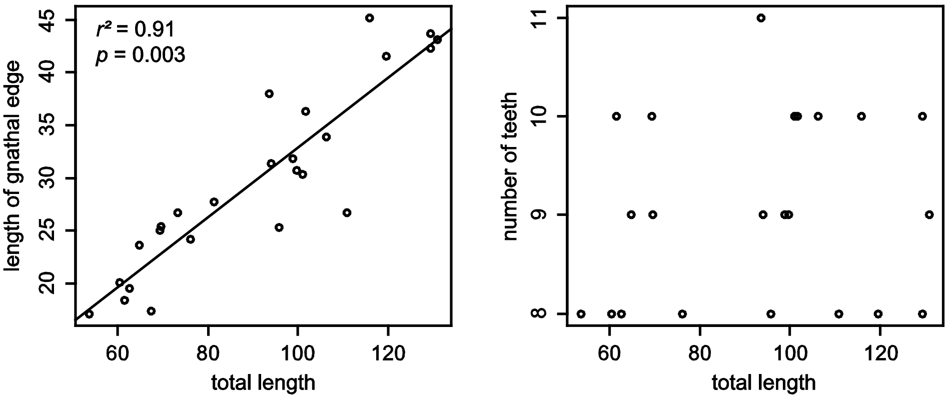
Figure 4



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Article VIII

Filamentous eukaryotic algae from the Winneshiek Lagerstätte in Iowa (Middle Ordovician)

Nowak, H., Harvey, T.H.P., Liu, H., McKay, R.M., Campbell, D. & Servais, T.

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Filamentous eukaryotic algae from the Winneshiek Lagerstätte in Iowa (Middle Ordovician)

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Abstract

Previous studies on the Darriwilian (Middle Ordovician) Konservat-Lagerstätte of the Winneshiek Shale in Iowa (USA) have reported various animal and trace fossils. A search for "small carbonaceous fossils" (SCFs) in palynological samples from the Winneshiek Shale has now led to the discovery of various kinds of organic-walled microfossils. Here we report on a particular group of filamentous eukaryotic algae. These algae are constituted by large, elongated cells and occasionally show branching. These features are typical of the Cladophorales, an order of green algae with a long, but sporadic fossil record, to which the Winneshiek microfossils are tentatively assigned.

Keywords: Winneshiek Lagerstätte, Middle Ordovician, Cladophorales, Small Carbonaceous Fossils

Introduction

The Darriwilian (Whiterockian, Middle Ordovician) Winneshiek Shale near the city of

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Decorah in Winneshiek County, northern Iowa (USA) has gained attention for its exceptionally preserved fossils (Liu *et al.*, 2006). First reports from this Konservat-Lagerstätte (*sensu* Seilacher, 1970) have documented, among others, the presence of phyllocarids, eurypterids, ostracods, and other arthropods, linguloids, mollusks, conodonts, possible jawless fish, bromalites and other trace fossils (Liu *et al.*, 2006; 2009; Lamsdell *et al.*, 2015). The lack of many elements of typical Ordovician marine faunas and indications of tidal influence led to an interpretation of the Winneshiek Shale as representing a restricted, possibly brackish, shallow marginal-marine environment (Liu *et al.*, 2006; 2013). Acritarchs and coenobial green algae were found by P. Zippi (unpublished report). Here we report on giant-celled, filamentous, eukaryotic algae from the Winneshiek Lagerstätte. These were isolated using a low-manipulation technique designed for the search for "small carbonaceous fossils" (SCFs; see Butterfield & Harvey, 2012), which are usually more fragile and larger than conventional palynomorphs (such as acritarchs or land-plant derived spores and pollen grains). The fossil record of comparable algae is rather limited, although they are known from Proterozoic Lagerstätten (Butterfield *et al.*, 1988; 1994; Podkovyrov, 2009).

Geological setting

The Winneshiek Shale is a greenish brown or medium to dark grey, slightly sandy, well laminated shale (Liu *et al*., 2006; Wolter *et al*., 2011). It only occurs around the city of Decorah and mostly below the surface, in a circular area with a diameter of ~5.6 km (Lamsdell *et al*., 2015), interpreted as an impact crater (Kass *et al*., 2013a; 2013b; Liu *et al*., 2009; McKay *et al*., 2010; 2011). The only known outcrop is in the riverbed of the Upper Iowa River (Liu *et al*., 2006). From two drill cores, the total thickness has been determined as 18-27 m (McKay *et al*., 2011). Underlying the Winneshiek Shale is an unnamed unit of breccia, conglomerate, sand and shale, while the St. Peter Sandstone Formation overlies the Winneshiek Shale (Liu *et al*., 2006; Wolter *et al*., 2011).

Materials and methods

Samples were taken from the upper 3.8 m of the Winneshiek Shale during an excavation by the Iowa Geological & Water Survey (now Geological Survey of Iowa) of the outcrop in the bed of the temporarily dammed Upper Iowa River in 2010 (nineteen samples, prefix WS) and from a drill core near the outcrop (nine samples, prefix H2). The rock samples (a few tens of grams each) were treated with hydrofluoric acid in a technique similar to that employed and described by Butterfield & Harvey (2012, supplementary information), but for security reasons with two courses of diluting and decanting before filtration with a mesh size of 51 µm. Fossils were hand-picked from the residue >51 µm under water by use of a pipette and placed on glass carriers. Photographs were made with a ZEISS AxioCam MRc mounted on an Axioplan2 microscope or a ZEISS AxioCam Erc5s mounted on an Axio Imager.A2. All figured and unfigured specimens are stored at the Geological Survey of Iowa.

Results

Parts of giant-celled algae (Pl. I) were found in most samples from the excavation and in the borehole H2 (Fig. 1). The cells occur isolated or connected in uniserial filaments, rarely with preserved branching. Where they are present, few well-defined specimens are usually accompanied by abundant, smaller fragments. The algae are very thin and usually clear transparent, indicating an excellent state of preservation. They are only faintly visible under a light microscope. The largest fragment measures a total length of 1.25 mm (Pl. I, 11). Individual cells have an observed length of 220-640 µm. Their outline can be rectangular or with bulging sides. The maximum width is in the range of 90-380 µm. To attain the original diameter, we can apply a correcting factor of $2/\pi$, assuming a perfect flattening of a cylindrical form. This gives values for original cell diameters of about 60-240 µm. The contacts between cells are often constricted relative to the middle of the cells, indicating that these parts potentially retained the original diameter due to cross walls. Cross walls are not always visible. Visible cross walls or constrictions show a width of 70-240 µm, which is well overlapping with the diameters calculated from maximum cell widths. However, individual cells may show a difference between the maximum width and width of cell contacts larger than would be expected from compaction of simple cylinders. This indicates that some cells originally had a barrelled shape.

Most cells contain internal bodies. These are light to dark brown, sometimes nearly opaque, grainy and considerably thicker than the rest of the cell. They can have oval/ovoid, rectangular, band-like or similar shapes, often somewhat reflecting the appearance of the surrounding cell. Their sizes in relation to the cells vary.

A few specimens bear outgrowths in the form of bulges or tubes (Pl. I, 6-8), the latter in at least one case with an opening at the distal end (Pl. I, 8). They appear brownish, granular and less transparent than the main cells.

The branching appears to be intercalary (sub-apical), judging from the few, incomplete specimens showing branching (Pl. I, 10, 11). In these cases, cell contacts are not conspicuous. Consequently, we cannot determine the branching position on the stem cells.

Discussion

Filamentous algae with similarly large and even larger cells are found among the Cladophorales (Ulvophycea, Chlorophyta) (compare e.g. *Cladophora vandenhoekii* Norris & Olsen, 1991). This extant group of green algae has a limited fossil record, but was reported from Lagerstätten as far back as the Mesoproterozoic Lakhanda Formation of Siberia (Podkovyrov, 2009) and the Neoproterozoic Svanbergfjellet Formation on Spitsbergen (Butterfield *et al.*, 1988; 1994). The genus *Cladophora* is known from modern-day freshwater, brackish and marine environments in high to low latitudes (Zulkifly *et al.*, 2013).

The outgrowths found on some specimen may represent early stages of branching or sexual reproductive organs. The longer, tubular outgrowths resemble antheridia (♂), the more spherical ones could be interpreted as oogonia (♀), although the latter do not show an opening, which may be a preservational effect.

Possible origins of internal bodies such as those observed here include cytoplasmic remains (e.g. Graham *et al.*, 2013) or pyrenoids (Oehler, 1977). In this case, the cytoplasm theory is supported by the way in which the form of internal bodies seems to mirror to some extent the outer shape of the cell; more well-rounded cells contain an ovoid body, longer cells contain ribbon-like bodies (compare Pl. I, 2-4 and 10).

Conclusions

Besides arthropod cuticles, acritarchs and a diverse assemblage of various microscopic algal groups, the Winneshiek Lagerstätte contains important amounts of a distinct type of giant-celled, filamentous eukaryotic algae. They are possibly assignable to the Cladophorales, which otherwise have a poor fossil record. Additional material might answer the remaining questions about their morphology and affinity. The preservation of relatively large, connected fragments suggests the possibility that even complete thalli might be preserved in the Winneshiek Shale, if not in large amounts.

Acknowledgments

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Plates and figures

Plate I. Fragments of giant-celled filamentous algae from the Winneshiek Shale. Scale bars = 200 µm.

Fig. 1 Two connected (and partly distorted) cells with internal bodies. Sample WS-6

Figs. 2-4 Isolated oval cells with internal bodies. Fig. 2, Sample H2 10'. Figs. 3-4, Sample WS-6.

Fig. 5 Ribbon-like fragment with elongate, paired internal bodies. Sample WS-7.

Figs. 6-8 At least two connected cells with outgrowths. Sample WS-13.

Fig. 7 Close-up showing a bulbous (lower) outgrowth and a small elongated one (upper).

Fig. 8 Close-up of a tubular outgrowth bearing an opening.

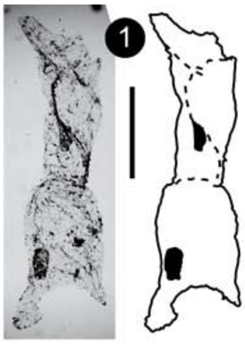
Fig. 9 Two connected cells showing both straight (lower cell) and convex (upper cell) outlines. Sample WS-12.

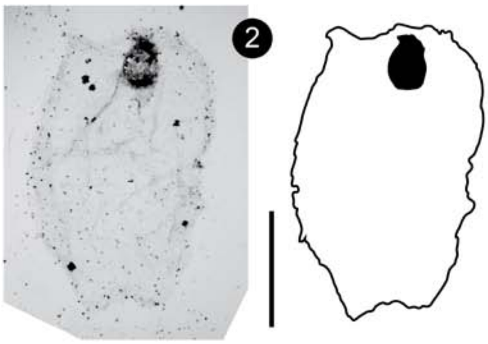
Fig. 10 Large fragment with branching. Note elongate intracellular body in the branch. Sample H2 15'.

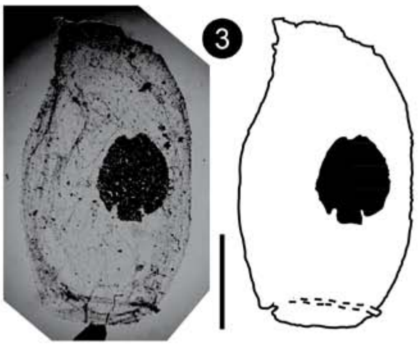
Fig. 11 Largest fragment, bearing two(?) branchings. Sample H2 15'.

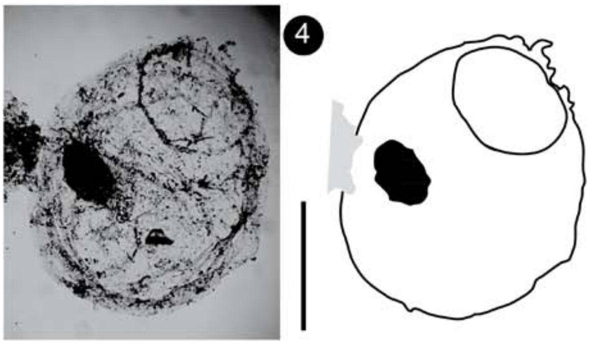
Fig. 1. Samples and stratigraphic distribution of giant-celled filamentous algae in the Winneshiek Shale. A, excavated outcrop in the Upper Iowa River. B, H2 drill core.

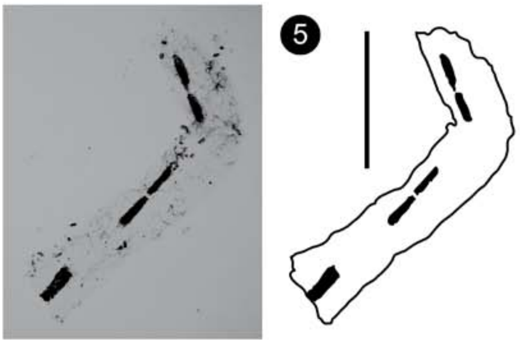
Plate 1

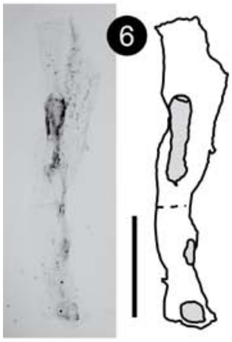


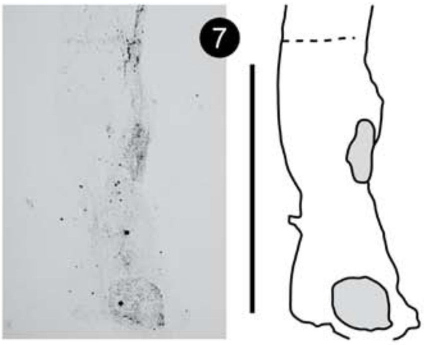


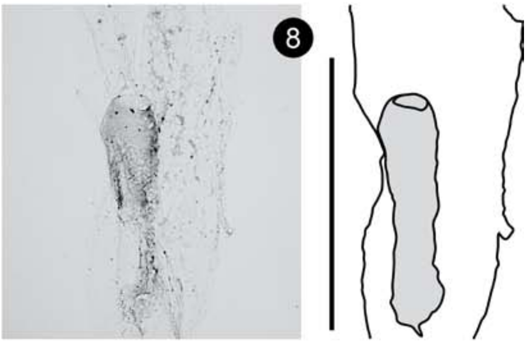


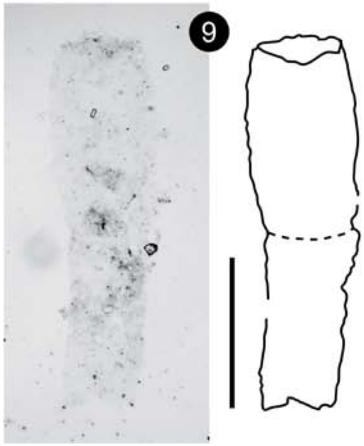


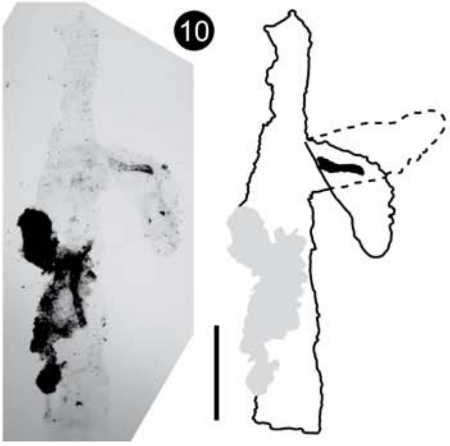












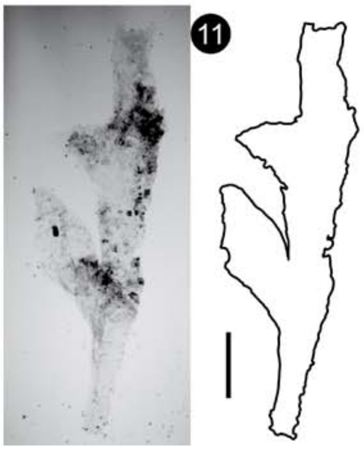


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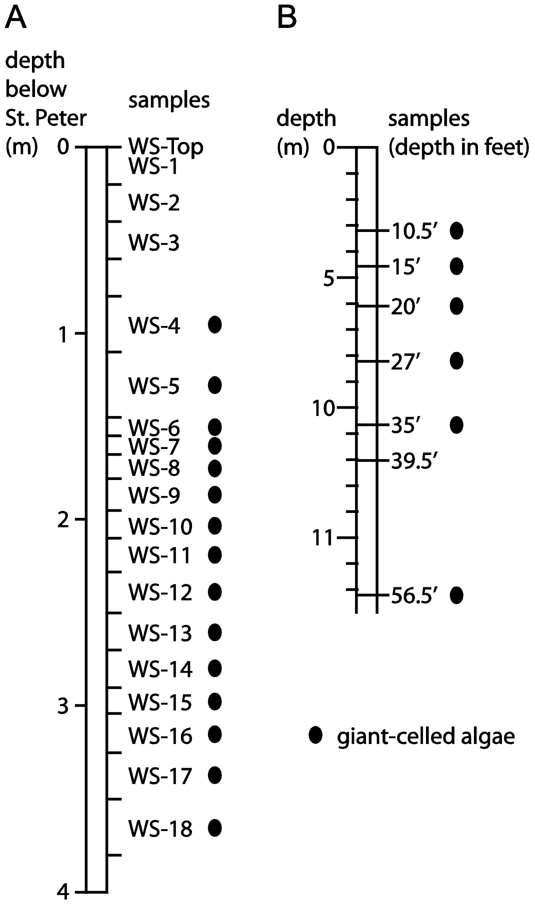
Figure 1


A
depth below St. Peter (m)
0
1
2
3
4
samples
WS-Top
WS-1
WS-2
WS-3
WS-4
WS-5
WS-6
WS-7
WS-8
WS-9
WS-10
WS-11
WS-12
WS-13
WS-14
WS-15
WS-16
WS-17
WS-18
B
depth (m)
0
5
10
11
samples (depth in feet)
10.5′
15′
20′
27′
35′
39.5′
56.5′
● giant-celled algae

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Appendix

Supplementary data for:

Article I – Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: A review of Cambrian acritarch diversity

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Supplementary material S1

Database of Cambrian acritarch occurrences. Available digitally:

http://www.sciencedirect.com/science/MiamiMultiMediaURL/1-s2.0-S0012825215300428/1-s2.0-S0012825215300428-mmc1.csv/271741/html/S0012825215300428/88e9f304e8f23b1286b58e6038ea2919/mmc1.csv

Supplementary material S2

List of source references, including bibliography, countries and palaeogeographical units corresponding to study areas.

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List of literary sources for the Cambrian acritarch database

[country/countries – palaeocontinent(s)]
* not included in the diversity analyses

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Supplementary material S3

List of acritarch genera and species reported from the Cambrian System, with marked known synynomies and homonymies, including references.

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Comments on systematic palaeontology

Among the so-called acritarchs reported from the Cambrian, the genera *Chuaria* Walcott 1899, *Cymatiosphaera* Wetzel 1933 *ex* Deflandre 1954, *Dictyotidium* Eisenack 1955, *Leiopsophosphaera* Naumova 1961 *ex* Naumova 1968, *Polyedryxium* Deunff 1954, *Pterospermella* Eisenack 1972, and *Tasmanites* Newton 1875 are now considered to be (likely) prasinophytes (e.g. Guy-Ohlson 1996, Traverse 2007). At least a part of the rather featureless sphaeromorphs, especially *Leiosphaeridia* Eisenack 1958 and *Protoleiosphaeridium* Timofeev 1959 *ex* Timofeev 1960, might also belong to this group (comp. e.g. Guy-Ohlson 1996, Strother 1996). *Huroniospora* Barghoorn in Barghoorn & Tyler 1965 and *Myxococcoides* Schopf 1968 have been identified as cyanobacteria (Chroococcales; e.g. Shukla et al. 2006, Schopf 1968). *Caryosphaeroides* Schopf 1968 was described as a chlorococcoid (Chlorophyceae) green alga (Schopf 1968). According to Butterfield (2005), *Germinosphaera* Mikhailova 1986 (considered by him to be a synonym of *Tappania* Yin 1997) belongs to the fungi. *Ceratophyton* Kiryanov in Volkova et al. 1979 has been established to comprise animal remains (Fatka & Konzalová 1995). Wang and Luo (1982) reported the artificial production of structures resembling *Trematosphaeridium* Timofeev 1959 and *Polyporata* Pykhova 1966, among others. They suggested that these genera might – at least in part – represent pseudofossils. Baudet et al. (1989) tentatively identified ?*Hemisphaerium* Hemer & Nygreen 1967 from the lower Cambrian Sekwi Formation of the Canadian Mackenzie Mountains. According to Grenfell (1995), *Hemisphaerium* is a probable synonym of *Brazilea* Tiwari & Navale 1967, which he classified as a zygnematacean spore. From the Sinian (Late Proterozoic-?lower Cambrian) of northern China, Timofeev (1966) described *Pulvinomorpha* Timofeev 1966, considered by Grenfell (1995) as a possible synonym of *Tetraporina* Naumova 1939, another zygnematacean spore. This tentative interpretation would make *Brazilea (Hemisphaerium)* and *Tetraporina (Pulvinomorpha)* the oldest recorded zygnemataceans by far, with a gap in the record ranging up to the Carboniferous (Grenfell 1995). The genus *Pseudozonosphaeridium* Andreeva 1966 and the species *P. fengxiangense* Zhong Guofang 1978 in particular have been reported from the Proterozoic and the Silurian, but not the Cambrian (Fensome et al. 1990). The existence of *Veryhachium* Deunff 1954 in the Cambrian was rejected by Raevskaya and Servais (2009), but several species reported from the Cambrian have been assigned to this genus and are currently not formally transferred to other genera. Moczydłowska (1991) proposed the transfer of Cambrian forms assigned to *Micrhystridium* Deflandre 1937 (which has received numerous emendations) to the new genera *Asteridium* Moczydłowska 1991 and *Heliosphaeridium* Moczydłowska 1991. Not all concerned species have been transferred so far and not all authors have followed the proposal (e.g. Sarjeant & Stancliffe 1994).

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List of acritarch genera and species reported from the Cambrian

names in “ ” have been found to be invalid

« → » indicates current name

“Abacum” Fombella 1978
→ *Virgatasporites* Combaz 1967 [acc. to Fensome et al. 1990]
type species: “*Abacum normale*” Fombella 1978
→ *Virgatasporites normalis* (Fombella 1978) Fensome et al. 1990

“*Abacum normale*” Fombella 1978
→ *Virgatasporites normalis* (Fombella 1978) Fensome et al. 1990

Acanthodiacrodium Timofeev 1958 emend. Deflandre & Deflandre-Rigaud 1962
restrict. Moczydłowska & Stockfors 2004
type species: *Acanthodiacrodium dentiferum* Timofeev 1958

“*Acanthodiacrodium achrasii*” (Martin 1972) Martin & Dean 1988
→ *Actinotodissus achrasii* (Martin 1972) Yin L. 1986

Acanthodiacrodium anceps Timofeev 1959b

Acanthodiacrodium angustum (Downie 1958) Combaz 1967

Acanthodiacrodium complanatum (Deunff 1961a) Vavrdová 1965

Acanthodiacrodium enodum Timofeev 1959b

Acanthodiacrodium golubii Fensome et al. 1990

Acanthodiacrodium cf. *ignoratum* (Deunff 1961a) Downie & Sarjeant 1965

Acanthodiacrodium lanatum Timofeev 1959b ex Downie & Sarjeant 1965

Acanthodiacrodium petrovii Timofeev 1959b

“*Acanthodiacrodium polymorphum*” Timofeev 1959b
→ *Actinotodissus polimorphus* (Timofeev 1959b) Moczydłowska & Stockfors 2004

“*Acanthodiacrodium secundarium*” Timofeev 1959b
→ *Actinotodissus secundarius* (Timofeev 1959b) Moczydłowska & Stockfors 2004

Acanthodiacrodium sinuosum Rasul 1979

Acanthodiacrodium snookense Parsons & Anderson 2000

Acanthodiacrodium cf. *spinum* Rasul 1979

“*Acanthodiacrodium spinutisum*” Timofeev 1959b
→ *Actinotodissus spinutisus* (Timofeev 1959b) Moczydłowska & Stockfors 2004

“*Acanthodiacrodium timofeevii*” Golub & Volkova in Volkova & Golub 1985

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→ *Acanthodiacrodium golubii* Fensome et al. 1990

Acanthodiacrodium tricorne (Timofeev 1959b ex Downie & Sarjeant 1965) Martin 1969

"Acanthodiacrodium tuberatum" (Downie 1958) Martin 1972
→ *Goniosphaeridium tuberatum* (Downie 1958) Welsch 1986

"Acanthodiacrodium ubuii" Martin 1969
→ *Actinotodissus ubuii* (Martin 1969) Fensome et al. 1990

"Acanthodiacrodium uniforme" Burmann 1968
[**senior homonym:** *Acanthodiacrodium uniforme* Timofeev 1959b, acc. to Fensome et al. 1990]
→ *Actinotodissus burmanniae* (Fensome et al. 1990) Moczydłowska & Stockfors 2004 [Moczydłowska & Stockfors 2004 gave authorship of this combination as "(Burmann 1968) Fensome et al. 1990 »]
→ {*pro parte* in Chen J. et al. 1985} *Actinotodissus achrasii* (Martin 1972) Yin L. 1986 [acc. to Martin & Dean 1988]
→ {*pro parte* in Chen J. et al. 1985} *Dasydiacrodium obsonum* Martin in Martin & Dean 1988 [acc. to Moczydłowska & Stockfors 2004]

Acanthodiacrodium sp. A Parsons & Anderson 2000

Acanthodiacrodium sp. B Parsons & Anderson 2000

Acanthodiacrodium sp. I Yin L. in Chen J. et al. 1985

Acrum Fombella 1977
type species: *Acrum novum* Fombella 1977

?*Acrum araxisii* Di Milia 1991

Acrum cylindriferum Downie 1982

Acrum radiale Fombella 1977

Actinotodissus Loeblich & Tappan 1978
type species: *Actinotodissus longitaleosus* Loeblich & Tappan 1978

Actinotodissus achrasii (Martin 1972) Yin L. 1986

Actinotodissus formosus (Górka 1967) Moczydłowska & Stockfors 2004

Actinotodissus polimorphus (Timofeev 1959b) emend. Moczydłowska & Stockfors 2004

Actinotodissus secundarius (Timofeev 1959b) Moczydłowska & Stockfors 2004

Actinotodissus spinutisus (Timofeev 1959b) Moczydłowska & Stockfors 2004

Actinotodissus ubuii (Martin 1969) Fensome et al. 1990

Actinotodissus sp. A Martin 1992

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Adara Fombella 1977 emend. Martin in Martin & Dean 1981
type species: *Adara mutatina* Fombella 1977

Adara alea Martin in Martin & Dean 1981
→ {in Albani et al. 1991} *Multiplicisphaeridium ?ancliforme* Fombella 1978 [acc. to Jachowicz-Zdanowska 2013]
→ {in Buła & Jachowicz 1996; Moczydłowska 1998} *Turrisphaeridium semireticulatum* (Timofeev 1959b) Jachowicz-Zdanowska 2013 [acc. to Jachowicz-Zdanowska 2013]

“*Adara denticulata*” Tongiorgi in Bagnoli et al. 1988
→ *Adara alea* Martin in Martin & Dean 1981 [acc. to Vanguestaine & Brück 2008]

Adara matutina Fombella 1977

“*Adara undulata*” Moczydłowska 1998
→ *Adara alea* Martin in Martin & Dean 1981 [acc. to Vanguestaine & Brück 2008]

Adara sp. A Baudet et al. 1989

Alliumella Fanderflit in Umnova & Fanderflit 1971
type species: *Alliumella baltica* Fanderflit in Umnova & Fanderflit 1971

Alliumella baltica Fanderflit in Umnova & Fanderflit 1971

Alliumella n. sp. Vanguestaine 1986

Ammonidium Lister 1970 emend. Sarjeant & Vavrdová 1997
type species: *Ammonidium microcladum* (Downie 1963) Lister 1970 emend. Sarjeant & Vavrdová 1997

Ammonidium bellulum (Moczydłowska 1998) Sarjeant & Stancliffe 2000

Ammonidium notatum (Volkova 1969) Jachowicz-Zdanowska 2013

Ammonidium oligum (Jankauskas in Jankauskas & Posti 1976) Jachowicz-Zdanowska 2013

Annulum Fombella 1978
type species: *Annulum difuminatum* Fombella 1978

“*Annulum squamaceum*” (Volkova 1968) emend. Martin in Martin & Dean 1983
→ *Granomarginata squamacea* Volkova 1968

Aranidium Jankauskas 1975
type species: *Aranidium izhoricum* Jankauskas 1975

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Aranidium granulatum Welsch 1986

Aranidium izhoricum Jankauskas 1975

Aranidium aff. *pycnacanthum* Jankauskas 1975

Aranidium sparsum Volkova in Volkova et al. 1979

Arbusculidium Deunff 1968a emend. Welsch 1986
type species: *Arbusculidium destombesii* Deunff 1968a

?*Arbusculidium adminiculum* Di Milia et al. 1989

Arbusculidium destombesii Deunff 1968a

Arbusculidium cf. *mamillosum* Welsch 1986

Arbusculidium ornatum (Combaz 1967) Fensome et al. 1990

Arbusculidium perlongum Di Milia et al. 1989

Arbusculidium polypus Di Milia et al. 1989

"*Arbusculidium rommelaerei*" Martin in Martin & Dean 1981
→ *Ladogella rommelaerei* (Martin in Martin & Dean 1981) Di Milia et al. 1989

Arbusculidium sp. 1 Volkova 1990

Archaeodiscina Naumova 1961 emend. Volkova 1968
type species: *Archaeodiscina granulata* Naumova 1961

Archaeodiscina bicostata Volkova in Volkova et al. 1979

Archaeodiscina umbonulata Volkova 1968

Archaeodiscina multipunctata Jachowicz-Zdanowska 2013

Archaeodiscina sp. A Baudet et al. 1989

?*Archaeodiscina* sp. B Baudet et al. 1989

Archaeosacculina Pykhova 1967
[**junior homonym:** "*Archaeosacculina*" Naumova 1968]
type species: *Archaeosacculina torosa* Pykhova 1967

"*Archaeosacculina atava*" Pykhova 1966
[not validly published acc. to Fensome et al. 1990]

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Aryballomorpha Martin and Yin L. 1988
type species: *Aryballomorpha grootaertii* (Martin 1984) emend. Martin and Yin L. 1988

Aryballomorpha albertana Martin 1992

Asperatopsophosphaera Shepeleva 1963 emend Kowalski 1983
type species: *Asperatopsophosphaera bavlensis* Shepeleva 1963 emend. Kowalski 1983

Asperatopsophosphaera bavlensis Shepeleva 1963

“*Asperatopsophosphaera partialis*” Shepeleva 1963
→ *Asperatopsophosphaera bavlensis* Shepeleva 1963 [acc. to Kowalski 1983]

Asperatopsophosphaera rugosa Ding
[cited without complete reference in Ding et al. 1992]

Asperatopsophosphaera umishanensis Xing & Liu 1973

Asteridium Moczydłowska 1991
type species: *Asteridium lanatum* (Volkova 1969) Moczydłowska 1991

Asteridium cerinum (Volkova 1968) Moczydłowska 1991

Asteridium lanatum (Volkova 1969) Moczydłowska 1991

Asteridium ordense (Downie 1982) emend. Vidal & Peel 1993

Asteridium pallidum (Volkova 1968) Moczydłowska 1991

Asteridium pilare Moczydłowska 1998

Asteridium solidum Moczydłowska 1998

Asteridium spinosum (Volkova 1969) Moczydłowska 1991

Asteridium tornatum (Volkova 1968) Moczydłowska 1991

Asteriscus Kowalski 1983
type species: *Asteriscus irregularis* Kowalski 1983

Asteriscus irregularis Kowalski 1983

Auritusphaera Strother 2008
type species: *Auritusphaera bifurcata* Strother 2008

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Auritusphaera bifurcata Strother 2008

Baltisphaeridium Eisenack 1958c ex Eisenack 1959a emend. Staplin et al. 1965 emend. Eisenack 1969 emend. Eiserhardt 1989
type species: *Baltisphaeridium longispinosum* (Eisenack 1931 ex Wetzel 1933) Eisenack 1959a

Baltisphaeridium acerosum Jankauskas & Posti 1976

“*Baltisphaeridium brachyspinosum*” Kiryanov 1974
→ *Ichnosphaera delicata* Jachowicz-Zdanowska 2013

“*Baltisphaeridium capillatum*” (Naumova 1950) Umnova 1975
[**senior homonym:** *Baltisphaeridium capillatum* Jardiné et al. 1974]

“*Baltisphaeridium cerinum*” Volkova 1968
→ *Globosphaeridium cerinum* (Volkova 1968) Moczydłowska 1991

“*Baltisphaeridium ciliosum*” Volkova 1969
→ *Skiagia ciliosa* (Volkova 1969) Downie 1982

Baltisphaeridium citrinum (Downie 1963) Stockmans & Willière 1974

“*Baltisphaeridium compressum*” Volkova 1968
→ *Skiagia compressa* (Volkova 1968) Downie 1982

Baltisphaeridium crinitum Martin in Dean & Martin 1978

Baltisphaeridium dictium Wang & Chen Q. 1987

“*Baltisphaeridium dubium*” Volkova 1968
→ “*Lophosphaeridium dubium*” (Volkova 1968) Moczydłowska 1991]

Baltisphaeridium ellipticum Wang et Chen
[cited without complete reference in Wang & Chen Q. 1987]

Baltisphaeridium emeiense Wang et Chen
[cited without complete reference in Wang & Chen Q. 1987]

Baltisphaeridium favosum Xing 1962

“*Baltisphaeridium implicatum*” Fridriksone 1971
→ *Solisphaeridium implicatum* (Fridriksone 1971) Moczydłowska 1998

“*Baltisphaeridium insigne*” (Fridriksone 1971) Volkova 1974
→ *Skiagia insignis* (Fridriksone 1971) Downie 1982

Baltisphaeridium jiulaodongense Wang & Chen Q. 1987

Baltisphaeridium jilinense Fensome et al. 1990

“*Baltisphaeridium latviense*” Volkova 1974
→ *Comasphaeridium latviense* (Volkova 1974) Hagenfeldt 1989a

Baltisphaeridium longispinosum (Eisenack 1931 ex Wetzel 1933) Eisenack 1959a

“*Baltisphaeridium orbiculare*” Volkova 1968
→ *Skiagia orbicularis* (Volkova 1968) Downie 1982

“*Baltisphaeridium ornatum*” Volkova 1968

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→ *Skiagia ornata* (Volkova 1968) Downie 1982

“Baltisphaeridium papillosum” (Timofeev 1959) ex Volkova 1968
→ *Filisphaeridium papillosum* (Timofeev 1959 ex Volkova 1968) Hu Yunxu 1986

“Baltisphaeridium pilosiusculum” Jankauskas in Volkova et al. 1979
→ *Skiagia pilosiuscula* (Jankauskas in Volkova et al. 1979) Jachowicz-Zdanowska 2013

“Baltisphaeridium primarium” Jankauskas in Volkova et al. 1979
→ *Goniosphaeridium primarium* (Jankauskas in Volkova et al. 1979) Downie 1982

Baltisphaeridium pseudofaveolatum Fridriksone 1971

Baltisphaeridium cf. *psilatum* Kjellström 1971a

“Baltisphaeridium pungens” Timofeev 1959b ex Martin 1969
→ *Polygonium pungens* (Timofeev 1959b ex Martin 1969) Albani 1989

Baltisphaeridium reticulum Wang & Chen Q. 1987

“Baltisphaeridium robustum” Yin L. in Chen J. et al. 1985
→ *Baltisphaeridium jilinense* Fensome et al. 1990

Baltisphaeridium simplex Deunff 1961a
[**junior homonym:** *“Baltisphaeridium simplex”* Stockmans & Willière 1962]

Baltisphaeridium solidum Xing 1962

“Baltisphaeridium stipaticum” Hagenfeldt 1989a
→ *Ichnosphaera stipaticum* (Hagenfeldt 1989a) Jachowicz-Zdanowska 2013

“?Baltisphaeridium strigosum” Jankauskas in Jankauskas & Posti 1976
→ *Comasphaeridium strigosum* (Jankauskas in Jankauskas & Posti 1976) Downie 1982

Baltisphaeridium tuberculatum Fridriksone 1971

“Baltisphaeridium varium” Volkova 1969
→ *Eklundia varia* (Volkova 1969) Jachowicz-Zdanowska 2013

Baltisphaeridium sp. 1 Volkova 1980

Baltisphaeridium sp. 1 Volkova et al. 1983

Baltisphaeridium sp. 1 Volkova et al. 1983

Baltisphaeridium sp. 2 Volkova 1980

Baltisphaeridium sp. 2 Volkova et al. 1983
→ *Goniosphaeridium volkovae* Hagenfeldt 1989a [acc. to Jachowicz-Zdanowska 2013]

Bavlinella Shepeleva 1962
[acc. to Muir 1977 “[...] objects like *Bavlinella* are not fossils. They are organic residua from framboids.”]
type species: *Bavlinella faveolata* Shepeleva 1962

Bavlinella faveolata Shepeleva 1962

“Bothroligtriletes” Timofeev 1958
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variant: *“Bothroligotriletum”*
no type species

“Bothroligotriletes exasperatus” Timofeev 1959b

Brevitrichoides Jankauskas 1980
type species: *Brevitrichoides bashkirius* Jankauskas 1980

Brevitrichoides crassus (Xing & Liu 1978) Zang 1992

Brochos
[cited without reference for the genus in Volkova 1995]
type species: ?

Brochos eisenackii Vanderflit et Mikhailova
[cited without complete reference in Volkova 1995]

Bubomorpha Yin L. in Chen J. et al. 1985
type species: *Bubomorpha hunjiangensis* Yin L. in Chen J. et al. 1985

Bubomorpha balangensis Yin L. et al. 2010

Bubomorpha hunjiangensis Yin L. in Chen J. et al. 1985

Buchinia Volkova 1990
type species: *Buchinia variabilis* Volkova 1990

Buchinia variabilis Volkova 1990

Buedingiisphaeridium Schaarschmidt 1963 emend. Lister 1970 emend. Sarjeant & Stancliffe 1994
type species: *Buedingiisphaeridium permicum* Schaarschmidt 1963

Buedingiisphaeridium tremadocum Rasul 1979

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Caldariola Molyneux in Molyneux & Rushton 1988
type species: *Caldariola glabra* (Martin 1972) Molyneux in Molyneux & Rushton 1988

Caldariola glabra (Martin 1972) Molyneux in Molyneux & Rushton 1988

Calyxiella Golub & Volkova in Volkova & Golub 1985
type species: *Calyxiella izhoriensis* Golub & Volkova in Volkova & Golub 1985

Calyxiella izhoriensis Golub & Volkova in Volkova & Golub 1985

Caryosphaeroides Schopf 1968
[Chlorococcales]
type species: *Caryosphaeroides pristina* Schopf 1968

Caryosphaeroides pristina Schopf 1968

Celtiberium Fombella 1977 emend. Sarjeant & Stancliffe 2000
type species: *Celtiberium geminum* Fombella 1977

Celtiberium cf. *clarum* Fombella 1978
→ {in Vanguestaine & Van Looy 1983} *Turrisphaeridium semireticulatum* (Timofeev 1959b) Jachowicz-Zdanowska 2013

Celtiberium dedalinum Fombella 1978

Celtiberium geminum Fombella 1977

Celtiberium cf. *geminum* Fombella 1977
→ {in Vanguestaine & Van Looy 1983} *Turrisphaeridium semireticulatum* (Timofeev 1959b) Jachowicz-Zdanowska 2013

?Celtiberium papillatum Moczydłowska 1998

Celtiberium robustum Hagenfeldt 1989b

Celtiberium n. sp. A Palacios 2010

Celtiberium sp. A Downie 1982

Celtiberium sp. B Downie 1982

Celtiberium sp. B Knoll & Swett 1987

Celtiberium sp. indet. B Jago et al. 2006

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Ceratophyton Kiryanov in Volkova et al. 1979
[SCF]
type species: *C. vernicosum* Kiryanov in Volkova et al. 1979

Chuaria Walcott 1899 emend. Vidal & Ford 1985
type species: *Chuaria circularis* Walcott 1899 emend. Vidal & Ford 1985

Chuaria circularis Walcott 1899 emend. Vidal & Ford 1985

Comasphaeridium Staplin et al. 1965 emend. Sarjeant & Stancliffe 1994
type species: *Comasphaeridium cometes* (Valensi 1949) Staplin et al. 1965

Comasphaeridium agglutinatum Moczydłowska 1988

Comasphaeridium annulare (Wang 1985) Yao et al. 2005

“Comasphaeridium brachyspinosum” (Kiryanov 1974) Moczydłowska & Vidal 1988
→ *Ichnosphaera delicata* Jachowicz-Zdanowska 2013

“Comasphaeridium caesariatum” Wood & Clendening 1982
[**senior homonym:** *Comasphaeridium caesariatum* Wicander 1974]
→ *Comasphaeridium woodii* Fensome et al. 1990

?Comasphaeridium densispinosum Vidal in Vidal & Peel 1993

“Comasphaeridium filiforme” Fombella 1979
[nomen nudum, acc. to Fensome et al. 1990]

Comasphaeridium formosum Moczydłowska 1988

Comasphaeridium francinae Jachowicz-Zdanowska 2013

Comasphaeridium gogense (Downie 1982) Sarjeant & Stancliffe 1994

Comasphaeridium latviense (Volkova 1974) Hagenfeldt 1989a

Comasphaeridium longispinosum Hagenfeldt 1989b
[**junior homonym:** *“Comasphaeridium longispinosum”* Vidal in Vidal & Peel 1993]

“Comasphaeridium longispinosum” Vidal in Vidal & Peel 1993
[**senior homonym:** *Comasphaeridium longispinosum* Hagenfeldt 1989b]

Comasphaeridium mackenzianum Baudet et al. 1989

Comasphaeridium molliculum Moczydłowska & Vidal 1988

“Comasphaeridium piliferum” Fombella 1979
[nomen nudum, acc. to Fensome et al. 1990]
→ *Parmasphaeridium implicatum* (Fridriksone 1971) Jachowicz-Zdanowska 2013

Comasphaeridium silesiense Moczydłowska 1998

Comasphaeridium soniae Jachowicz-Zdanowska 2013

Comasphaeridium spinosum Jachowicz-Zdanowska 2013

Comasphaeridium strigosum (Jankauskas in Jankauskas & Posti 1976) Downie 1982

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→ {in Szczepanik 2000} *Comasphaeridium silesiense* Moczydłowska 1998 [acc. to Jachowicz-Zdanowska 2013]

Comasphaeridium velvetum Moczydłowska 1988

Comasphaeridium vozmedianum Fombella 1978 ex Jachowicz-Zdanowska 2013

Comasphaeridium woodii Fensome et al. 1990

Comasphaeridium n. sp. 3 Moczydłowska & Vidal 1986

Comasphaeridium n. sp. 4 Moczydłowska & Vidal 1986

Comasphaeridium n. sp. A Palacios 2010
→ *Comasphaeridium francinae* Jachowicz-Zdanowska 2013

Comasphaeridium n. sp. Vidal 1981

Comasphaeridium sp. 2 Moczydłowska & Vidal 1986

Comasphaeridium sp. A Downie 1982

Comasphaeridium sp. A Palacios et al. 2009

Comasphaeridium sp. B Palacios et al. 2009

Comasphaeridium sp. indet. A Jago et al. 2006

Corollasphaeridium Martin in Dean & Martin 1982 emend. Yin L. 1986
type species: *Corollasphaeridium wilcoxianum* Martin in Dean & Martin 1982

Corollasphaeridium wilcoxianum Martin in Dean & Martin 1982

Corrugasphaera Fensome et al. 1990
type species: *Corrugasphaera terranovana* (Martin in Martin & Dean 1988) Fensome et al. 1990

Corrugasphaera terranovana (Martin in Martin & Dean 1988) Fensome et al. 1990

Coryphidium Vavrdová 1972
type species: *Coryphidium bohemicum*Vavrdová 1972

Coryphidium sichuanense Wang & Chen Q. 1987

Cristallinium Vanguestaine 1978
type species: *Cristallinium cambriense* (Slavíková 1968) Vanguestaine 1978

Cristallinium aciculatum Tongiorgi in Bagnoli et al. 1988

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Cristallinium baculatum Volkova 1990

Cristallinium cambriense (Slavíková 1968) Vanguestaine 1978

Cristallinium compactum Jachowicz-Zdanowska 2013

?Cristallinium delicatum Yin L. in Chen J. et al. 1985

Cristallinium dubium Volkova 1990

Cristallinium locale Volkova 1990

“Cristallinium ovillense” (Cramer & Díez 1972) Fensome et al. 1990
→ *Cristallinium cambriense* (Slavíková 1968) Vanguestaine 1978 [acc. to Moczydłowska 1998]

“Cristallinium ovillense” (Cramer & Díez 1972) Martin in Martin & Dean 1981
→ *Retisphaeridium ovillense* (Cramer & Díez 1972) Vanguestaine 2002

Cristallinium pilosum Golub & Volkova in Volkova & Golub 1985

Cristallinium cf. randomense Martin in Martin & Dean 1981 emend. Martin in Martin & Dean 1988

Cymatiogalea Deunff 1961a emend. Deunff 1964
type species: *Cymatiogalea margaritata* Deunff 1961a

Cymatiogalea aspergillum Martin in Martin & Dean 1988

Cymatiogalea bellicosa Deunff 1961a

Cymatiogalea bouvardii Martin 1972
→ {in Martin & Dean 1981} *Stelliferidium* sp. A Parsons & Anderson 2000

“Cymatiogalea columellifera” (Deunff 1961a) Eisenack et al. 1973
→ *Cymatiogalea cuvillieri* (Deunff 1961a) Deunff 1964 [acc. to Rasul 1974]

Cymatiogalea cristata (Downie 1958) Rauscher 1973

Cymatiogalea cuvillieri (Deunff 1961a) Deunff 1964

“Cymatiogalea cylindrata” Rasul 1974
→ *Stelliferidium cylindratum* (Rasul 1974) Elaouad-Debbaj 1988

Cymatiogalea dentalea Paalits 1992b

Cymatiogalea fascicularis Yin L. in Chen J. et al. 1985

Cymatiogalea fimbriata Volkova 1990

Cymatiogalea geometrica Di Milia et al. 1989

Cymatiogalea gorkae Rauscher 1973

Cymatiogalea hunjiangensis Yin L. in Chen J. et al. 1985 emend Yin L. 1986

Cymatiogalea membranispina Deunff 1961a

?Cymatiogalea membranula Martin in Dean & Martin 1978

Cymatiogalea multarea (Deunff 1961a) Eisenack et al. 1973

Cymatiogalea parvivela Di Milia 1991

Cymatiogalea regularis Yin L. in Chen J. et al. 1985 emend. Yin L. 1986

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Cymatiogalea velifera (Downie 1958) Martin 1969

Cymatiogalea virgulta Martin in Martin & Dean 1988

Cymatiogalea wironica Paalits 1992b

Cymatiogalea sp. 1 Paalits 1992b

Cymatiogalea sp. 2 Paalits 1992b

Cymatiogalea sp. 3 Paalits 1992b

Cymatiosphaera Wetzel 1933 ex Deflandre 1954
type species: *Cymatiosphaera radiata* Wetzel 1933

Cymatiosphaera baarstadi Eklund 1990

“Cymatiosphaera capsulara” Jankauskas in Jankauskas & Posti 1976
→ *Retisphaeridium capsulatum* (Jankauskas in Jankauskas & Posti 1976) Vanguestaine in Brück & Vanguestaine 2005

Cymatiosphaera crameri Slavíková 1968

Cymatiosphaera cristata Jankauskas 1976

“Cymatiosphaera favosa” Jankauskas 1976
→ *Cristallinium cambriense* (Slavíková 1968) Vanguestaine 1978

Cymatiosphaera gotlandica Hagenfeldt 1989a

“Cymatiosphaera luminosa” Fombella 1978
→ *Duplisphaera luminosa* (Fombella 1978) Moczydłowska 1998

“?Cymatiosphaera membranacea” Kiryanov 1974
→ *Fimbriaglomerella membranacea* Kiryanov 1974 ex Moczydłowska & Vidal 1988

“Cymatiosphaera minuta” Jankauskas in Volkova et al. 1979
→ *Fimbriaglomerella minuta* (Jankauskas in Volkova et al. 1979) Moczydłowska & Vidal 1988

Cymatiosphaera cf. *mirabilis* Deunff 1959

Cymatiosphaera cf. *nebulosa* (Deunff 1954b) Deflandre 1954

“Cymatiosphaera nerisica” Jankauskas 1976
→ *Cristallinium cambriense* (Slavíková 1968) Vanguestaine 1978 [acc. to Welsch 1986]

“Cymatiosphaera ovillensis” Cramer & Díez 1972
→ *Cristallinium cambriense* (Slavíková 1968) Vanguestaine 1978

Cymatiosphaera aff. *pavimenta* (Deflandre 1945) Deflandre 1954

“Cymatiosphaera postii” Jankauskas in Volkova et al. 1979
→ *Retisphaeridium postae* (Jankauskas in Volkova et al. 1979) Vanguestaine in Brück & Vanguestaine 2004

“Cymatiosphaera pusilla” Moczydłowska 1998
→ *Retisphaeridium pusillum* (Moczydłowska 1998) Vanguestaine in Brück & Vanguestaine 2005

Cymatiosphaera sp. 1 Hagenfeldt 1989b

Cymatiosphaera sp. 1 Volkova et al. 1979

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Cymatiosphaera sp. 2 Hagenfeldt 1989a

Cymatiosphaera sp. A Moczydłowska & Stockfors 2004

Cymatiosphaera sp. A Moczydłowska 1998

Cymatiosphaera sp. A Vanguestaine 1978
[dated 1977 in Baudet et al. 1989]

Cymatiosphaera sp. A Vanguestaine 1986

Dactylofusa Brito & Santos 1965 emend Combaz et al. 1967 emend Cramer 1970
type species: *Dactylofusa maranhensis* Brito & Santos 1965

"Dactylofusa simplex" Combaz 1967
→ *Leiofusa simplex* (Combaz 1967) Martin 1975

"Dactylofusa squama" (Deunff 1961a) Rauscher 1973
→ *Poikilofusa squama* (Deunff 1961a) Martin 1973

Dasydiacrodium Timofeev 1959b ex Deflandre & Deflandre-Rigaud 1962 emend. Moczydłowska & Stockfors 2004
type species: *Dasydiacrodium eichwaldii* Timofeev 1959b

Dasydiacrodium cf. *angulare* Timofeev 1959b ex Downie & Sarjeant 1965

"Dasydiacrodium caudatum" Vanguestaine 1973b
→ *Ninadiacrodium caudatum* (Vanguestaine 1973b) Raevskaya & Servais 2009

Dasydiacrodium obsonum Martin in Martin & Dean 1988

Dasydiacrodium palmatilobum Timofeev 1959b ex Downie & Sarjeant 1965

?Dasydiacrodium setuensis Paalits 1992a

"Dasydiacrodium tricorne" Timofeev 1959b ex Downie & Sarjeant 1965
→ *Acanthodiacrodium tricorne* (Timofeev 1959b ex Downie & Sarjeant 1965) Martin 1969

Dasydiacrodium tumidum (Deunff 1961a) Tongiorgi in Bagnoli et al. 1988

Dasydiacrodium veryhachioides Di Milia et al. 1989

Dasydiacrodium sp. A Moczydłowska & Stockfors 2004

Dasydiacrodium sp. B Moczydłowska & Stockfors 2004

Deunffia Downie 1960 emend. Thusu 1973
type species: *Deunffia monospinosa* (Deunff 1951) Downie 1960

"Deunffia dentifera" Volkova 1969
→ *Volkovia dentifera* (Volkova 1969) Downie 1982

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"Dichasphaira" Vanguestaine 1973a
[not validly published, acc. to Fensome et al. 1990]
type species: ?

"Dichasphaira vorax" Vanguestaine 1973a
[not validly published, acc. to Fensome et al. 1990]

Dichotisphaera Turner 1984
type species: *Dichotisphaera* caradocensis Turner 1984

Dichotisphaera gregalis (Hagenfeldt 1989a) Vanguestaine 1991

Dicrodiacrodium Burmann 1968
type species: *Dicrodiacrodium ancoriforme* Burmann 1968

Dicrodiacrodium ramusculosum (Combaz 1967) Volkova 1990

Dictyotidium Eisenack 1955 emend. Staplin 1961
type species: *Dictyotidium dictyotum* (Eisenack 1938a) Eisenack 1955

Dictyotidium birvetense Paškevičienė in Volkova et al. 1979

"Dictyotidium cambriense" Slavíková 1968
→ *Cristallinium cambriense* (Slavíková 1968) Vanguestaine 1978

Dictyotidium hasletianum Vanguestaine 1974

"Dictyotidium microreticulatum" Hagenfeldt 1989b
[**senior homonym:** *Dictyotidium microreticulatum* Jiabo 1978 (= Song et al. 1978)]

Dictyotidium perforatum Vidal in Vidal & Peel 1993

Dictyotidium priscum Kiryanov & Volkova in Volkova et al. 1979

Dictyotidium sp. 1 Hagenfeldt 1989b

Dictyotidium sp. 1 Volkova 1980

Dictyotidium sp. 1 Volkova et al. 1979

Dominopolia Kiryanov 1974
type species: *Dominopolia longispinosa* Kiryanov 1974

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Dominopolia lata Kiryanov 1974

Dominopolia longispinosa Kiryanov 1974

Duplisphaera Moczydłowska 1998
type species: *Duplisphaera luminosa* (Fombella 1978) Moczydłowska 1998

Duplisphaera luminosa (Fombella 1978) Moczydłowska 1998

Eklundia Jachowicz-Zdanowska 2013
type species: *Eklundia campanula* (Eklund 1990) Jachowicz-Zdanowska 2013

Eklundia campanula (Eklund 1990) Jachowicz-Zdanowska 2013

Eklundia florentinata Jachowicz-Zdanowska 2013

Eklundia pusilla Jachowicz-Zdanowska 2013

Eklundia varia (Volkova 1969) Jachowicz-Zdanowska 2013

Elektoriskos Loeblich 1970
type species: *Elektoriskos aurora* Loeblich 1970

“Elektoriskos cerinus” (Volkova 1968) Vanguestaine 1978
→ *Globosphaeridium cerinum* (Volkova 1968) Moczydłowska 1991

“Elektoriskos flexuosus” Eklund 1990
→ *Ichnosphaera flexuosa* (Eklund 1990) Jachowicz-Zdanowska 2013
→ {in Brück & Vanguestaine 2004} *Ichnosphaera robusta* Jachowicz-Zdanowska 2013

Elektoriskos sp. A Vidal & Peel 1993

Elenia Volkova 1984
type species: *Elenia armillata* Fanderflit in Umnova & Fanderflit 1971 ex Volkova 1984

Elenia armillata Fanderflit in Umnova & Fanderflit 1971 ex Volkova 1984

Eliasum Fombella 1977
type species: *Eliasum llaniscum* Fombella 1977

Eliasum asturicum Fombella 1977

Eliasum hutchinsonii Martin in Martin & Dean 1984

Eliasum jennessii Martin in Martin & Dean 1984

Eliasum llaniscum Fombella 1977

“Eliasum microgranulatum” Hagenfeldt 1989b
→ *Eliasum llaniscum* Fombella 1977 [acc. to Vanguestaine & Brück 2008]

Eliasum pisciforme Fombella 1977

Eliasum pisiformis
[cited without reference in Palacios 2008, 2010; presumably a misspelling of *Eliasum pisciforme* Fombella 1977]

Eliasum n. sp. A Palacios 2010

Eliasum sp. 1 Volkova 1990

Eliasum sp. A Żylińska & Szczepanik 2009

Eomicrhystridium Deflandre 1968
type species: *Eomicrhystridium barghoornii* Deflandre 1968

Estiastra Eisenack 1959a emend. Sarjeant & Stancliffe 1994
type species: *Estiastra magna* Eisenack 1959a

Estiastra minima Volkova 1969

“Eupoikilofusa” Cramer 1970
→ *Dactylofusa* Brito & Santos 1965 [acc. to Fensome et al. 1990]
type species: *“Eupoikilofusa striatifera”* (Cramer 1964a) Cramer 1970
→ *Dactylofusa striatifera* (Cramer 1964a) Fensome et al. 1990

“Eupoikilofusa squama” (Deunff 1961a) Eisenack et al. 1979
→ *Poikilofusa squama* (Deunff 1961a) Martin 1973

Evittia Brito 1967a emend. Lister 1970
type species: *Evittia sommeri* Brito 1967a

Evittia irregulare Downie 1982

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Filisphaeridium Staplin et al. 1965 emend. Sarjeant & Stancliffe 1994 (emend. rejected by Mullins 2001)
type species: *Filisphaeridium setasessitante* (Jansonius 1962) Staplin et al. 1965

Filisphaeridium hirtum (Timofeev 1959b ex Umnova 1975) Sarjeant & Stancliffe 1994

Filisphaeridium papillosum (Timofeev 1959b ex Volkova 1968) Hu Yunxu 1986

Filisphaeridium sp. A Jago et al. 2006

Fimbriaglomerella Loeblich & Drugg 1968
type species: *Fimbriaglomerella divisa* Loeblich & Drugg 1968

Fimbriaglomerella gothlandica
[cited without reference in Jago et al. 2006]

Fimbriaglomerella membranacea Kiryanov 1974 ex Moczydłowska & Vidal 1988

Fimbriaglomerella minuta (Jankauskas in Volkova et al. 1979) Moczydłowska & Vidal 1988

Germinosphaera Mikhailova 1986
[fungi]
type species: *Germinosphaera bispinosa* Mikhailova 1986

Globosphaeridium Moczydłowska 1991
type species: *Globosphaeridium cerinum* (Volkova 1968) Moczydłowska 1991

Globosphaeridium arenulum Jachowicz-Zdanowska 2013

Globosphaeridium cerinum (Volkova 1968) Moczydłowska 1991

Globus Vidal *in* Moczydłowska & Vidal 1988
type species: *Globus gossipinus* Vidal *in* Moczydłowska & Vidal 1988

Globus gossipinus Vidal *in* Moczydłowska & Vidal 1988

Gloeocapsomorpha Zalessky 1917 emend. Foster et al. 1989
[incertae sedis]
type species: *Gloeocapsomorpha prisca* Zalessky 1917

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Goniomorpha Yin L. 1986
type species: *Goniomorpha rara* Yin L. 1986

Goniosphaeridium Eisenack 1969 emend. Kjellström 1971a emend. Turner 1984
type species: *Goniosphaeridium polygonale* (Eisenack 1931 ex Eisenack 1938a) Eisenack 1969

“Goniosphaeridium aff. *akrochordum”* (Rasul 1979) Dean & Martin 1982
[misspelled as *“akrochodermum”* in Dean & Martin 1982 and Martin 1992]
→ {in Dean & Martin 1982; *pro parte* in Martin 1992} *Polygonium martinae* Moczydłowska & Crimes 1995 [acc. to Moczydłowska & Stockfors 2004]
→ {*pro parte* in Martin 1992} *Solisphaeridium akrochordum* (Rasul 1979) Moczydłowska & Stockfors 2004

Goniosphaeridium canningia (Combaz & Peniguel 1972) Playford & Martin 1984

“Goniosphaeridium aff. *dentatum”* (Timofeev 1959b ex Konzalová-Mazancová 1969) Rauscher 1973
→ *Polygonium pungens* (Timofeev 1959b ex Martin 1969) Albani 1989 [acc. to Moczydłowska & Stockfors 2004]

“Goniosphaeridium implicatum” (Fridriksone 1971) Downie 1982
→ *Parmasphaeridium implicatum* (Fridriksone 1971) Jachowicz-Zdanowska 2013

Goniosphaeridium primarium (Jankauskas in Volkova et al. 1979) Downie 1982

Goniosphaeridium rasulii Welsch 1986

“Goniosphaeridium regulare” Yin L. in Chen J. et al. 1985
→ *Stellechinatum uncinatum* (Downie 1958) Molyneux 1987 [acc. to Yin L. 1986]

Goniosphaeridium tener Timofeev 1959b ex Elaouad-Debbaj 1988

Goniosphaeridium tuberatum (Downie 1958) Welsch 1986
[comb. not validly published in Wolf 1980]

“Goniosphaeridium uncinatum” (Downie 1958) Kjellström 1971b
→ *Stellechinatum uncinatum* (Downie 1958) Molyneux 1987

“Goniosphaeridium varium” (Volkova 1969) Downie 1982
→ *Eklundia varia* (Volkova 1969) Jachowicz-Zdanowska 2013

Goniosphaeridium volkovae Hagenfeldt 1989a

Goniosphaeridium sp. A Downie 1982

Goniosphaeridium sp. A Vidal & Peel 1993

Goniosphaeridium sp. B Downie 1982

Gorgonisphaeridium Staplin et al. 1965 emend. Kiryanov 1978
type species: *Gorgonisphaeridium winslowiae* Staplin et al. 1965

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?Gorgonisphaeridium sp. A Wood & Clendening 1982

?Gorgonisphaeridium sp. B Wood & Clendening 1982

?Gorgonisphaeridium sp. C Wood & Clendening 1982

?Gorgonisphaeridium sp. D Wood & Clendening 1982

?Gorgonisphaeridium sp. E Wood & Clendening 1982

?Gorgonisphaeridium sp. F Wood & Clendening 1982

Granomarginata Naumova 1961
type species: *Granomarginata prima* Naumova 1961

Granomarginata parva Jachowicz-Zdanowska 2013

Granomarginata prima Naumova 1961

Granomarginata squamacea Volkova 1968

Granomarginata vulgaris Naumova 1968

Granularia Kowalski 1983
type species: *Granularia saccoformis* Kowalski 1983

Granularia saccoformis Kowalski 1983

Heliosphaeridium Moczydłowska 1991
type species: *Heliosphaeridium dissimilare* (Volkova 1969) Moczydłowska 1991

Heliosphaeridium ampliatum (Wang 1985) Yao et al. 2005

“Heliosphaeridium bellulum” Moczydłowska 1998
→ *Ammonidium bellulum* (Moczydłowska 1998) Sarjeant & Stancliffe 2000

Heliosphaeridium coniferum (Downie 1982) Moczydłowska 1991

Heliosphaeridium dissimilare (Volkova 1969) Moczydłowska 1991

Heliosphaeridium exile Moczydłowska 1998

Heliosphaeridium lanceolatum (Vanguestaine 1974) Moczydłowska 1998

“?Heliosphaeridium llynense” Martin in Young et al. 1994
→ *Multiplicisphaeridium llynense* (Martin in Young et al. 1994) Jachowicz-Zdanowska 2013

Heliosphaeridium longum (Moczydłowska 1988) Moczydłowska 1998

Heliosphaeridium lubomlense (Kiryanov 1974) Moczydłowska 1991

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Heliosphaeridium nodosum Moczydłowska 1998

“Heliosphaeridium notatum” (Volkova 1969) Moczydłowska 1991
→ *Ammonidium notatum* (Volkova 1969) Jachowicz-Zdanowska 2013

Heliosphaeridium obscurum (Volkova 1969) Moczydłowska 1991

“Heliosphaeridium oligum” (Jankauskas in Jankauskas & Posti 1976) Moczydłowska 1998
→ *Ammonidium oligum* (Jankauskas in Jankauskas & Posti 1976) Jachowicz-Zdanowska 2013

Heliosphaeridium radzynicum (Volkova in Volkova et al. 1979) Moczydłowska 1991

Heliosphaeridium serridentatum Moczydłowska 1998

Heliosphaeridium n. sp. B Moczydłowska & Crimes 1995

Hemisphaerium Hemer & Nygreen 1967
→ *Brazilea* Tiwari & Navale 1967 [acc. to Grenfell 1995; Zygnemataceae]
type species: *Hemisphaerium inornatum* Hemer & Nygreen 1967

Hubeisphaera Xing & Liu 1978
type species: *Hubeisphaera radiata* Xing & Liu 1978

Hubeisphaera radiata Xing & Liu 1978

Huroniospora Barghoon in Barghoorn & Tyler 1965
type species: *Huroniospora microreticulata* Barghoorn in Barghoorn & Tyler 1965

Huroniospora microreticulata Barghoorn in Barghoorn & Tyler 1965

Ichnosphaera Jachowicz-Zdanowska 2013
type species: *Ichnosphaera flexuosa* (Eklund 1990) Jachowicz-Zdanowska 2013

Ichnosphaera aranea Jachowicz-Zdanowska 2013

Ichnosphaera delicata Jachowicz-Zdanowska 2013

Ichnosphaera flexuosa (Eklund 1990) Jachowicz-Zdanowska 2013

Ichnosphaera robusta Jachowicz-Zdanowska 2013

Ichnosphaera stipatica (Hagenfeldt 1989a) Jachowicz-Zdanowska 2013

Impluviculus Loeblich & Tappan 1969 emend. Martin 1975
type species: *Impluviculus milonii* (Deunff 1968b) Loeblich & Tappan 1969

?Impluviculus bibulbulus Parsons & Anderson 2000

Impluviculus cleae (Martin 1972) Martin 1975

Impluviculus lenticularis Martin 1975

Impluviculus milonii (Deunff 1968b) Loeblich & Tappan 1969

Impluviculus multiangularis (Umnova in Umnova & Fanderflit 1971) Volkova 1990

Impluviculus stellaris Martin 1975

Impluviculus villosiusculus Volkova 1990

Impluviculus sp. A Martin & Dean 1988

?Impluviculus sp. A Parsons & Anderson 2000

Izhoria Golub & Volkova in Volkova & Golub 1985
type species: *Izhoria angulata* Golub & Volkova in Volkova & Golub 1985

Izhoria angulata Golub & Volkova in Volkova & Golub 1985

“Kildinella” Shepeleva & Timofeev 1963 ex Timofeev 1966
→ *Leiosphaeridia* Eisenack 1958a [acc. to Volkova 1968 and Lindgren 1982]
type species: “*Kildinella hyperboreica*” Timofeev 1966
→ *Leiosphaeridia hyperboreica* (Timofeev 1966) Fensome et al. 1990

“Kildinosphaera” Vidal in Vidal & Siedlecka 1983
→ *Valeria* Jankauskas 1982 [acc. to Fensome et al. 1990]
type species: “*Kildinosphaera chagrinata*” Vidal in Vidal & Siedlecka 1983
→ *Valeria sinica* (Timofeev 1966) Fensome et al. 1990

“*Kildinosphaera chagrinata*” Vidal in Vidal & Siedlecka 1983
→ *Valeria sinica* (Timofeev 1966) Fensome et al. 1990

“*Kildinosphaera granulata*” Vidal in Vidal & Siedlecka 1983
→ *Megasacculina atava* Naumova 1961

Ladogella Golub & Volkova in Volkova & Golub 1985
type species: *Ladogella rotundiformis* Golub & Volkova in Volkova & Golub 1985

?Ladogella aries Di Milia et al. 1989

Ladogella filifera Di Milia et al. 1989

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?Ladogella intermedia Parsons & Anderson 2000

Ladogella rommelaerei (Martin in Martin & Dean 1981) Di Milia et al. 1989

Ladogella rotundiformis Golub & Volkova in Volkova & Golub 1985

Ladogella saharica Vecoli & Playford 1997

Ladogella volkovae Di Milia et al. 1989

Ladogella sp. A Parsons & Anderson 2000

Lechistania Jachowicz-Zdanowska 2013
type species: *Lechistania magna* Jachowicz-Zdanowska 2013

Lechistania magna Jachowicz-Zdanowska 2013

Leiofusa Eisenack 1938a emend. Eisenack 1965a emend. Combaz et al. 1967 emend. Cramer 1970
type species: *Leiofusa fusiformis* Eisenack 1934 ex Eisenack 1938a

Leiofusa cf. *bicornuta* Xing & Liu 1973

Leiofusa cf. *gravida* Pittau 1985

“Leiofusa pristina” Potter in Baudelot & Géry 1979
[nomen nudum, acc. to Fensome et al. 1990; Baudelot & Géry 1979 gave authorship as “Potter 1974”, refering to an unpublished thesis]

Leiofusa simplex (Combaz 1967) Martin 1975

“Leiofusa squama” Deunff 1961a
→ *Poikilofusa squama* (Deunff 1961a) Martin 1973

Leiofusa stoumonensis Vanguestaine 1973b

“Leioligotriletes” Timofeev 1958
[not validly published acc. to Fensome et al. 1990]
variant: *“Leioligotriletum”*
type species: *“Leioligotriletes crassus”* (Naumova 1949) Timofeev 1958 [not validly published, acc. to Fensome et al. 1990]

“Leioligotriletes crassus” (Naumova 1949) Timofeev 1958
[not validly published, acc. to Fensome et al. 1990]

Leiomarginata Naumova 1961
type species: *Leiomarginata simplex* Naumova 1961

Leiomarginata simplex Naumova 1961

“*Leiominuscula*” Naumova 1961
→ *Leiosphaeridia* Eisenack 1958a [acc. to Cramer & Díez 1979]
type species: “*Leiominuscula minuta*” Naumova 1961
→ *Leiosphaeridia riphiana* Fensome et al. 1990

“*Leiominuscula minuta*” Naumova 1961
→ *Leiosphaeridia riphiana* Fensome et al. 1990

“*Leiopsophosphaera*” Naumova 1961 ex Naumova 1968
→ *Leiosphaeridia* Eisenack 1958a [acc. to Volkova 1968 and Lindgren 1982]
type species: “*Leiopsophosphaera convexiplicata*” Naumova 1968

“*Leiopsophosphaera indefinita*” Pichova
[cited as “*Leiopsophosphaera indefinitus* Pichova” without complete reference in Pykhova 1967]

“*Leiopsophosphaera infriata*” Shepeleva
[cited without complete reference in Ding et al. 1992]
[possible homonym: “*Leiopsophosphaera infriata* (Andr.) Sin et Liu (comb. nov.)” in Xing & Liu 1978, wherein the basionym was not properly referenced; Fensome et al. 1990 also reported citations of “*Leiopsophosphaera infriata*” without complete references and authorship given as: “(Andreeva)” in Xing et al. 1979; “(Timofeev)” in Xing & Liu 1980]

“*Leiopsophosphaera pseudozonalis*” Wang et Chen
[cited without complete reference in Wang & Chen Q. 1987]

“*Leiopsophosphaera rotunda*” Pykhova 1967
[not validly published, acc. to Fensome et al. 1990]

“*Leiopsophosphaera solida*” (Liu et Sin) Xing & Liu 1978
[the basionym was not properly referenced in Xing & Liu 1978, most likely *Protoleiosphaeridium solidum* Liu & Xing in Xing & Liu 1973]

Leiosphaeridia Eisenack 1958a emend. Downie & Sarjeant 1963 emend. Turner 1984
type species: *Leiosphaeridia baltica* Eisenack 1958a

Leiosphaeridia annulata Yin L. in Chen J. et al. 1985

Leiosphaeridia asperata (Naumova 1950) Lindgren 1982

“*Leiosphaeridia atava*” (Naumova 1961) Cramer & Díez 1979

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→ *Megasacculina atava* Naumova 1961

Leiosphaeridia bicrura Jankauskas in Jankauskas & Posti 1976

Leiosphaeridia cerebriformis Volkova 1969

Leiosphaeridia crassa (Naumova 1949) Jankauskas in Jankauskas et al. 1989
[**junior homonym:** *“Leiosphaeridia crassa”* (Pykhova 1973) Fensome et al. 1990]

Leiosphaeridia dehisca Paškevičienė in Volkova et al. 1979

“Leiosphaeridia densa” (Timofeev 1966) Pyatiletov 1978
[**junior homonym:** *Leiosphaeridia densa* (Maithy 1975) Nautiyal 1983]
→ *Protoleiosphaeridium laccatum* (Timofeev 1966) Fensome et al. 1990 [acc. to Vidal 1974]

Leiosphaeridia desmosa Yin L. in Chen J. et al. 1985

“Leiosphaeridia fragile” Downie 1982
→ *Saharidia fragilis* (Downie 1958) Combaz 1967

Leiosphaeridia fumiana Vanguestaine 1974

“Leiosphaeridia gregalis” Hagenfeldt 1989a
→ *Dichotisphaera gregalis* (Hagenfeldt 1989a) Vanguestaine 1991

Leiosphaeridia macrostomata Yin L. in Chen J. et al. 1985

Leiosphaeridia minutissima (Naumova 1949) Jankauskas in Jankauskas et al. 1989

“Leiosphaeridia papillata” (Staplin 1961) Downie & Sarjeant 1965
→ *Lophosphaeridium papillatum* (Staplin 1961) Martin 1969

Leiosphaeridia pylomifera Paškevičienė in Volkova et al. 1979

Leiosphaeridia subgranulata Kiryanov 1974

Leiosphaeridia tenuissima Eisenack 1958b

Leiosphaeridia ternata (Timofeev 1966) Mikhailova & Jankauskas in Jankauskas et al. 1989

Leiosphaeridia tubulosa Eisenack 1963

Leiosphaeridia sp. 1 Cramer & Díez 1972

Leiosphaeridia sp. 1 Eklund 1990

Leiosphaeridia sp. 1 Moczydłowska & Vidal 1986

Leiosphaeridia sp. 1 Volkova et al. 1979

Leiosphaeridia sp. 2 Moczydłowska & Vidal 1986

Leiosphaeridia sp. A Parsons & Anderson 2000

Leiovalia Eisenack 1965a ex Górka 1969
type species: *Leiovalia ovalis* (Eisenack 1938a) Górka 1969

Leiovalia tenera Kiryanov 1974

Liepaina Jankauskas and Volkova in Volkova et al. 1979

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type species: *Liepaina plana* Jankauskas and Volkova in Volkova et al. 1979

Liepaina plana Jankauskas and Volkova in Volkova et al. 1979

Liepaina rigida Eklund 1990

?Liepaina n. sp. Vidal 1981
→ *Turrisphaeridium semireticulatum* (Timofeev 1959b) Jachowicz-Zdanowska 2013

Lophodiacrodium Timofeev 1958 emend. Deflandre & Deflandre-Rigaud 1962
type species: *Lophodiacrodium obtusum* Timofeev 1958

Lophodiacrodium valdaicum (Timofeev 1959b) Downie & Sarjeant 1965

"Lopholigotriletum" Timofeev 1959b
[not validly published, acc. to Fensome et al. 1990]
no type species

"Lopholigotriletum spathaeforme" Timofeev 1959b
→ *Lophosphaeridium spathaeforme* Timofeev 1959b ex Hu Yunxu 1986

Lophominuscula Naumova 1961
type species: *Lophominuscula prima* Naumova 1961

Lophominuscula acietata Sun in Sun & Zhai 1989
[complete reference only available in Chinese]

Lophominuscula crassa Xing & Liu 1978

Lophominuscula prima Naumova 1961

Lophopsophosphaera Naumova
[cited without complete reference in Pykhova 1967; most likely a misspelling of *Leiopsophosphaera* Naumova 1961]
type species: ?

Lophosphaeridium Timofeev 1959b ex Downie 1963 emend. Lister 1970
type species: *Lophosphaeridium rarum* Timofeev 1959b ex Downie 1963

Lophosphaeridium acietatum Xing & Liu 1978

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Lophosphaeridium bacilliferum Vanguestaine 1974

Lophosphaeridium bottnicum Hagenfeldt 1989b

“Lophosphaeridium citrinum” Downie 1963
→ *Baltisphaeridium citrinum* (Downie 1963) Stockmans & Willière 1974

“Lophosphaeridium dubium” (Volkova 1968) Moczydłowska 1991
[**senior hymonym:** *Lophosphaeridium dubium* Jankauskas & Vaitekunene 1972, acc. to Molyneux et al. 1996]

Lophosphaeridium kryptoradiatum Vanguestaine 1974

Lophosphaeridium latviense (Volkova 1974) Moczydłowska 1998

Lophosphaeridium orbiculatum Xing 1962

Lophosphaeridium papillatum (Staplin 1961) Martin 1969

Lophosphaeridium spathaeforme Timofeev 1959b ex Hu Yunxu 1986

Lophosphaeridium tentativum Volkova 1968

Lophosphaeridium truncatum Volkova 1969

Lophosphaeridium tynnii Hagenfeldt 1989b

Lophosphaeridium variabile Volkova 1974

Lophosphaeridium yichangense Xing & Liu 1978

Lophosphaeridium sp. A Potter 1974

Lusatia Burmann 1970 emend. Sarjeant & Vavrdová 1997
type species: *Lusatia dendroidea* Burmann 1970 emend. Albani et al. 2007

Lusatia dendroidea Burmann 1970 emend. Albani et al. 2007

“Lusatia triangularis” (Umnova 1975) Volkova 1990
→ *Lusatia dendroidea* Burmann 1970 emend. Albani et al. 2007

Macroptycha Timofeev 1973a ex Timofeev et al. 1976
type species: *Macroptycha uniplicata* Timofeev in Timofeev et al. 1976

Macroptycha uniplicata Timofeev in Timofeev et al. 1976

Margominuscula Naumova 1961
type species: *Margominuscula rugosa* Naumova 1961

Margominuscula rugosa Naumova 1961

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Medousapalla Wood & Clendening 1982
type species: *Medousapalla choanoklosma* Wood & Clendening 1982

Medousapalla choanoklosma Wood & Clendening 1982

Megasacculina Naumova 1961
type species: *Megasacculina atava* Naumova 1961

Megasacculina atava Naumova 1961

Micrhystridium Deflandre 1937 emend. Staplin 1961 emend. Downie & Sarjeant 1963 emend. Staplin et al. 1965 emend. Sarjeant 1967 emend. Lister 1970 emend. Sarjeant & Stancliffe 1994
type species: *Micrhystridium inconspicuum* (Deflandre 1935) Deflandre 1937

Micrhystridium ampliatum Wang 1985
[**junior homonym:** “*Micrhystridium ampliatum*” Wicander & Playford 1985, acc. to Fensome et al. 1990]
→ *Heliosphaeridium ampliatum* (Wang 1985) Yao et al. 2005

Micrhystridium breviacanthum Slavíková 1968

Micrhystridium brevicornum Jankauskas 1976
→ {in Welsch 1986} *Heliosphaeridium serridentatum* Moczydłowska 1998

Micrhystridium cerinum
[cited without reference in Yang & Yin L. 2001]

Micrhystridium confusum (Jankauskas 1975) Fensome et al. 1990
[acc. to Fensome et al. 1990, this combination was not validly published in Pozaryski et al. 1981]

“*Micrhystridium coniferum*” Downie 1982
→ *Heliosphaeridium coniferum* (Downie 1982) Moczydłowska 1991

Micrhystridium cf. *coronatum* Stockmans & Willière 1963

“*Micrhystridium dissimilare*” Volkova 1969
→ *Heliosphaeridium dissimilare* (Volkova 1969) Moczydłowska 1991

Micrhystridium dubium
[cited without reference in Yang & Yin L. 2001]

Micrhystridium echinulatum Luo & Wang in Wang & Luo 1984

Micrhystridium ellaense Downie 1982

“*Micrhystridium ellipticum*” Downie 1982
→ *Heliosphaeridium obscurum* (Volkova 1969) Moczydłowska 1991

Micrhystridium flexispinosum Downie 1982

“*Micrhystridium gogense*” Downie 1982
→ *Comasphaeridium gogense* (Downie 1982) Sarjeant & Stancliffe 1994

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Micrhystridium guizhouense Fensome et al. 1990

Micrhystridium henryi Paris & Deunff 1970

“Micrhystridium lanatum” Volkova 1969
→ *Asteridium lanatum* (Volkova 1969) Moczydłowska 1991

“Micrhystridium lanceolatum” Vanguestaine 1974
[**junior homonym:** *“Micrhystridium lanceolatum”* Yin L. 1985, acc. to Palacios & Vidal 1992]
→ *Heliosphaeridium lanceolatum* (Vanguestaine 1974) Moczydłowska 1998

“Micrhystridium lanceolatum” Yin L. 1985
[**senior homonym:** *“Micrhystridium lanceolatum”* Vanguestaine 1974, **now** *Asteridium lanceolatum* (Vanguestaine 1974) Moczydłowska 1998, acc. to Palacios & Vidal 1992]

Micrhystridium longispiniferum Wang & Luo 1984

“Micrhystridium longum” Moczydłowska 1988
→ *Heliosphaeridium longum* (Moczydłowska 1988) Moczydłowska 1998

“Micrhystridium lubomlense” Kiryanov 1974
→ *Heliosphaeridium lubomlense* (Kiryanov 1974) Moczydłowska 1991

Micrhystridium maidingense Wang & Chen Q. 1987

Micrhystridium minimum Xing
[cited without complete reference in Yin C. & Gao 1996]

Micrhystridium minutum Downie 1982
[**junior homonym:** *“Micrhystridium minutum”* Luo & Wang in Wang & Luo 1984, acc. to Fensome et al. 1990]

“Micrhystridium minutum” Luo &Wang in Wang & Luo 1984
[**senior homonym:** *Micrhystridium minutum* Downie 1982, acc. to Fensome et al. 1990]
→ *Micrhystridium guizhouense* Fensome et al. 1990

Micrhystridium ningqiangense Xing
[cited without complete reference in Yin C. & Gao 1996]

“Micrhystridium notatum” Volkova 1968
→ *Ammonidium notatum* (Volkova 1969) Jachowicz-Zdanowska 2013

Micrhystridium obscurum Volkova 1969
→ *Heliosphaeridium obscurum* (Volkova 1969) Moczydłowska 1991

“Micrhystridium oligum” Jankauskas in Jankauskas & Posti 1976
→ *Ammonidium oligum* (Jankauskas in Jankauskas & Posti 1976) Jachowicz-Zdanowska 2013

“Micrhystridium ordense” Downie 1982
→ *Asteridium ordense* (Downie 1982) Vidal & Peel 1993

“Micrhystridium pallidum” Volkova 1968
→ *Asteridium pallidum* (Volkova 1968) Moczydłowska 1991

?Micrhystridium profusum Wicander 1974

Micrhystridium pseudozonale Wang & Chen Q. 1987

“Micrhystridium radzynicum” Volkova in Volkova et al. 1979
→ *Heliosphaeridium radzynicum* (Volkova in Volkova et al. 1979) Moczydłowska 1991

Micrhystridium regulare Yin L. 1987

Micrhystridium resistens Timofeev 1959b ex Deflandre & Deflandre-Rigaud 1965

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Micrhystridium semiapertum Welsch 1986

Micrhystridium setulerum Wang et al. 1987
[cited as "in press" in Wang & Chen Q. 1987]

Micrhystridium shinetonense Downie 1958

"Micrhystridium sinuosum" Potter in Baudelot & Géry 1979
[nomen nudum, acc. to Fensome et al. 1990; Baudelot & Géry 1979 gave authorship as "Potter 1974", refering to an unpublished thesis]

"Micrhystridium spinosum" Volkova 1969
→ *Asteridium spinosum* (Volkova 1969) Moczydłowska 1998

Micrhystridium stellatum Deflandre 1945

"Micrhystridium tornatum" Volkova 1968
→ *Asteridium tornatum* (Volkova 1968) Moczydłowska 1991

Micrhystridium varium
[cited without reference in Yang & Yin L. 2001]

Micrhystridium villosum Kiryanov 1974

Micrhystridium n. sp. Vidal 1981

Micrhystridium sp. 1 Cramer & Díez 1972

Micrhystridium sp. 1 Hagenfeldt 1989b

Micrhystridium sp. 1 Paalits 2005

Micrhystridium sp. 2 Hagenfeldt 1989b

Micrhystridium sp. 2 Paalits 2005

Micrhystridium sp. A Albani et al. 1991

Micrhystridium sp. A Knoll & Swett 1987

Micrhystridium sp. A Parsons & Anderson 2000

Micrhystridium sp. B Albani et al. 1991

Micrhystridium sp. B Potter 1974

Microconcentrica Naumova 1961 ex Naumova 1968
type species: *Microconcentrica atava* Naumova 1961 ex Naumova 1968

Microconcentrica atava Naumova 1961 ex Naumova 1968

Microconcentrica induplicata Liu & Xing in Xing & Liu 1973

Monocrodium Pittau 1985
type species: *Monocrodium mediterraneum* Pittau 1985

Monotrematosphaeridium Sin in Xing & Liu 1978

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[authorship in Xing & Liu 1978 was given as "Sin 1962 (MS)", presumably referencing an unpublished manuscript or Xing 1962]
type species: *Monotrematosphaeridium asperum* Xing & Liu 1978

"Monotrematosphaeridium quadratum" Sin 1962
[probably not validly published]

Monotrematosphaeridium simplex Wang et Chen
[cited without complete reference in Wang & Chen Q. 1987]

Multiplicisphaeridium Staplin 1961 emend. Staplin et al. 1965 emend. Eisenack 1969 emend. Lister 1970 emend. Eiserhardt 1992 emend. Sarjeant & Vavrdová 1997
type species: *Multiplicisphaeridium ramispinosum* Staplin 1961

Multiplicisphaeridium ?ancliforme Fombella 1978

"Multiplicisphaeridium campanulum" Eklund 1990
→ *Eklundia campanula* (Eklund 1990) Jachowicz-Zdanowska 2013

Multiplicisphaeridium cervinacornuum Welsch 1986

Multiplicisphaeridium chakor Vanguestaine & Van Looy 1983

Multiplicisphaeridium constipatum Eklund 1990

Multiplicisphaeridium dactilum Vidal in Moczydłowska & Vidal 1988

"Multiplicisphaeridium dendroideum" (Jankauskas 1976) Jankauskas & Kiryanov in Volkova et al. 1979
[**senior homonyms:** *Multiplicisphaeridium dendroidium* Morbey 1975; *Multiplicisphaeridium dendroideum* (Burmann 1970) Eisenack et al. 1976, acc. to Fensome et al. 1990]
→ *Multiplicisphaeridium xianum* Fombella 1977 [acc. to Moczydłowska 1998]

Multiplicisphaeridium cf. *eodigitatum* Fombella 1978

Multiplicisphaeridium cf. *eopiriferum* Fombella 1978

"?Multiplicisphaeridium cf. *furcatum"* (Deunff 1961a) Eisenack et al. 1973
→ *Stelliferidium* cf. *furcatum* (Deunff 1961a) emend. Deunff et al. 1974

Multiplicisphaeridium jaroslavicum Volkova 1990

"Multiplicisphaeridium lancarae" Cramer & Díez 1972
→ *Timofeevia lancariae* (Cramer & Díez 1972) Vanguestaine 1978

Multiplicisphaeridium llynense (Martin in Young et al. 1994) Jachowicz-Zdanowska 2013

Multiplicisphaeridium martae Cramer & Díez 1972

Multiplicisphaeridium ramosum Moczydłowska 1998

"Multiplicisphaeridium raquelinae" Cramer & Díez 1972
→ *Timofeevia raquelinae* (Cramer & Díez 1972) Cramer & Díez 1979

Multiplicisphaeridium parvum (Hagenfeldt 1989b) Moczydłowska 1998

Multiplicisphaeridium sosnowiecense Moczydłowska 1998

Multiplicisphaeridium varietatis Moczydłowska 1998

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“Multiplicisphaeridium vilnense” (Jankauskas 1976) Jankauskas in Volkova et al. 1979

→ *Timofeevia lancariae* (Cramer & Díez 1972) Vanguestaine 1978

Multiplicisphaeridium waltonii Downie 1982

Multiplicisphaeridium xianum Fombella 1977

Multiplicisphaeridium yankauskasii Fensome et al. 1990

Multiplicisphaeridium sp. 1 Volkova 1990

Myxococcoides Schopf 1968
type species: *Myxococcoides minor* Schopf 1968

Myxococcoides inornata Schopf 1968

Myxococcoides minor Schopf 1968

Myxococcoides staphylidion Lo 1980

Nanocyclopia Loeblich & Wicander 1976
type species: *Nanocyclopia aspratilis* Loeblich & Wicander 1976

Nanocyclopia sp. 1 Uutela 2008

Navifusa Combaz et al. 1967 ex Eisenack 1976
type species: *Navifusa navis* (Eisenack 1938b) Eisenack 1976

Nellia Golub & Volkova in Volkova & Golub 1985
type species: *Nellia longiuscula* Golub & Volkova in Volkova & Golub 1985

Nellia acifera (Umnova in Umnova & Fanderflit 1971) Volkova 1990

?Nellia longispinata Parsons & Anderson 2000

Nellia longiuscula Golub & Volkova in Volkova & Golub 1985

Nellia magna Volkova 1990

Nellia sukatschevii (Timofeev 1959b) Volkova 1990

Neoveryhachium Cramer 1970
type species: *Neoveryhachium carminae* (Cramer 1964b) Cramer 1970

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Ninadiacrodium Raevskaya & Servais 2009
type species: *Ninadiacrodium dumontii* (Vanguestaine 1973b) Raevskaya & Servais 2009

Ninadiacrodium caudatum (Vanguestaine 1973b) Raevskaya & Servais 2009

Ninadiacrodium dumontii (Vanguestaine 1973b) Raevskaya & Servais 2009

Nodosus Hagenfeldt 1989b
type species: *Nodosus irregulare* Hagenfeldt 1989b

Nodosus irregulare Hagenfeldt 1989b

Nucellosphaeridium Timofeev 1966
type species: *Nucellosphaeridium deunffii* Timofeev 1966

Nucellosphaeridium sp. A Martin & Dean 1983

“Ocridoligotriletes” Timofeev 1958
variant: *“Ocridoligotriletum”*
→ *Trachytriletes* Naumova 1939 ex Naumova 1949 [acc. to Fensome et al. 1990]
type species: *O. kryshtofovichii* (Naumova 1949) Timofeev 1958 [comb. illegitimate acc. to Fensome et al. 1990]
→ *Trachytriletes kryshtofovichii* Naumova 1949

“Ocridoligotriletum kryshtofovichi” (Naumova 1949) Timofeev 1958 [comb. illegitimate acc. to Fensome et al. 1990]
→ *Trachytriletes kryshtofovichii* Naumova 1949

Octaedryxium Rudavskaya 1973a
or *Octoedryxium* Rudavskaya 1973b [uncertain seniority acc. to Fensome et al. 1990]
type species: *Octaedryxium truncatum* Rudavskaya 1973a or Rudavskaya 1973b

Octaedryxium minutum Wang & Chen Q. 1987

Octaedryxium simplex Wang & Chen Q. 1987

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Ooidium Timofeev 1957 emend. Norris & Sarjeant 1965
type species: *Ooidium rossicum* Timofeev 1957

?Ooidium clavigerum Parsons & Anderson 2000

"Ooidium aff. *revinium"* Vanguestaine 1973b
→ *Trunculumarium* aff. *revinium* (Vanguestaine 1973b) Loeblich & Tappan 1976

Ooidium rossicum Timofeev 1957

Ooidium timofeevii Loeblich 1970

Ooidium sp. A Vanguestaine 1986

?Ooidium sp. A Martin & Dean 1981

Orthosphaeridium Eisenack 1968 emend. Kjellström 1971a emend. Turner 1984
type species: *Orthosphaeridium rectangulare* (Eisenack 1963) Eisenack 1968

?Orthosphaeridium extensum Parsons & Anderson 2000
→ {*pro parte* in Parsons & Anderson 2000} *Lusatia dendroidea* Burmann 1970 emend. Albani et al. 2007

"?Orthosphaeridium triangulare" (Umnova 1975) Parsons & Anderson 2000
→ *Lusatia dendroidea* Burmann 1970 emend. Albani et al. 2007

Orygmatosphaeridium Timofeev 1959b
type species: *Orygmatosphaeridium ruminatum* Timofeev 1959b

Orygmatosphaeridium holtedahlii (Timofeev 1966) Fensome et al. 1990

"Orygmatosphaeridium semireticulatum" Andreeva 1966
→ *Orygmatosphaeridium holtedahlii* (Timofeev 1966) Fensome et al. 1990

"Ovulum" Jankauskas 1975
[not validly published, acc. to Fensome et al. 1990]
→ *Revinotesta* Vanguestaine 1974 [acc. to Cramer & Díez 1979]
type species: *Ovulum saccatum* Jankauskas 1975
→ *Revinotesta saccata* (Jankauskas 1975) ex Fensome et al. 1990

"Ovulum lanceolatum" Jankauskas 1975
→ *Revinotesta lanceolata* Jankauskas 1975 ex Fensome et al. 1990

"Ovulum saccatum" Jankauskas 1975
→ *Revinotesta saccata* Jankauskas 1975 ex Fensome et al. 1990

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Paracymatiosphaera Wang 1985
type species: *Paracymatiosphaera regularis* Wang 1985

Paracymatiosphaera annularis Wang 1985

Paracymatiosphaera hunnanensis Wang 1985

Paracymatiosphaera irregularis Wang 1985

Paracymatiosphaera regularis Wang 1985

Paracymatiosphaera spinosa Yin C. in Yin C. & Liu 1988

Parmasphaeridium Jachowicz-Zdanowska 2013
type species: *Parmasphaeridium implicatum* (Fridriksone 1971) Jachowicz-Zdanowska 2013

Parmasphaeridium implicatum (Fridriksone 1971) Jachowicz-Zdanowska 2013

Parmasphaeridium robustispinosum Jachowicz-Zdanowska 2013

Peramorpha Martin in Martin & Dean 1983
type species: *Peramorpha manuelsensis* Martin in Martin & Dean 1983

Peramorpha manuelsensis Martin in Martin & Dean 1983

Petaloferidium Jacobson 1978
type species: *Petaloferidium stigii* Jacobson 1978

Petaloferidium lacrimiferum Palacios et al. 2009

Peteinosphaeridium Staplin et al. 1965
type species: *Peteinosphaeridium bergstroemii* Staplin et al. 1965

Phenacoon Vecoli & Playford 1997
type species: *Phenacoon imperfectum* Vecoli & Playford 1997

Phenacoon imperfectum Vecoli & Playford 1997

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Pirea Vavrdová 1972
type species: *Pirea dubia* Vavrdová 1972

Pirea orbicularis Volkova 1990

“Plicatosphaera” Potter in Baudelot & Géry 1979
[nomen nudum, acc. to Fensome et al. 1990]
type species: *“Plicatosphaera elementaria”* Potter in Baudelot & Géry 1979 [nomen nudum acc. to Fensome et al. 1990]

“Plicatosphaera elementaria” Potter in Baudelot & Géry 1979
[nomen nudum, acc. to Fensome et al. 1990; Baudelot & Géry 1979 gave authorship as “Potter 1974”, refering to an unpublished thesis]

Poikilofusa Staplin et al. 1965
type species: *Poikilofusa spinata* Staplin et al. 1965

Poikilofusa chalaza Rasul 1979

Poikilofusa squama (Deunff 1961a) Martin 1972

Polyedryxium Deunff 1954a emend. Deunff 1971
type species: *Polyedryxium deflandrei* Deunff 1954a ex Deunff 1961b

“Polyedryxium sarjeantii” Slavíková 1968
[not validly published, acc. to Fensome et al. 1990]

Polygonium Vavrdová 1966 restrict. Le Hérissé 1989 emend. Sarjeant & Stancliffe 1994 emend. Moczydłowska & Stockfors 2004
type species: *Polygonium gracile* Vavrdová 1966

“Polygonium dentatum” (Timofeev 1959b ex Konzalová-Mazancová 1969) Albani 1989
→ *Polygonium pungens* (Timofeev 1959b ex Martin 1969) Albani 1989 [acc. to Moczydłowska & Stockfors 2004]

Polygonium gracile Vavrdová 1966 emend. Jacobson & Achab 1985 emend. Sarjeant & Stancliffe 1996

Polygonium martinae Moczydłowska & Crimes 1995

Polygonium minimum Timofeev 1959b ex Volkova 1990

Polygonium pellicidum (Timofeev 1959b ex Tynni 1975) Volkova 1990 emend.

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Moczydłowska & Stockfors 2004

Polygonium pungens (Timofeev 1959b ex Martin 1969) Albani 1989
[this combination was not validly published by Baudelot & Bessiere 1977, acc. to Fensome et al. 1990]

Polygonium sexradiatum (Timofeev 1959b) Volkova 1990

"Polygonium varium" (Volkova 1969) Sarjeant & Stancliffe 1994
[Sarjeant & Stancliffe 1994 tentatively assigned this species to *Polygonium*; Moczydłowska 1998 marked this as a new combination]
→ *Eklundia varia* (Volkova 1969) Jachowicz-Zdanowska 2013

Polygonium sp. A Vanguestaine 1973a

"Polyporata" Pykhova 1966
[nomen nudum, acc. to Fensome et al. 1990]
[**homonym:** *Polyporata* Xing & Liu 1973]
no type species

"Polyporata nidia" Pykhova 1966
[not validly published, acc. to Fensome et al. 1990]

"Polyporata verrucosa" Pykhova 1966
[not validly published, acc. to Fensome et al. 1990]

Priscogalea Deunff 1961a emend. Rasul 1974
type species: *Priscogalea barbara* Deunff 1961a

"Priscogalea cortinula" Deunff 1961a
→ *Stelliferidium cortinulum* (Deunff 1961a) emend. Deunff et al. 1974

"Priscogalea cuvillieri" Deunff 1961a
→ *Cymatiogalea cuvillieri* (Deunff 1961a) Deunff 1964

"Priscogalea gautieri" Martin 1972
→ *Stelliferidium gautieri* (Martin 1972) Pittau 1985

"Priscogalea multarea" Deunff 1961a
→ *Cymatiogalea multarea* (Deunff 1961a) Eisenack et al. 1973

Priscogalea primordialis Yin L. in Chen J. et al. 1985 emend. Yin L. 1986

Priscogalea promptusa Yin L. in Chen J. et al. 1985

?Priscogalea sp. A Vanguestaine 1986

Priscotheca Deunff 1961a
type species: *Priscotheca raia* Deunff 1961a

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Priscotheca notata Volkova 1988

Protoarchaeosacculina Naumova 1961
type species: *Protoarchaeosacculina atava* Naumova 1961

Protoleiosphaeridium Timofeev 1959b ex Timofeev 1960
type species: *Protoleiosphaeridium conglutinatum* Timofeev 1959b ex Timofeev 1960

Protoleiosphaeridium conglutinatum Timofeev 1959b ex Timofeev 1960

Protoleiosphaeridium crassum Timofeev 1963

“Protoleiosphaeridium densum” (Timofeev 1966) Yin L. 1979
→ *Protoleiosphaeridium laccatum* (Timofeev 1966) Fensome et al. 1990

Protoleiosphaeridium laccatum (Timofeev 1966) Fensome et al. 1990

Protoleiosphaeridium minutissimum Timofeev
[cited without complete reference in Jagielska 1965]

Protoleiosphaeridium papyraceum (Timofeev 1966) Zang 1992

Protoleiosphaeridium rugulosum (Fombella 1978) Fensome et al. 1990

Protoleiosphaeridium sp. forme A Potter 1974

Protolophosphaeridium Timofeev 1963
type species: *Protolophosphaeridium faetonum* Timofeev 1963

Protolophosphaeridium crispum Timofeev
[cited without complete reference in Jagielska 1965]

Protolophosphaeridium grumosum Timofeev
[cited without complete reference in Jagielska 1965]

Protomyceterosphaeridium Timofeev 1963
type species: *Protomyceterosphaeridium marmoratum* Timofeev 1963

Protomycterosphaeridium marmoratum Timofeev 1963

“Protosphaeridium” Timofeev 1966
→ *Protoleiosphaeridium* Timofeev 1959b ex Timofeev 1960 [acc. to Loeblich & Tappan 1976]

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type species: “*Protosphaeridium densum*” Timofeev 1966
→ *Protoleiosphaeridium laccatum* (Timofeev 1966) Fensome et al. 1990

“*Protosphaeridium flexuosum*” Timofeev 1966
→ *Orygmatosphaeridium holtedahlii* (Timofeev 1966) Fensome et al. 1990

Prototrachysphaeridium Timofeev 1963
type species: *Prototrachysphaeridium staplinii* Timofeev 1963

Prototrachysphaeridium nevelense Timofeev
[cited without complete reference in Jagielska 1965]

Pseudotasmanites Kiryanov 1974
type species: *Pseudotasmanites parvus* Kiryanov 1974

Pseudotasmanites parvus Kiryanov 1974

Pseudozonosphaera Xing & Liu 1973
type species: *Pseudozonosphaera verrucosa* Xing & Liu 1973

Pseudozonosphaera asperella Xing & Liu 1978
[authorship in Xing & Liu 1978 was given as “Sin et Liu (MS)”, presumably referencing an unpublished manuscript]

Pseudozonosphaera sinica Xing & Liu 1973

Pseudozonosphaera verrucosa Xing & Liu 1973

Pseudozonosphaeridium Andreeva 1966
type species: *Pseudozonosphaeridium populosum* Andreeva 1966

Pseudozonosphaeridium fengxiangense Zhong Guofang 1978
[not reported from the Cambrian, but from the Proterozoic and the Silurian]

Psophosphaera Naumova 1939 ex Ishchenko 1952 emend. Potonié 1958
[gymnospermous palynomorphs]
type species: ?

Psophosphaera obscura Pykhova 1967

Pterospermella Eisenack 1972
type species: *Pterospermella aureolata* (Cookson & Eisenack 1958) Eisenack 1972

Pterospermella gigantea Jachowicz-Zdanowska 2013

Pterospermella inordinata Jachowicz-Zdanowska 2013

Pterospermella solida (Volkova 1969) Volkova in Volkova et al. 1979

Pterospermella velata Moczydłowska 1988

Pterospermella vitalis Jankauskas in Volkova et al. 1979

Pterospermella vitrea (Volkova 1974) Fensome et al. 1990

"Pterospermella wolynica" Kiryanov
[cited in Vidal 1981 as "*P. wolynica* Kiryanov", "*P.*" implicitly representing
Pterospermella in the context, but it should be *Pterospermopsimorpha*]
→ *Pterospermopsimorpha wolynica* Kiryanov 1974

Pterospermella n. sp. 1 Moczydłowska & Vidal 1986

Pterospermella sp. A Palacios & Vidal 1992

Pterospermella sp. B Moczydłowska & Stockfors 2004

Pterospermopsimorpha Timofeev 1966
type species: *Pterospermopsimorpha pileiformis* Timofeev 1966

Pterospermopsimorpha rugulosa Jachowicz-Zdanowska 2013

Pterospermopsimorpha wolynica Kiryanov 1974

Pulvinosphaeridium Eisenack 1954a
type species: *Pulvinosphaeridium pulvinellum* Eisenack 1954a

Pulvinosphaeridium antiquum Paškevičienė 1980

Pulvinosphaeridium delicatum Yin L. in Chen J. et al. 1985

Raphesphaera Volkova 1990
type species: *Raphesphaera spinulifera* Volkova 1990

Raphesphaera obsoleta Volkova 1990

Raphesphaera spinulifera Volkova 1990

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→ *Vulcanisphaera spinulifera* (Volkova 1990) Parsons & Anderson 2000

Raphesphaera striatula Volkova 1993a

“Raphesphaera turbata” (Martin in Martin & Dean 1981) Volkova 1990
→ *Vulcanisphaera turbata* Martin in Martin & Dean 1981

Retisphaeridium Staplin et al. 1965
type species: *Retisphaeridium dichamerum* Staplin et al. 1965

Retisphaeridium brayense (Gardiner & Vanguestaine 1971) Moczydłowska & Crimes 1995

Retisphaeridium capsulatum (Jankauskas in Jankauskas & Posti 1976) Vanguestaine in Brück & Vanguestaine 2005

Retisphaeridium densum Paškevičienė in Volkova et al. 1979

Retisphaeridium dichamerum Staplin et al. 1965

“Retisphaeridium howellii” Martin in Martin & Dean 1983
→ *Retisphaeridium postae* (Jankauskas in Volkova et al. 1979) Vanguestaine in Brück & Vanguestaine 2004 [acc. to Vanguestaine in Brück & Vanguestaine 2004]

Retisphaeridium lechistanium Jachowicz-Zdanowska 2013

Retisphaeridium ovillense (Cramer & Díez 1972) Vanguestaine 2002

Retisphaeridium postae (Jankauskas in Volkova et al. 1979) Vanguestaine in Brück & Vanguestaine 2004

Retisphaeridium pusillum (Moczydłowska 1998) Vanguestaine in Brück & Vanguestaine 2005

Revinotesta Vanguestaine 1974 emend. Moczydłowska 1998
type species: *Revinotesta microspinosa* Vanguestaine 1974

Revinotesta izhorica (Jankauskas 1975) Moczydłowska 1998

“Revinotesta laevigata” Vanguestaine in Baudelot & Géry 1979
[nomen nudum, acc. to Fensome et al. 1990; Baudelot & Géry 1979 gave authorship as “Vanguestaine 1973”, refering to an unpublished thesis (Vanguestaine 1973a)]

Revinotesta lanceolata Jankauskas 1975 ex Fensome et al. 1990

Revinotesta microspinosa Vanguestaine 1974

Revinotesta ordensis Downie 1982

Revinotesta saccata Jankauskas 1975 ex Fensome et al. 1990

Revinotesta n. sp. Vanguestaine 1986

“Rugasphaera” Martin in Martin & Dean 1988
[**senior homonym:** *Rugasphaera* Jiabo 1978 (= Song et al. 1978), acc. to Fensome et al. 1990]

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→ *Corrugasphaera* Fensome et al. 1990
type species: “*Rugasphaera terranovana*” Martin in Martin & Dean 1988
→ *Corrugasphaera terranovana* Fensome et al. 1990

“*Rugasphaera terranova*” Martin in Martin & Dean 1988
→ *Corrugasphaera terranovana* Fensome et al. 1990

Sagatum Vavrdová & Bek 2001
type species: *Sagatum priscum* (Kiryanov & Volkova in Volkova et al. 1979) Vavrdová & Bek 2001

Sagatum priscum (Kiryanov & Volkova in Volkova et al. 1979) Vavrdová & Bek 2001

Saharidia Combaz 1967
type species: *Saharidia downiei* Combaz 1967

Saharidia fragilis (Downie 1958) Combaz 1967

Saharidia sp. A Parsons & Anderson 2000

Schizodiacrodium Burmann 1968
type species: *Schizodiacrodium ramiferum* Burmann 1968

Schizodiacrodium armatum Volkova 1990

Schizodiacrodium brevicrinitum Golub & Volkova in Volkova & Golub 1985

Schizodiacrodium digermulense (Welsch 1986) Parsons & Anderson 2000

Schizodiacrodium fibrosum Golub & Volkova in Volkova & Golub 1985

Sinianella Yin L. 1980 emend. Zang in Zang & Walter 1992
type species: *Sinianella uniplicata* Yin L. 1980 emend. Zang in Zang & Walter 1992

Sinianella uniplicata Yin L. 1980 emend. Zang in Zang & Walter 1992

Skiagia Downie 1982 emend. Moczydłowska 1991
type species: *Skiagia scottica* Downie 1982

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Skiagia brachyspinosa (Kiryanov 1974) Jachowicz-Zdanowska 2013

“Skiagia brevispinosa” Downie 1982
→ *Skiagia brachyspinosa* (Kiryanov 1974) Jachowicz-Zdanowska 2013

Skiagia ciliosa (Volkova 1969) Downie 1982

Skiagia compressa (Volkova 1968) Downie 1982

Skiagia insignis (Fridriksone 1971) Downie 1982

Skiagia orbicularis (Volkova 1968) Downie 1982

Skiagia ornata (Volkova 1968) Downie 1982

Skiagia pilosiuscula (Jankauskas in Volkova et al. 1979) Jachowicz-Zdanowska 2013

Skiagia pura Moczydłowska 1988

Skiagia scottica Downie 1982

Skiagia sp. A Knoll & Swett 1987

Solisphaeridium Staplin et al. 1965 emend. Sarjeant 1968 emend. Moczydłowska 1998
type species: *Solisphaeridium stimuliferum* (Deflandre 1938) Staplin et al. 1965 [Fensome et al. 1990 gave authorship for this comb. as “(Deflandre 1938) Pocock 1972”]

Solisphaeridium akrochordum (Rasul 1979) Moczydłowska & Stockfors 2004

“Solisphaeridium baltoscandium” Eklund 1990 emend. Moczydłowska 1998
→ *Goniosphaeridium volkovae* Hagenfeldt 1989a

Solisphaeridium bimodulentum Moczydłowska 1998

Solisphaeridium chinese Moczydłowska & Stockfors 2004

Solisphaeridium cylindratum Moczydłowska 1998

Solisphaeridium elegans Moczydłowska 1998

Solisphaeridium flexipilosum Slavíková 1968 emend. Moczydłowska 1998

“Solisphaeridium implicatum” (Fridriksone 1971) Moczydłowska 1998
→ *Parmasphaeridium implicatum* (Fridriksone 1971) Jachowicz-Zdanowska 2013

Solisphaeridium lucidum (Deunff 1959) Turner 1985

Solisphaeridium multiflexipilosum Slavíková 1968 emend. Moczydłowska 1998

Solisphaeridium sp. A Moczydłowska 1998

“Sphaerocongregus” Moorman 1974
→ *Bavlinella* Shepeleva 1962 [acc. to Vidal 1976]
type species: *“Sphaerocongregus variabilis”* Moorman 1974
→ *Bavlinella faveolata* Shepeleva 1962 [acc. to Vidal 1976]

“Sphaerocongregus variabilis” Moorman 1974

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→ *Bavlinella faveolata* Shepeleva 1962 [acc. to Vidal 1976]

Spumosopsophosphaera Naumova
[cited without complete reference in Pykhova 1967]
?= *Spumososphaera* Naumova [cited without complete reference in Naumova 1968, acc. to Fensome et al. 1990]
type species: ?

Stellechinatum Turner 1984
type species: *Stellechinatum celestum* (Martin 1969) Turner 1984

Stellechinatum uncinatum (Downie 1958) Molyneux 1987

Stelliferidium Deunff et al. 1974
type species: *Stelliferidium striatulum* (Vavrdová 1966) Deunff et al. 1974

?Stelliferidium anomalum Di Milia et al. 1989

Stelliferidium cortinulamorphum Paalits 1995

Stelliferidium cortinulum (Deunff 1961a) emend. Deunff et al. 1974

Stelliferidium cylindratum (Rasul 1974) Elaouad-Debbaj 1988

Stelliferidium distinctum (Rasul 1974) Pittau 1985

?Stelliferidium cf. *furcatum* (Deunff 1961a) emend. Deunff et al. 1974

Stelliferidium gautieri (Martin 1972) Pittau 1985

Stelliferidium magnum Palacios et al. 2009

Stelliferidium pingiculum Martin in Martin & Dean 1988

Stelliferidium aff. *pseudoornatum* Pittau 1985

Stelliferidium robustum Moczydłowska 1998

Stelliferidium striatulum Vavrdová 1966) Deunff et al. 1974

Stelliferidium sp. 1 Volkova 1990

Stelliferidium sp. A Di Milia 1991

Stelliferidium sp. A Parsons & Anderson 2000

Stelliferidium sp. A Parsons & Anderson 2000

Stelliferidium sp. A Parsons & Anderson 2000

Stelliferidium sp. B Di Milia 1991

Stelliferidium sp. B Parsons & Anderson 2000

Stelliferidium sp. C Di Milia 1991

Stellinium Jardiné et al. 1972
type species: *Stellinium octoaster* (Staplin 1961) Jardiné et al. 1972

?Stellinium n. sp. Vidal 1981

Stictosphaeridium Timofeev 1962 ex Timofeev 1966
type species: *Stictosphaeridium sinapticuliferum* Timofeev 1966

“Stictosphaeridium brayense” Gardiner & Vanguestaine 1971
→ *Retisphaeridium brayense* (Gardiner & Vanguestaine 1971) Moczydłowska & Crimes 1995

“Stictosphaeridium implexum” Timofeev 1966
→ *Protoleiosphaeridium laccatum* (Timofeev 1966) Fensome et al. 1990

Stictosphaeridium sinapticuliferum Timofeev 1966

Striatotheca Burmann 1970
type species: *Striatotheca principalis* Burmann 1970

?Striatotheca loculifera Volkova 1990

?Striatotheca randomensis Parsons & Anderson 2000

Symplassosphaeridium Timofeev 1959b ex Timofeev 1969
type species: *Symplassosphaeridium tumidulum* Timofeev 1959b

Symplassosphaeridium cambriense Slavíková 1968 ex Fensome et al. 1990

Synsphaeridium Eisenack 1965b
[**junior homonym:** *“Synsphaeridium”* Timofeev 1966, acc. to Fensome et al. 1990]
type species: *Synsphaeridium gotlandicum* Eisenack 1965b

“Synsphaeridium conglutinatum” (Timofeev 1959b ex Timofeev 1960) Timofeev 1969
→ *Protoleiosphaeridium conglutinatum* Timofeev 1959b ex Timofeev 1960

Synsphaeridium cf. *paulum* Potter in Baudelot & Géry 1979
[nomen nudum, acc. to Fensome et al. 1990; Baudelot & Géry 1979 gave authorship as

"Potter 1974", refering to an unpublished thesis]

Synsphaeridium switjasium Kiryanov 1974

Synsphaeridium sp. 1 Cramer & Díez 1972

Synsphaeridium sp. 1 Young et al. 1994

Tasmanites Newton 1875
type species: *Tasmanites punctatus* Newton 1875

Tasmanites bobrowskae Ważyńska 1967

Tasmanites convolutus Volkova & Piskun 1985
[cited without complete reference in Jankauskas & Lendzion 1992 as "*Tasmanites convolutus* Volkova et Pisk."; in Jankauskas 2002 as "*T. convoliutum*" (p. 81), "*Tasmanites convolatus*" (p. 83), "*Tasmanites convuliutus* Volkova et Piskun, 1985" (p. 110); in Vetluzhskikh et al. 2009 as "*Tasmanites convolutus* Volk. et Pisk"]

Tasmanites piritaensis Posti & Jankauskas in Jankauskas & Posti 1976

Tasmanites tenellus Volkova 1968

"*Tasmanites variabilis*" Volkova 1968
→ *Tasmanites bobrowskae* Ważyńska 1967

Tasmanites volkovae Kiryanov 1974

Tasmanites sp. A Vanguestaine 1986

Tawuia Hofmann in Hofmann & Aitken 1979
type species: *Tawuia dalensis* Hofmann Hofmann & Aitken 1979

Tectitheca Burmann 1968
type species: *Tectitheca valida* Burmann 1968

Tectitheca cf. *filigera* Burmann 1968

?Tectitheca multispinula Yin L. in Chen J. et al. 1985 emend. Yin L. 1986

Teophipolia Kiryanov in Volkova et al. 1979
type species: *Teophipolia lacerata* Kiryanov in Volkova et al. 1979

Teophipolia lacerata Kiryanov in Volkova et al. 1979

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Thymadora Clendening & Wood 1981
type species: *Thymadora kerka* Clendening & Wood 1981

Thymadora kerka Clendening & Wood 1981

Timofeevia Vanguestaine 1978
type species: *Timofeevia lancariae* (Cramer & Díez 1972) Vanguestaine 1978

Timofeevia estonica Volkova 1990
Timofeevia ianischewskyi (Timofeev 1959b ex Vavrdová 1976) Volkova 1990
Timofeevia lancariae (Cramer & Díez 1972) Vanguestaine 1978
Timofeevia manata Albani et al. 1991
Timofeevia microretis Martin in Martin & Dean 1981
Timofeevia parva Hagenfeldt 1989b
Timofeevia pentagonalis (Vanguestaine 1974) Vanguestaine 1978
Timofeevia phosphoritica Vanguestaine 1978
Timofeevia raquelinae (Cramer & Díez 1972) Cramer & Díez 1979
Timofeevia tacheddirtensis Vanguestaine & Van Looy 1983
Timofeevia n. sp. A Palacios 2010
Timofeevia n. sp. B Palacios 2010
Timofeevia sp. 1 Paalits 2005
Timofeevia sp. 1 Volkova 1990
Timofeevia sp. 1 Volkova 1993b
Timofeevia sp. 1 Volkova 1995
Timofeevia sp. A Raevskaya & Golubkova 2006
Timofeevia sp. A Vanguestaine 1986

Trachydiacrodium Timofeev 1959b emend. Deflandre & Deflandre-Rigaud 1962
type species: *Trachydiacrodium productum* Timofeev 1959b

Trachydiacrodium coarctatum Timofeev 1959b

Trachyoligotriletes Timofeev 1958 ex Timofeev 1960
[**variant:** *Trachyoligotriletum*]
type species: *Trachyoligotriletes nevelensis* Timofeev 1958

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Trachyoligotriletes incrassatus (Naumova 1949) Timofeev 1960

Trachyoligotriletes laminaritus Timofeev 1958 ex Timofeev 1960

Trachyoligotriletes obsuletes (Naumova 1949) Timofeev 1960

Trachyoligotriletes planus Timofeev 1958

Trachysphaeridium Timofeev 1959b ex Timofeev 1966
[**junior synonym:** *Menneria* Lopukhin 1971, acc. to Vidal 1974]
type species: *Trachysphaeridium attenuatum* Timofeev 1959b

“*Trachysphaeridium cultum*” (Andreeva 1966) Xing in Xing & Liu 1973
→ *Leiosphaeridia culta* (Andreeva 1966) Paškevičienė 1980 [acc. to Fensome et al. 1990]

Trachysphaeridium hyalinum Xing & Liu 1973

Trachysphaeridium laminaritum Timofeev 1966

Trachysphaeridium leve (Lopukhin 1971) Vidal 1974

Trachysphaeridium minor Liu & Xing in Xing & Liu 1973

Trachysphaeridium rude Xing & Liu 1978

Trachysphaeridium rugosum Xing in Xing & Liu 1973

Trachysphaeridium simplex Xing 1962

“*Trachysphaeridium stipticum*” Sin et Liu
[cited without complete reference in Ding et al. 1992, presumably referring to Xing & Liu 1973. In that publication, authorship is given as “Sin (in litt.)”, apparently referring to an unpublished document. Since no type specimen was designated by Xing & Liu 1973, the species was not validly published]

Trachysphaeridium timofeevii Vidal 1976

Trachytriletes Naumova 1939
type species: *Trachytriletes kryshtofovichii* Naumova 1949

Trachytriletes kryshtofovichii Naumova 1949

Trachytriletes timofeevii Fensome et al. 1990

Trematosphaeridium Timofeev 1959b
type species: *Trematosphaeridium decoratum* Timofeev 1959b

“*Trematosphaeridium holtedahlii*” Timofeev 1966
→ *Orygmatosphaeridium holtedahlii* (Timofeev 1966) Fensome et al. 1990

Trematosphaeridium minutum Xing & Liu 1978

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Trematosphaeridium simplex Wang et Chen
[cited without complete reference in Wang & Chen Q. 1987; possible homonym of "*Trematosphaeridium simplex*" Pykhova 1973, which was not validly published acc. to Fensome et al. 1990]

Trichosphaeridium Timofeev 1966
type species: *Trichosphaeridium annolovaense* Timofeev 1966

Trichosphaeridium annolovaense Timofeev 1966

Trichosphaeridium hirtum Timofeev 1959b ex Fensome et al. 1990
→ *Filisphaeridium hirtum* (Timofeev 1959b ex Umnova 1975) Sarjeant & Stancliffe 1994

Trunculumarium Loeblich & Tappan 1976
type species: *Trunculumarium revinium* (Vanguestaine 1973b) Loeblich & Tappan 1976

Trunculumarium revinium (Vanguestaine 1973b) Loeblich & Tappan 1976

Tubulosphaera Palacios in Palacios & Moczydłowska 1998
type species: *Tubulosphaera perfecta* Palacios in Palacios & Moczydłowska 1998

Tubulosphaera n. sp. A Palacios 2010

Turrisphaeridium (Timofeev 1959b) Jachowicz-Zdanowska 2013
type species: *Turrisphaeridium semireticulatum* (Timofeev 1959b) Jachowicz-Zdanowska 2013

Turrisphaeridium semireticulatum (Timofeev 1959b) Jachowicz-Zdanowska 2013

Turrisphaeridium turgidum Jachowicz-Zdanowska 2013

"Uniporata" Naumova in Pykhova 1969
[not validly published, acc. to Fensome et al. 1990]
type species: "*Uniporata typica*" Naumova in Pykhova 1969 [nomen nudum, acc. to Fensome et al. 1990]

"*Uniporata nidia*" Pykhova 1966

[not validly published, acc. to Fensome et al. 1990]

“*Uniporata torosa*” Pykhova 1966
[not validly published, acc. to Fensome et al. 1990]

Valeria Jankauskas 1982
type species: *Valeria lophostriata* (Jankauskas 1979b) Jankauskas 1982

Valeria granulata (Vidal in Vidal & Siedlecka 1983) Fensome et al. 1990

Valeria sinica (Timofeev 1966) Fensome et al. 1990

Veryhachium Deunff 1954c emend. Downie & Sarjeant 1963 emend. Turner 1984 emend. Sarjeant & Stancliffe 1994
type species: *Veryhachium trisulcum* Deunff 1951 ex Deunff 1959

“*Veryhachium dumontii*” Vanguestaine 1973b
→ *Ninadiacrodium dumontii* (Vanguestaine 1973b) Raevskaya & Servais 2009

Veryhachium incus Paalits 1992a

Veryhachium cf. *minutum* Downie 1958

Veryhachium mutabile Di Milia et al. 1989

“*Veryhachium primaevum*” Deunff 1967
[nomen nudum, acc. to Fensome et al. 1990]

Veryhachium cf. *rhomboideum* Downie 1959

“*Veryhachium setuensis*” Paalits 1992a
→ *?Dasydiacrodium setuensis* Paalits 1992a

“*Veryhachium* cf. *trapezionarion*” Loeblich 1970
→ *Veryhachium* cf. *rhomboideum* Downie 1959 [acc. to Turner 1984]

Veryhachium trisentium Zang in Gravestock et al. 2001

Veryhachium sp. A Martin in Martin & Dean 1981

Veryhachium sp. A Parsons & Anderson 2000

Virgatasporites Combaz 1967
type species: *Virgatasporites rudii* Combaz 1967

Virgatasporites normale (Fombella 1978) Fensome et al. 1990

Virgatasporites rudii Combaz 1967

Vogtlandia Burmann 1970 emend. Sarjeant & Vavrdová 1997
type species: *Vogtlandia ramificata* Burmann 1970

Vogtlandia carvinacornua (Welsch 1986) Sarjeant & Vavrdová 1997

Vogtlandia notabilis Volkova 1990

Vogtlandia petropolitana (German 1974) Volkova 1990

Vogtlandia simplex Moczydłowska 1998

Volkovia Downie 1982
type species: *Volkovia dentifera* (Volkova 1969) Downie 1982

Volkovia conifera (Jankauskas 1975) Downie 1982

Volkovia dentifera (Volkova 1969) Downie 1982

Volkovia flagellata (Jankauskas 1975) Downie 1982

Vulcanisphaera Deunff 1961a emend. Rasul 1976
type species: *Vulcanisphaera africana* Deunff 1961a

Vulcanisphaera africana Deunff 1961a

Vulcanisphaera britannica Rasul 1976

Vulcanisphaera capillata Jardiné et al. 1974

“*Vulcanisphaera cirrita*” Rasul 1976
→ *Vulcanisphaera africana* Deunff 1961a [acc. to Elaouad-Debbaj 1988]

Vulcanisphaera fermosa Fombella 1977

Vulcanisphaera frequens Górka 1967

Vulcanisphaera lanugo Martin in Martin & Dean 1988

Vulcanisphaera nebulosa Deunff 1961a

Vulcanisphaera spinulifera (Volkova 1990) Parsons & Anderson 2000

“*Vulcanisphaera tuberata*” (Downie 1958) Eisenack et al. 1973
→ *Goniosphaeridium tuberatum* (Downie 1958) Welsch 1986

Vulcanisphaera turbata Martin in Martin & Dean 1981

Vulcanisphaera sp. 1 Volkova 1980

?Vulcanisphaera sp. 1 Paalits 2005

Yurtusia Dong et al. 2009
type species: *Yurtusia uniformis* Dong et al. 2009

Yurtusia uniformis Dong et al. 2009

“Zonosphaeridium” Timofeev 1959b
→ *Tasmanites* Newton 1875 [acc. to Timofeev 1966]
no type species

“Zonosphaeridium ovillensis” Cramer & Díez 1972
→ *Retisphaeridium ovillense* (Cramer & Díez 1972) Vanguestaine 2002

Acritarch gen. et sp. nov. Martin & Dean 1984
→ *Comasphaeridium francinae* Jachowicz-Zdanowska 2013

Acritarch gen. et sp. nov. Martin & Dean 1988

Acritarch gen. et sp. nov. Young et al. 1994

Acritarch sp. 1 Hagenfeldt 1989b

Acritarch sp. Wood & Clendening 1982

Gen. et sp. ind. A Di Milia 1991

Gen. et sp. ind. B Di Milia 1991

Gen. et sp. indet. 1 Paalits 2005

Gen. et sp. indet. 2 Paalits 2005

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Gen. et sp. indet. C Jago et al. 2006

Gen. et sp. indet. Żylińska & Szczepanik 2009

Genus et species ind. A Di Milia et al. 1989

Genus et species ind. B Di Milia et al. 1989

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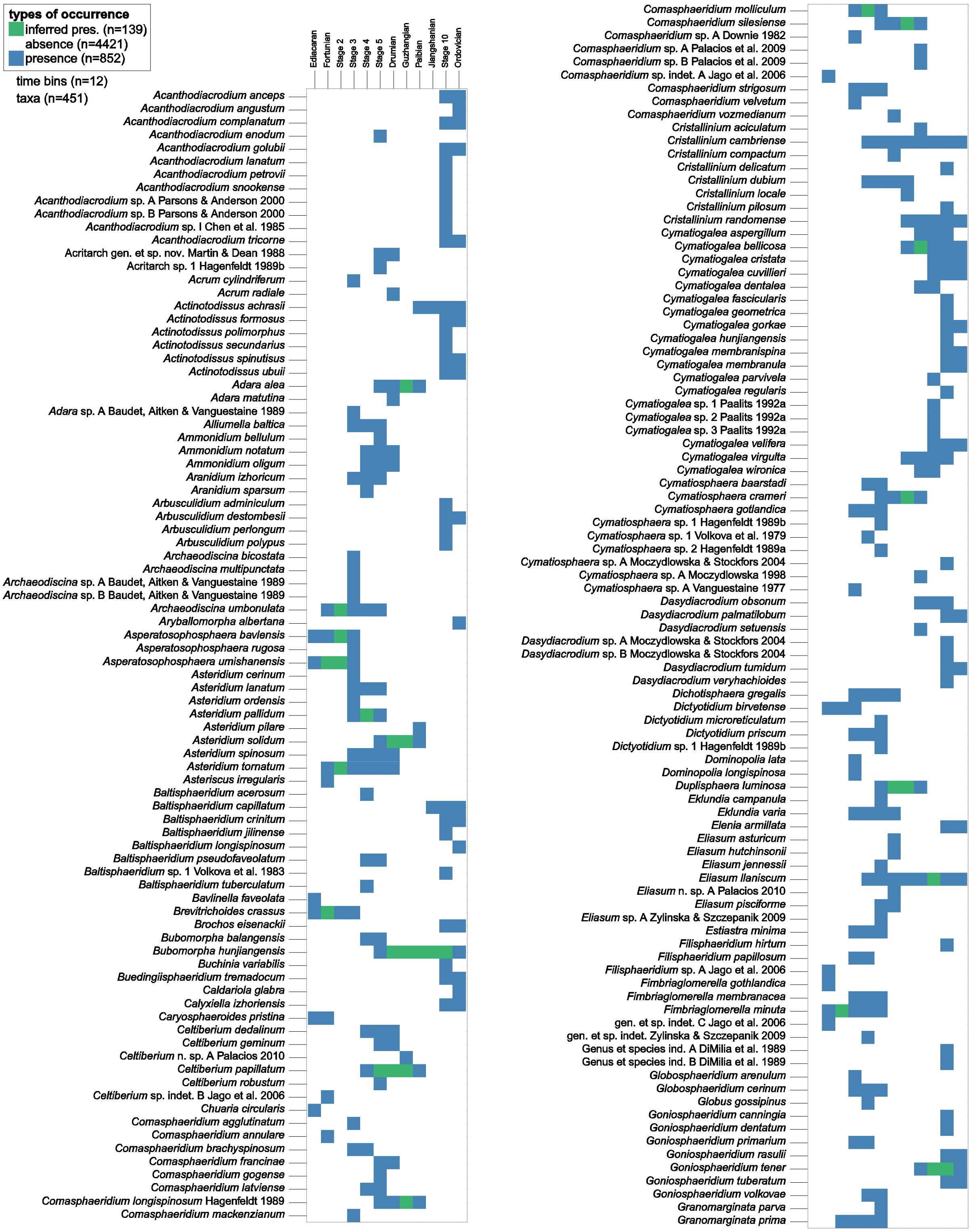
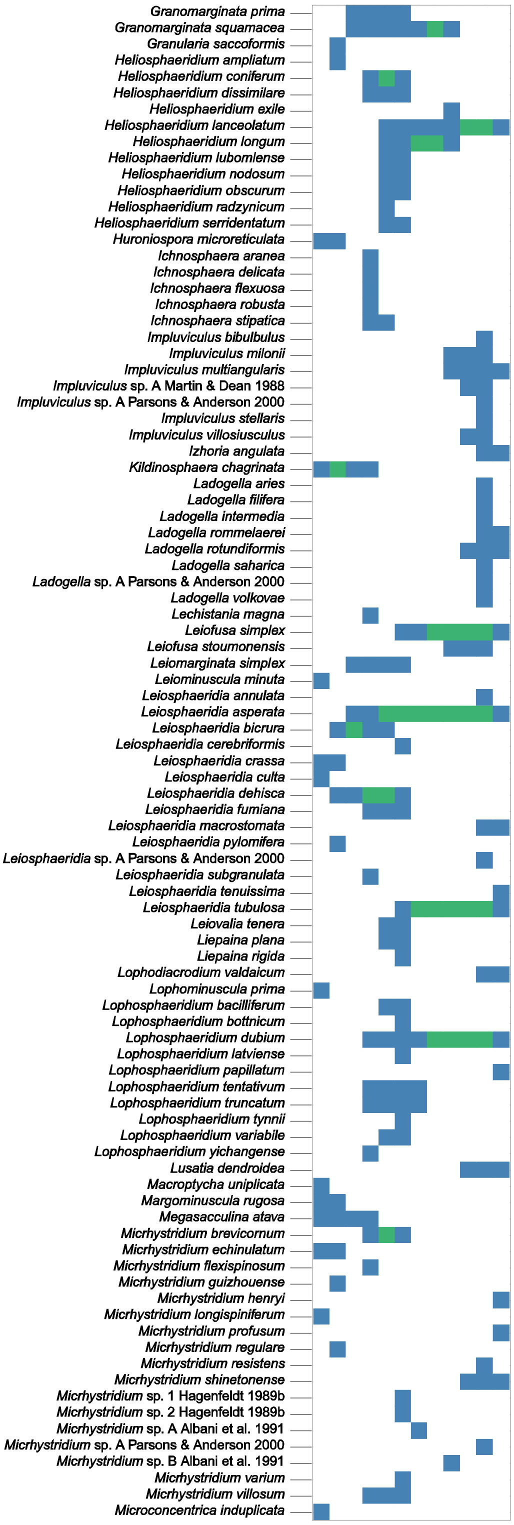
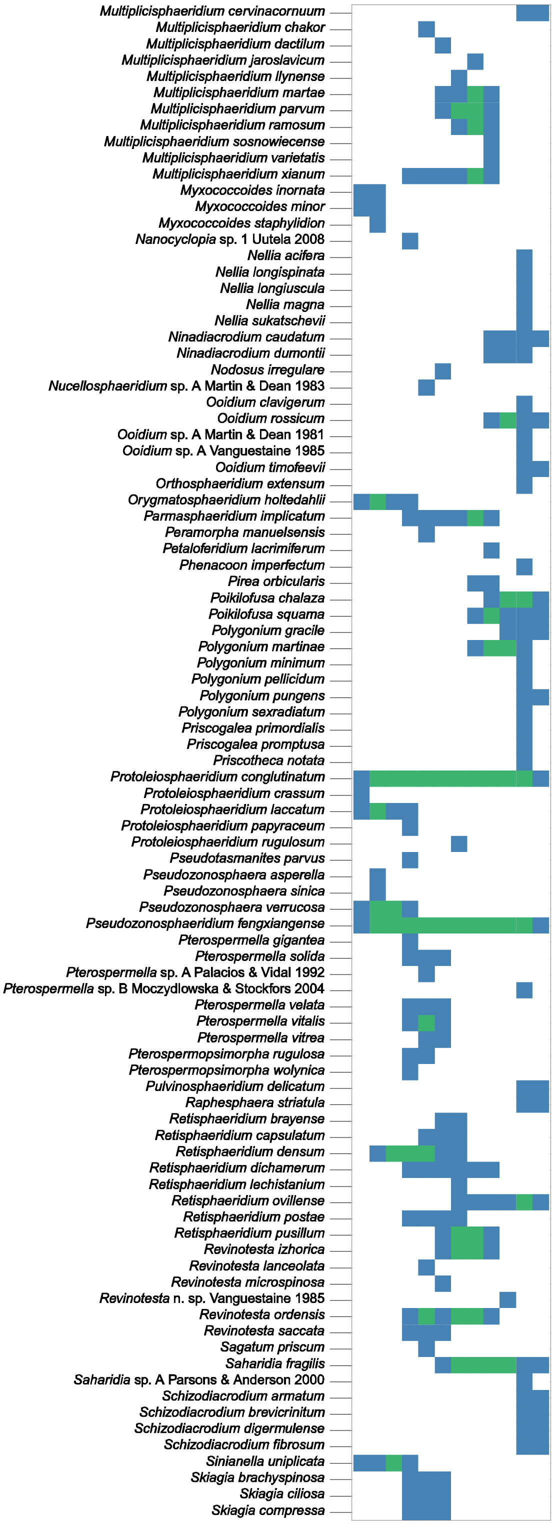
Supplementary material S4

Global species range charts based on stages, blue = presence reported; green = presence inferred; white = absence.







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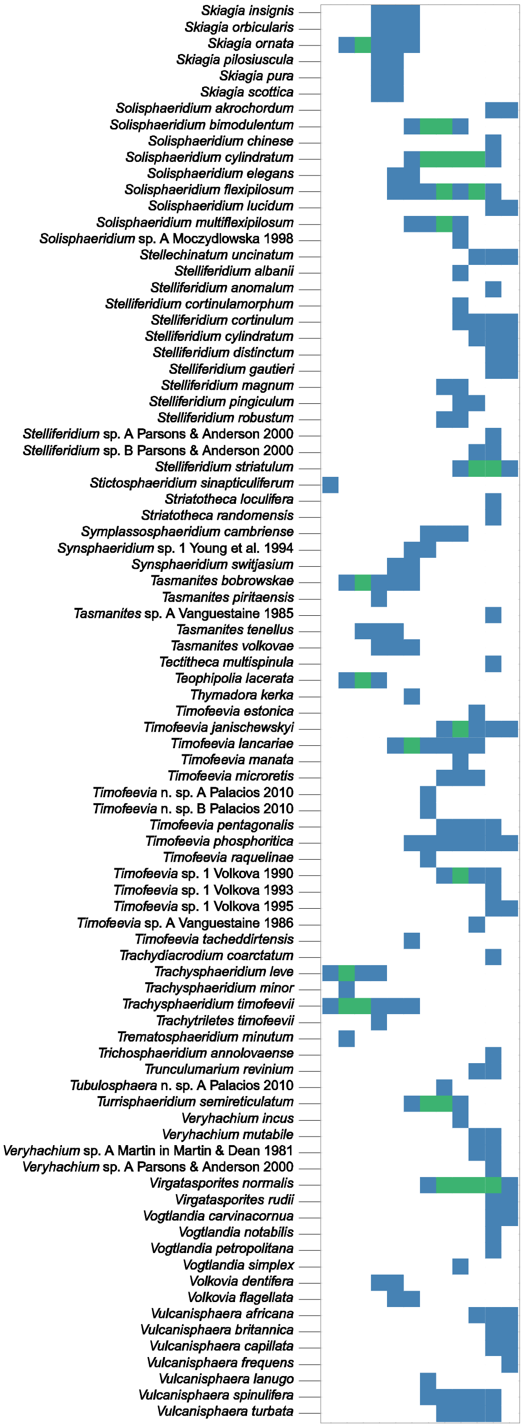
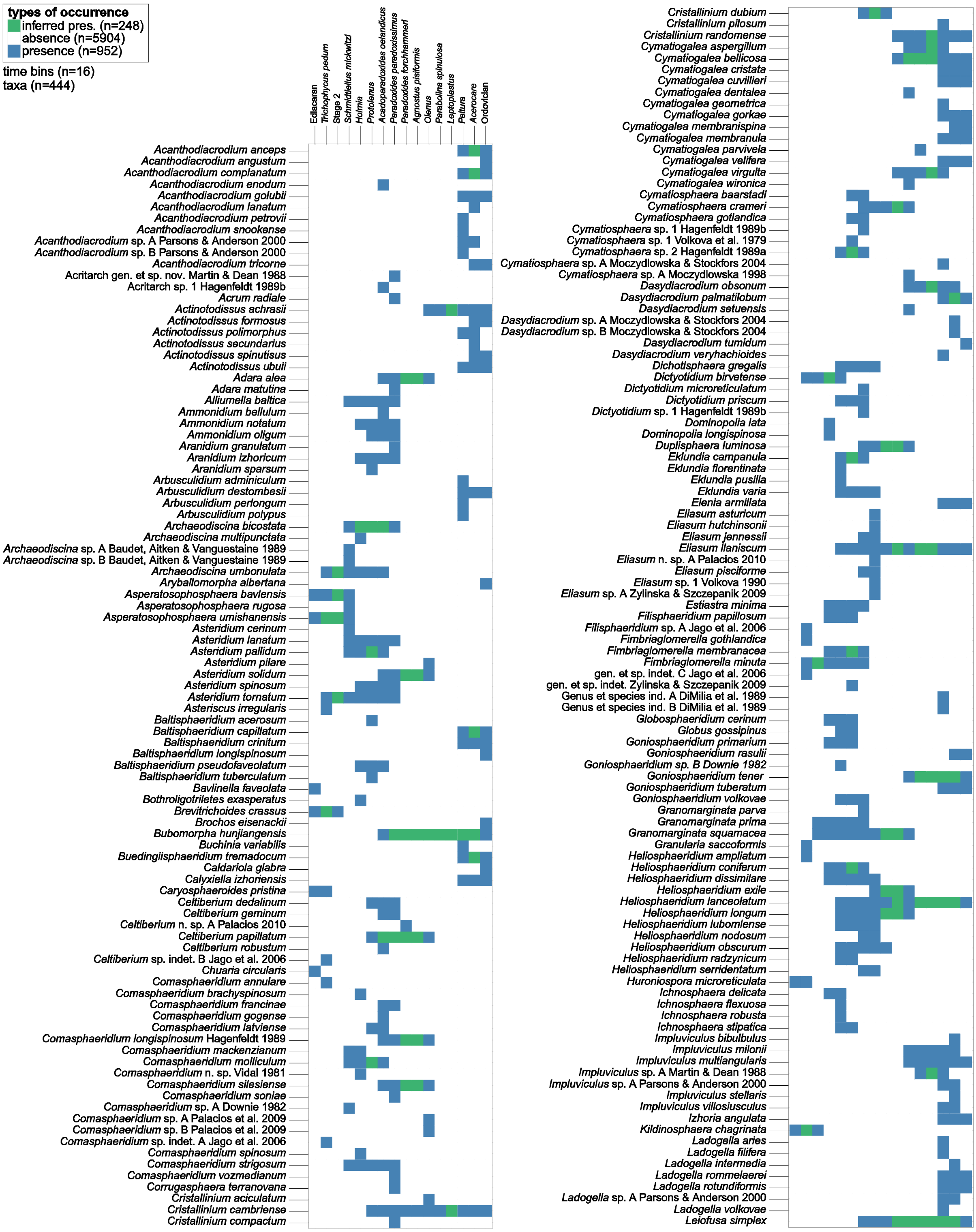

Skiagia insignis
Skiagia orbicularis
Skiagia ornata
Skiagia pilosiuscula
Skiagia pura
Skiagia scottica
Solisphaeridium akrochordum
Solisphaeridium bimodulentum
Solisphaeridium chinese
Solisphaeridium cylindratum
Solisphaeridium elegans
Solisphaeridium flexipilosum
Solisphaeridium lucidum
Solisphaeridium multiflexipilosum
Solisphaeridium sp. A Moczydlowska 1998
Stellechinatum uncinatum
Stelliferidium albanii
Stelliferidium anomalum
Stelliferidium cortinulamorphum
Stelliferidium cortinulum
Stelliferidium cylindratum
Stelliferidium distinctum
Stelliferidium gautieri
Stelliferidium magnum
Stelliferidium pingiculum
Stelliferidium robustum
Stelliferidium sp. A Parsons & Anderson 2000
Stelliferidium sp. B Parsons & Anderson 2000
Stelliferidium striatulum
Stictosphaeridium sinapticuliferum
Striatotheca loculifera
Striatotheca randomensis
Symplassosphaeridium cambriense
Synsphaeridium sp. 1 Young et al. 1994
Synsphaeridium switjasium
Tasmanites bobrowskae
Tasmanites piritaensis
Tasmanites sp. A Vanguestaine 1985
Tasmanites tenellus
Tasmanites volkovae
Tectitheca multispinula
Teophipolia lacerata
Thymadora kerka
Timofeevia estonica
Timofeevia janischewskyi
Timofeevia lancariae
Timofeevia manata
Timofeevia microretis
Timofeevia n. sp. A Palacios 2010
Timofeevia n. sp. B Palacios 2010
Timofeevia pentagonalis
Timofeevia phosphoritica
Timofeevia raquelinae
Timofeevia sp. 1 Volkova 1990
Timofeevia sp. 1 Volkova 1993
Timofeevia sp. 1 Volkova 1995
Timofeevia sp. A Vanguestaine 1986
Timofeevia tacheddirtensis
Trachydiacrodium coarctatum
Trachysphaeridium leve
Trachysphaeridium minor
Trachysphaeridium timofeevii
Trachytriletes timofeevii
Trematosphaeridium minutum
Trichosphaeridium annolovaense
Trunculumarium revinium
Tubulosphaera n. sp. A Palacios 2010
Turrisphaeridium semireticulatum
Veryhachium incus
Veryhachium mutabile
Veryhachium sp. A Martin in Martin & Dean 1981
Veryhachium sp. A Parsons & Anderson 2000
Virgatasporites normalis
Virgatasporites rudii
Vogtlandia carvinacornua
Vogtlandia notabilis
Vogtlandia petropolitana
Vogtlandia simplex
Volkovia dentifera
Volkovia flagellata
Vulcanisphaera africana
Vulcanisphaera britannica
Vulcanisphaera capillata
Vulcanisphaera frequens
Vulcanisphaera lanugo
Vulcanisphaera spinulifera
Vulcanisphaera turbata

Supplementary material S5

Global species range charts based on biozones, blue = presence reported; green = presence inferred; white = absence.



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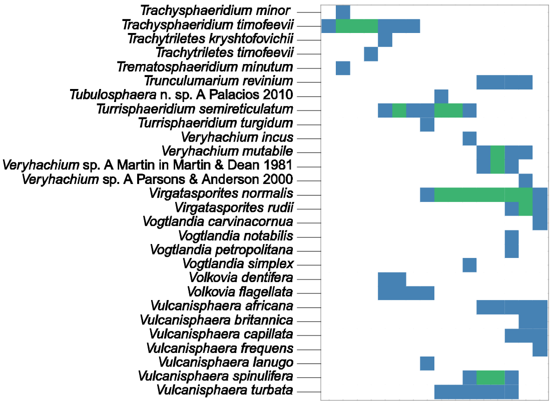
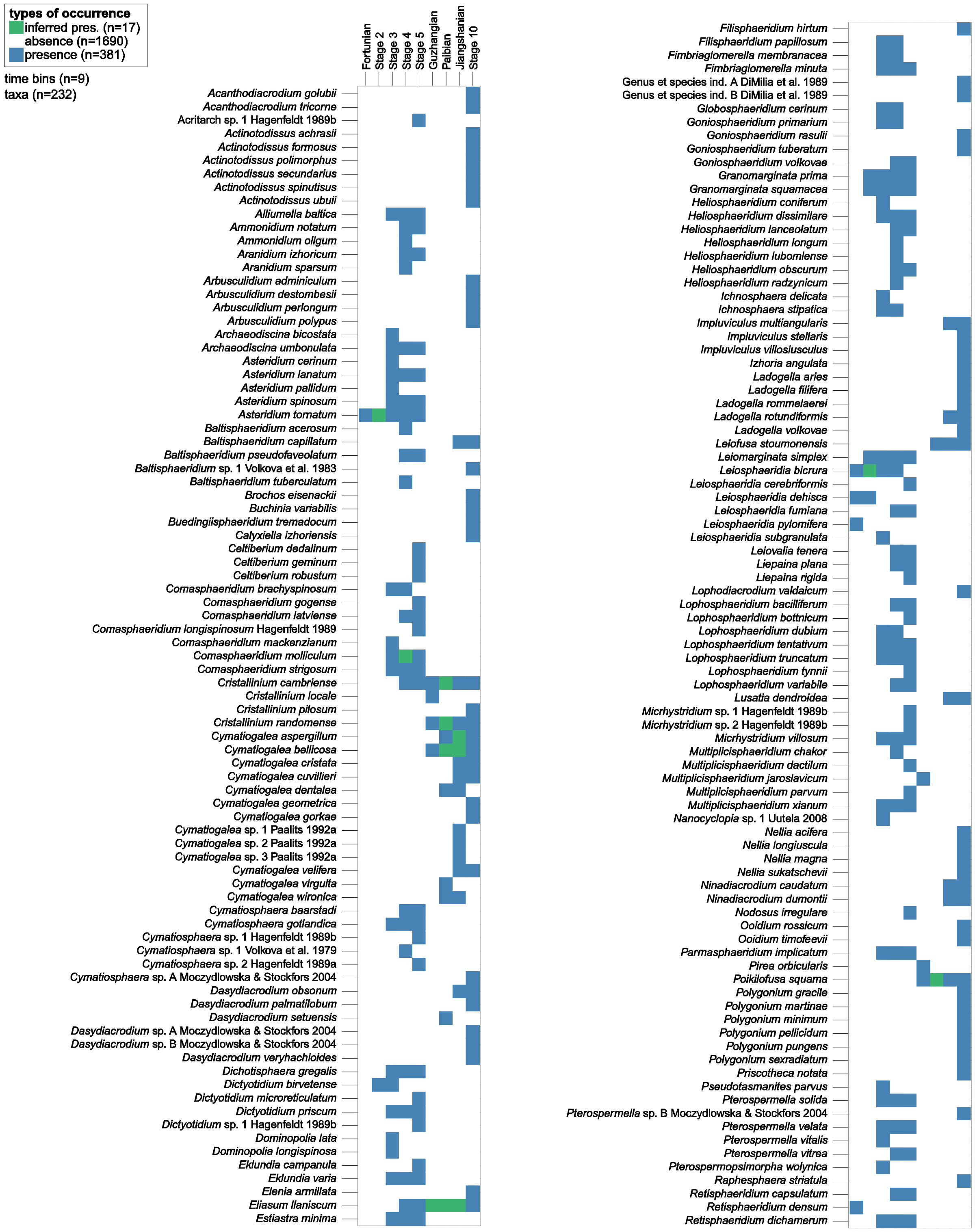
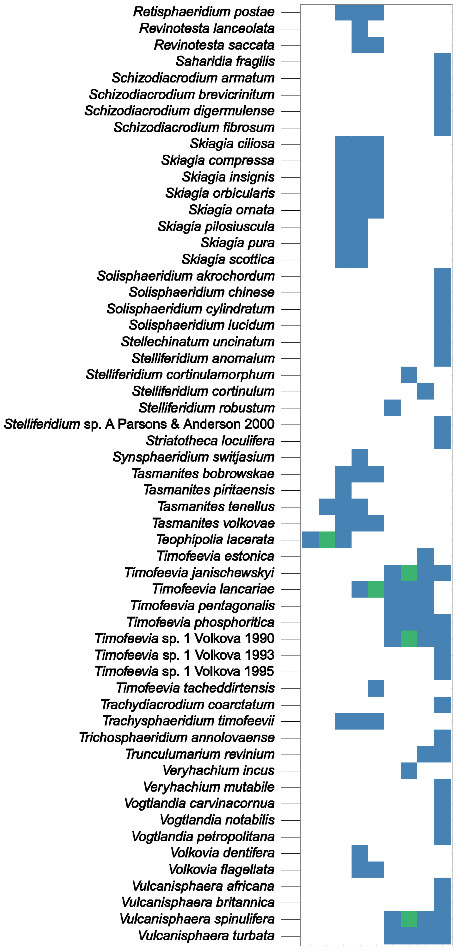

Trachysphaeridium minor
Trachysphaeridium timofeevii
Trachytriletes kryshtofovichii
Trachytriletes timofeevii
Trematosphaeridium minutum
Trunculumarium revinium
Tubulosphaera n. sp. A Palacios 2010
Turrisphaeridium semireticulatum
Turrisphaeridium turgidum
Veryhachium incus
Veryhachium mutabile
Veryhachium sp. A Martin in Martin & Dean 1981
Veryhachium sp. A Parsons & Anderson 2000
Virgatasporites normalis
Virgatasporites rudii
Vogtlandia carvinacornua
Vogtlandia notabilis
Vogtlandia petropolitana
Vogtlandia simplex
Volkovia dentifera
Volkovia flagellata
Vulcanisphaera africana
Vulcanisphaera britannica
Vulcanisphaera capillata
Vulcanisphaera frequens
Vulcanisphaera lanugo
Vulcanisphaera spinulifera
Vulcanisphaera turbata

Supplementary material S6

Baltica species range charts based on stages, blue = presence reported; green = presence inferred; white = absence.

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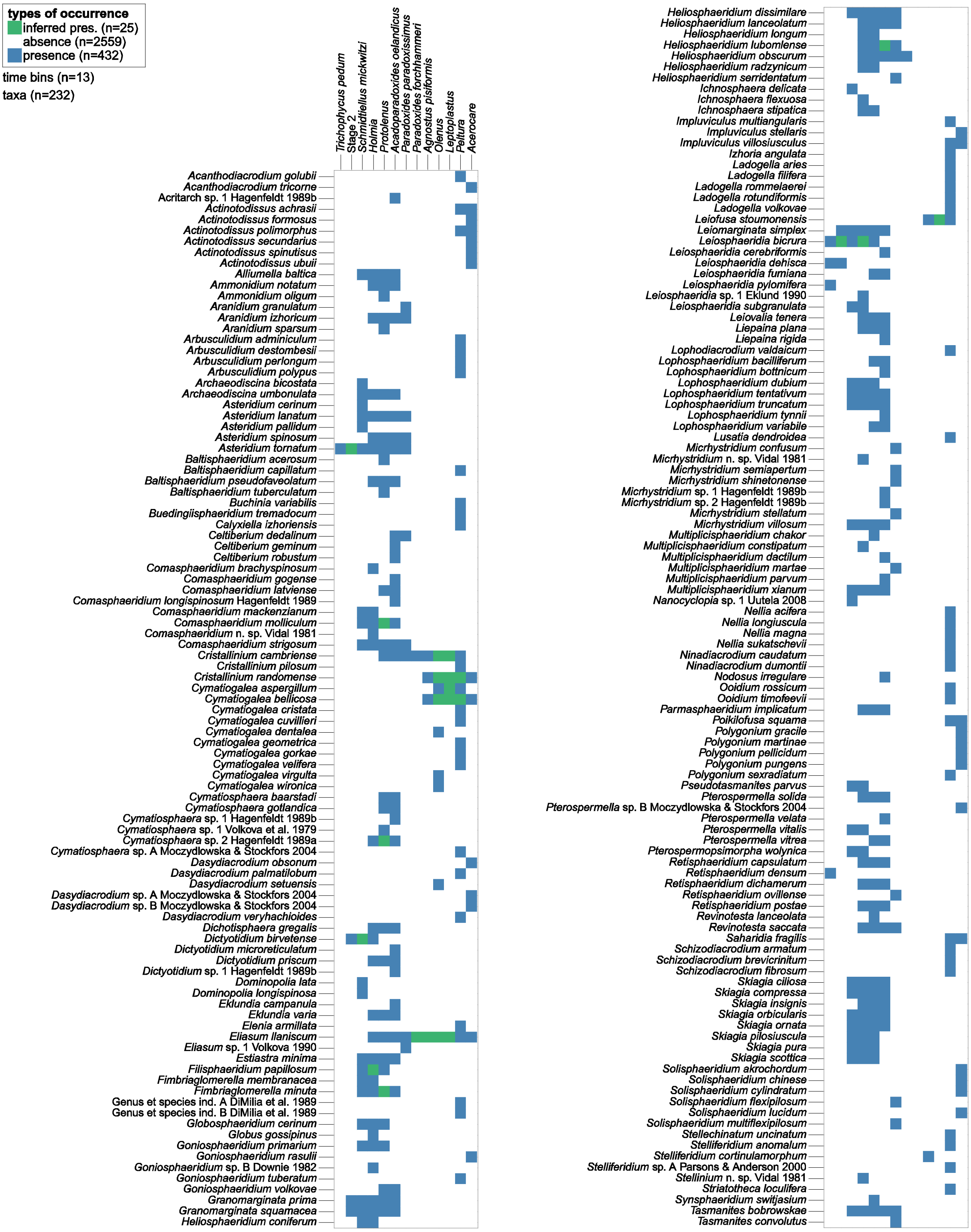
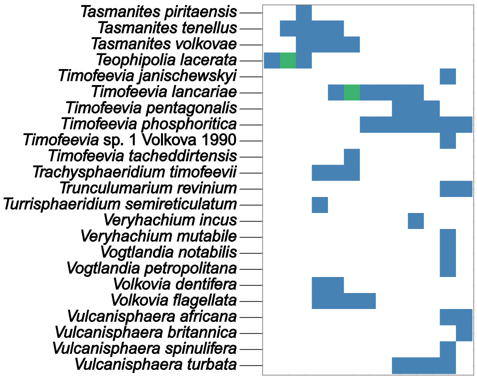
Revinotesta lanceolata
Revinotesta saccata
Saharidia fragilis
Schizodiacrodium armatum
Schizodiacrodium brevicrinitum
Schizodiacrodium digermulense
Schizodiacrodium fibrosum
Skiagia ciliosa
Skiagia compressa
Skiagia insignis
Skiagia orbicularis
Skiagia ornata
Skiagia pilosiuscula
Skiagia pura
Skiagia scottica
Solisphaeridium akrochordum
Solisphaeridium chinese
Solisphaeridium cylindratum
Solisphaeridium lucidum
Stellechinatum uncinatum
Stelliferidium anomalum
Stelliferidium cortinulamorphum
Stelliferidium cortinulum
Stelliferidium robustum
Stelliferidium sp. A Parsons & Anderson 2000
Striatotheca loculifera
Synsphaeridium switjasium
Tasmanites bobrowskae
Tasmanites piritaensis
Tasmanites tenellus
Tasmanites volkovae
Teophipolia lacerata
Timofeevia estonica
Timofeevia janischewskyi
Timofeevia lancariae
Timofeevia pentagonalis
Timofeevia phosphoritica
Timofeevia sp. 1 Volkova 1990
Timofeevia sp. 1 Volkova 1993
Timofeevia sp. 1 Volkova 1995
Timofeevia tacheddirtensis
Trachydiacrodium coarctatum
Trachysphaeridium timofeevii
Trichosphaeridium annolovaense
Trunculumarium revinium
Veryhachium incus
Veryhachium mutabile
Vogtlandia carvinacornua
Vogtlandia notabilis
Vogtlandia petropolitana
Volkovia dentifera
Volkovia flagellata
Vulcanisphaera africana
Vulcanisphaera britannica
Vulcanisphaera spinulifera
Vulcanisphaera turbata

Supplementary material S7

Baltica species range charts based on biozones, blue = presence reported; green = presence inferred; white = absence.





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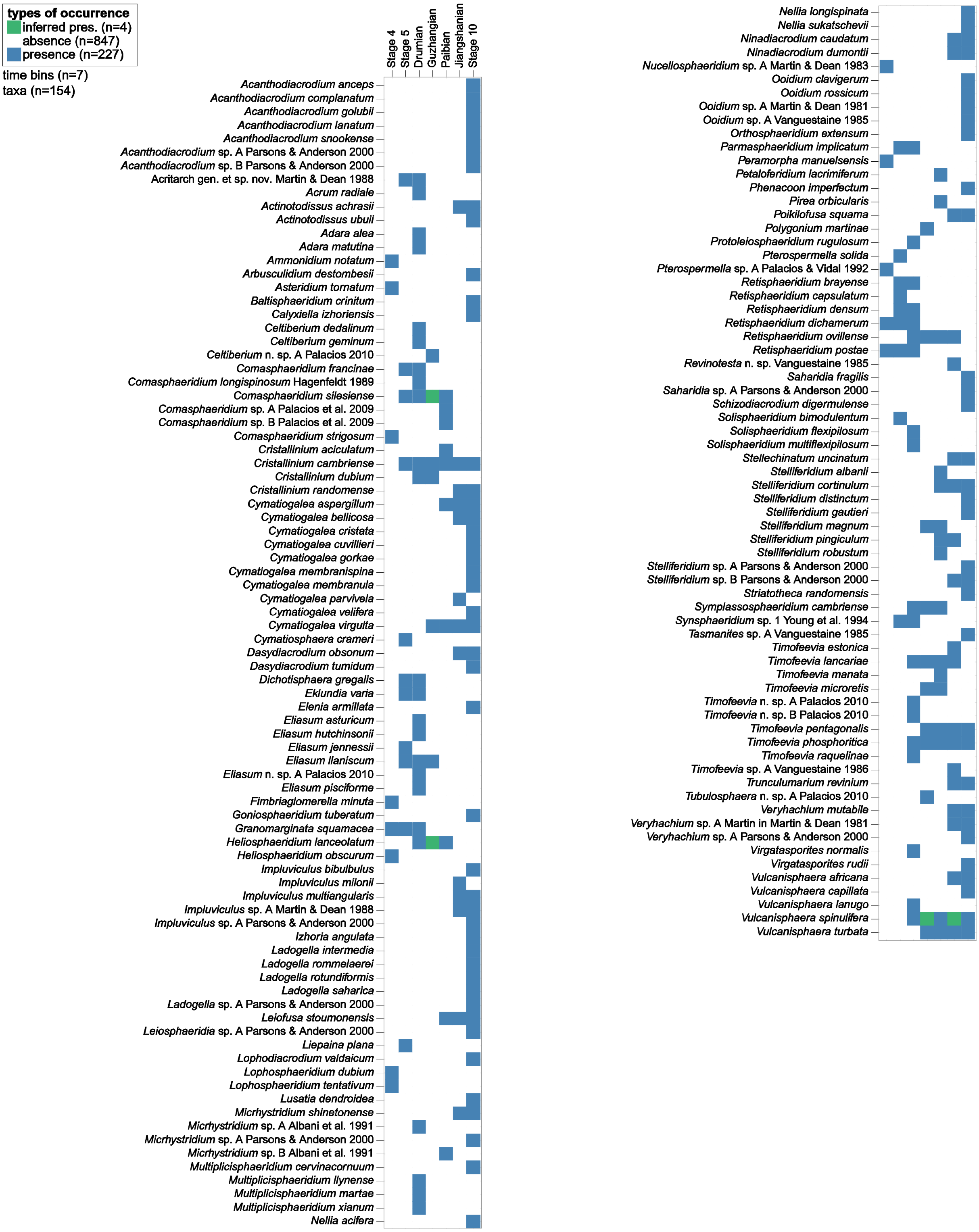
Supplementary material S8

Gondwana species range charts based on stages, blue = presence reported; green = presence inferred; white = absence.



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Supplementary material S9

Gondwana species range charts based on biozones, blue = presence reported; green = presence inferred; white = absence.

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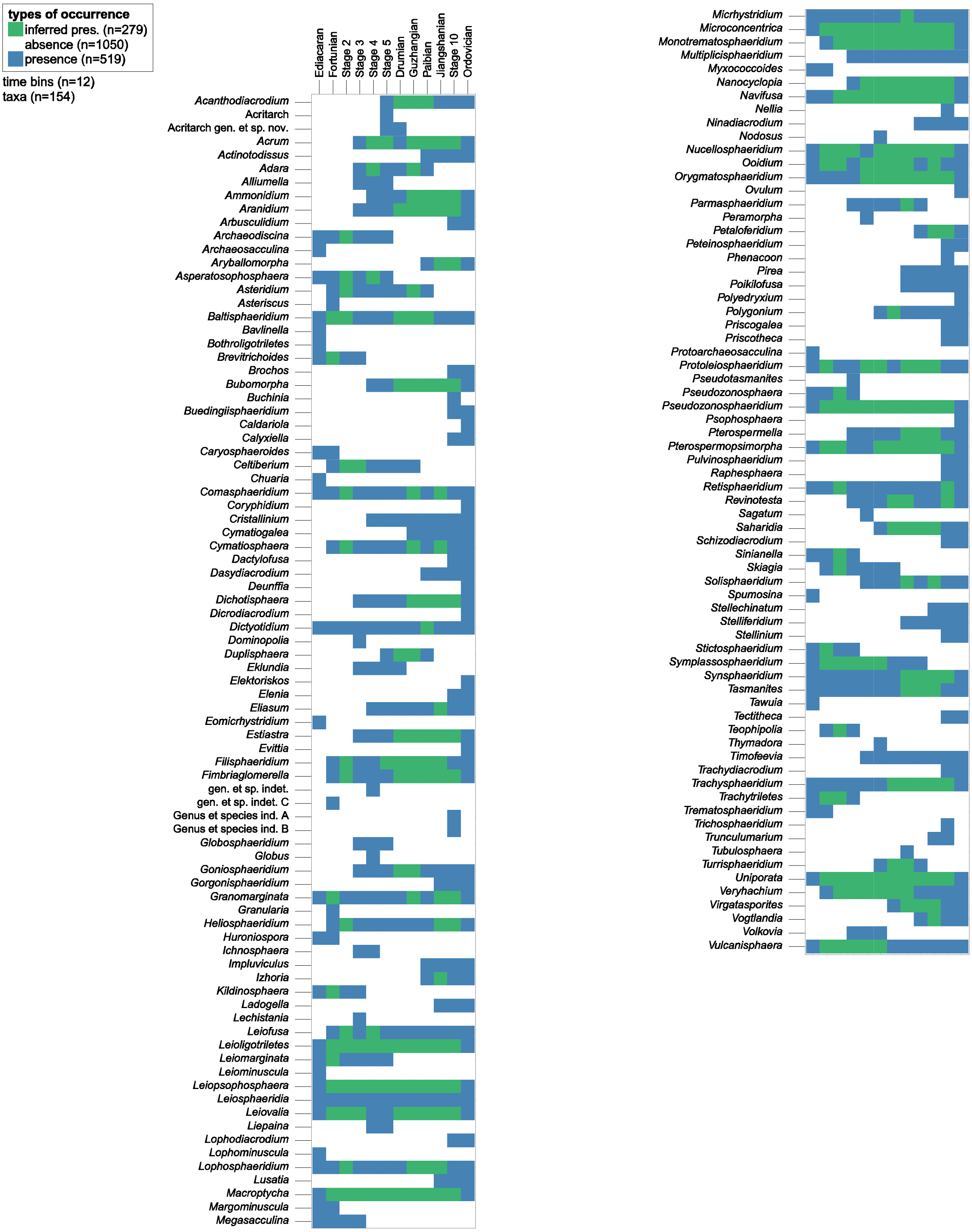
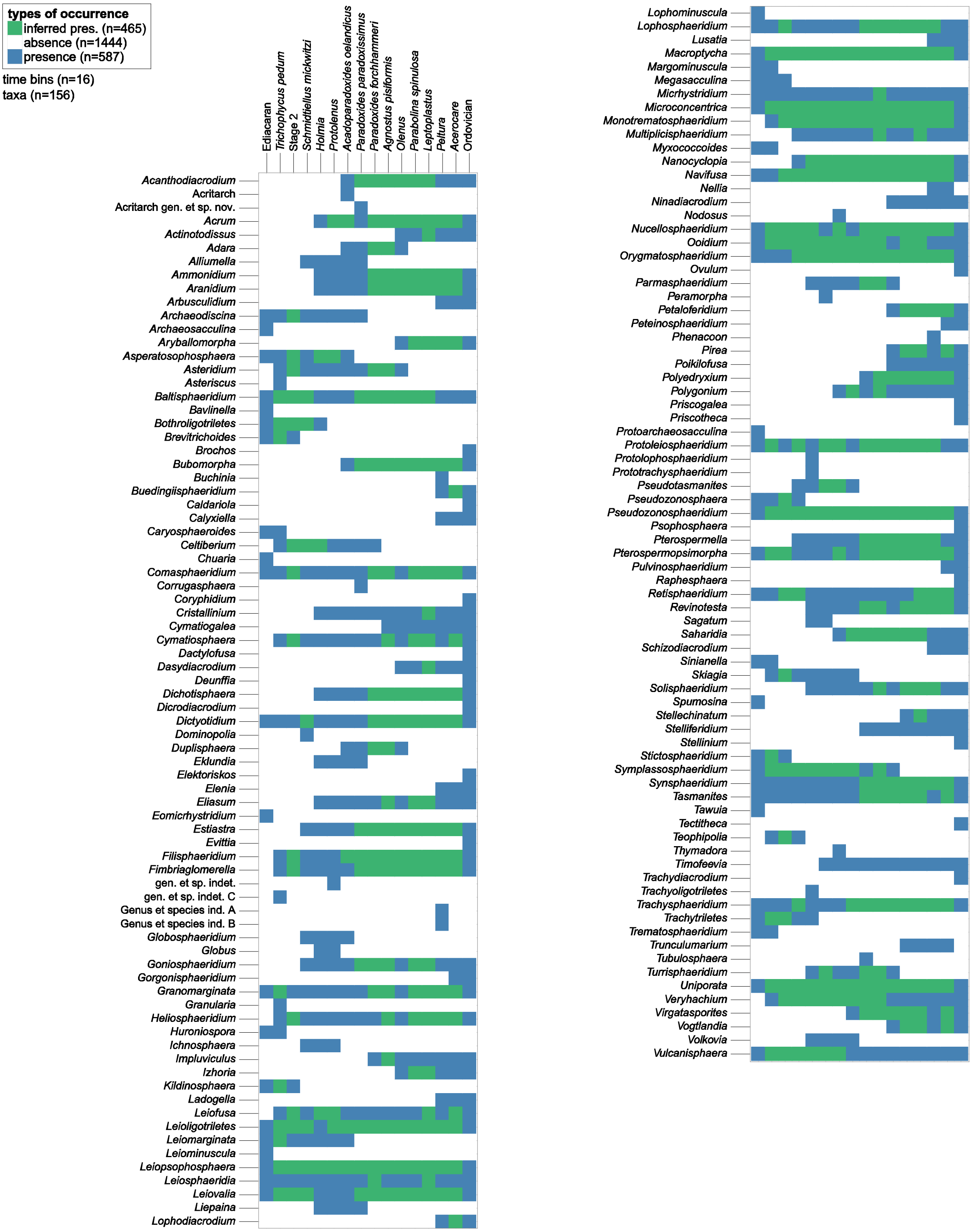
Supplementary material S10

Global genus range chart based on stages; blue = presence reported; green = presence inferred; white = absence.



Supplementary material S11

Global genus range chart based on biozones; blue = presence reported; green = presence inferred; white = absence.



Supplementary material S12

Values of diversity indices based on stages.

Diversity by stages												
Geography	**Taxonomy**	**Diversity index**	Fortunian	Stage 2	Stage 3	Stage 4	Stage 5	Drumian	Guzhangian	Paibian	Jiangshanian	Stage 10
global	species	sampled-in-bin	37	13	102	93	126	57	27	71	50	158
		total	47	28	106	104	131	74	58	86	68	171
		total without singletons	30	28	74	91	105	59	54	69	61	98
		normalized	30	25.5	61	77.5	80	55	49	57	53.5	104
		singletons	17	0	32	13	26	15	4	17	7	73
		crossovers	13	23	16	51	29	36	40	28	39	37
		origination	10	5	46	29	25	5	13	16	17	42
		extinction	7	0	12	11	51	18	1	25	5	19
		turnover	17	5	58	40	76	23	14	41	22	61
		origination rate	0.83	625	6.57	5.8	5.56	1.25	3.71	5.33	3.78	10.2
		extinction rate	0.58	0	1.71	2.2	11.3	4.5	0.29	8.33	1.11	4.63
		turnover rate	1.42	625	8.29	8	16.9	5.75	4	13.7	4.89	14.9
	genera	sampled-in-bin	35	14	52	47	51	32	18	37	28	62
		total	55	47	66	66	70	61	63	69	68	90
		total without singletons	52	47	63	62	67	61	62	69	68	84
		normalized	45.5	47	52.5	60	62	59	60	62	65.5	78.5
		singletons	3	0	3	4	3	0	1	0	0	6
		crossovers	36	47	39	54	54	57	57	55	63	67
		origination	11	0	16	7	6	1	4	8	5	16
		extinction	5	0	8	1	7	3	1	6	0	1
		turnover	16	0	24	8	13	4	5	14	5	17
		origination rate	0.92	0	2.29	1.4	1.33	0.25	1.14	2.67	1.11	3.9
		extinction rate	0.42	0	1.14	0.2	1.56	0.75	0.29	2	0	0.24
		turnover rate	1.33	0	3.43	1.6	2.89	1	1.43	4.67	1.11	4.15
	studies per stage		7	3	18	15	18	10	6	10	11	18
Baltica	species	sampled-in-bin	6	6	62	77	74		15	12	29	100
		total	6	9	62	78	75		16	20	32	100
		total without singletons	4	9	48	66	54		12	16	27	23
		normalized		6	34	56	39		9.5	16	22	
		singletons	2	0	14	12	21		4	4	5	77
		crossovers		3	6	34	3		3	12	12	
		origination		5	40	20	0		9	4	11	
		extinction		1	2	12	51		0	0	4	
		turnover		6	42	32	51		9	4	15	
		origination rate		0.63	5.71	4	0		2.57	1.33	2.44	
		extinction rate		0.13	0.29	2.4	11.3		0	0	0.89	
		turnover rate		0.75	6	6.4	11.3		2.57	1.33	3.33	
	genera	sampled-in-bin	4	5	34	39	38		10	8	19	53
		total	4	8	34	39	39		21	20	30	53
		total without singletons	4	8	31	39	36		20	20	30	30
		normalized		6	20.5	33	27		17.5	19.5	25	
		singletons	0	0	3	0	3		1	0	0	23
		crossovers		4	7	27	15		14	19	20	
		origination		4	23	9	0		5	1	10	
		extinction		0	1	3	21		1	0	0	
		turnover		4	24	12	21		6	1	10	
		origination rate		0.5	3.29	1.8	0		1.43	0.33	2.22	
		extinction rate		0	0.14	0.6	4.67		0.29	0	0	
		turnover rate		0.5	3.43	2.4	4.67		1.71	0.33	2.22	
	studies per stage		1	2	9	9	5		2	1	3	6

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Diversity by stages

Geography	Taxonomy	Diversity index	Fortunian	Stage 2	Stage 3	Stage 4	Stage 5	Drumian	Guzhangian	Paibian	Jiangshanian	Stage 10
Gondwana	species	sampled-in-bin				13	20	43	15	26	32	78
		total				13	20	43	18	26	33	78
		total without singletons				3	14	21	15	17	28	25
		normalized					11.5	23	13	17	21	
		singletons				10	6	22	3	9	5	53
		crossovers					3	3	8	8	9	
		origination					11	7	5	4	16	
		extinction					0	11	2	5	3	
		turnover					11	18	7	9	19	
		origination rate					2.44	1.75	1.43	1.33	3.56	
		extinction rate					0	2.75	0.57	1.67	0.67	
		turnover rate					2.44	4.5	2	3	4.22	
	genera	sampled-in-bin				16	18	25	12	14	20	35
		total				16	21	26	18	19	24	35
		total without singletons				10	20	23	17	17	22	21
		normalized					14.5	17.5	15	15.5	18.5	
		singletons				6	1	3	1	2	2	14
		crossovers					8	9	12	12	13	
		origination					10	5	3	2	8	
		extinction					2	9	2	3	1	
		turnover					12	14	5	5	9	
		origination rate					2.22	1.25	0.86	0.67	1.78	
		extinction rate					0.44	2.25	0.57	1	0.22	
		turnover rate					2.67	3.5	1.43	1.67	2	
	studies per stage					2	5	6	3	6	5	9

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Supplementary material S13

Values of diversity indices based on biozones.

Diversity by biozones

Geography	**Taxonomy**	**Diversity index**	*T. pedum*	Stage 2	*S. mickwitzi*	*Holmia*	*Protolenus*	*Ac. oelandicus*	*Pa. paradoxissimus*	*Pa. forchhammeri*	*Ag. pisiformis*	*Olenus*	*Pb. spinulosa*	*Leptoplastus*	*Peltura*	*Acerocare*
global	species	sampled-in-bin	37	13	56	106	85	121	88	25	10	71	32	11	103	76
		total	48	28	65	113	102	128	98	53	49	83	50	45	117	103
		total without singletons	31	28	54	86	92	104	73	49	49	64	48	45	87	90
		normalized	31	23	42	78	84	85	67	46	48	53	43	45	77	82
		singletons	17	0	11	27	10	24	25	4	0	19	2	0	30	13
		crossovers	13	18	19	43	65	41	36	39	46	23	35	45	36	60
		origination	10	5	31	36	13	26	6	7	3	15	10	0	42	12
		extinction	8	5	4	7	14	37	31	3	0	26	3	0	9	18
		turnover	18	10	35	43	27	63	37	10	3	41	13	0	51	30
		origination rate	0.8	0.6	8.9	6	5.2	12	1.4	1.8	1.8	5	4.5	0	20	6
		extinction rate	0.7	0.6	1.1	1.2	5.6	17	7.2	0.8	0	8.7	1.4	0	4.3	9
		turnover rate	1.5	1.3	10	7.2	11	29	8.6	2.6	1.8	14	5.9	0	24	15
	genera	sampled-in-bin	35	14	31	51	46	50	43	18	8	37	19	11	43	38
		total	56	47	53	68	66	70	67	62	61	70	66	66	79	78
		total without singletons	53	47	52	65	64	67	65	61	61	70	66	66	75	78
		normalized	46	45	47	58	63	64	62	60	61	63	65	66	73	76
		singletons	3	0	1	3	2	3	2	1	0	0	0	0	4	0
		crossovers	36	43	41	48	60	58	57	57	60	55	64	66	66	73
		origination	11	0	9	15	1	6	1	3	1	9	2	0	9	3
		extinction	6	4	2	2	3	3	7	1	0	6	0	0	0	2
		turnover	17	4	11	17	4	9	8	4	1	15	2	0	9	5
		origination rate	0.9	0	2.6	2.5	0.4	2.7	0.2	0.8	0.6	3	0.9	0	4.3	1.5
		extinction rate	0.5	0.5	0.6	0.3	1.2	1.4	1.6	0.3	0	2	0	0	0	1
		turnover rate	1.4	0.5	3.1	2.8	1.6	4.1	1.9	1.1	0.6	5	0.9	0	4.3	2.5
	studies per biozone		7	3	12	19	13	14	16	7	4	10	6	2	12	5
Baltica	species	sampled-in-bin	6	6	47	74	73	74	29	4	7	12		3	66	31
		total	6	9	48	76	76	76	29	5	8	16		9	68	31
		total without singletons	4	9	40	66	68	56	17	5	8	10		9	15	11
		normalized		6	28	54	61	46	17	4.5	6	12		8.5	36	
		singletons	2	0	8	10	8	20	12	0	0	6		0	53	20
		crossovers		3	7	31	45	15	4	4	4	7		8	4	
		origination		5	32	27	10	1	1	0	4	2		0	7	
		extinction		1	1	8	13	40	12	1	0	1		1	4	
		turnover		6	33	35	23	41	13	1	4	3		1	11	
		origination rate		0.6	9.1	4.5	4	0.5	0.2	0	2.4	0.7		0	3.3	
		extinction rate		0.1	0.3	1.3	5.2	18	2.8	0.3	0	0.3		0.4	1.9	
		turnover rate		0.8	9.4	5.8	9.2	19	3	0.3	2.4	1		0.4	5.2	
	genera	sampled-in-bin	4	5	27	40	37	38	18	3	5	8		3	37	21
		total	4	8	29	41	38	38	23	12	14	17		16	40	21
		total without singletons	4	8	27	39	38	36	22	12	14	17		16	23	19
		normalized		6	18	33	36	29	17	12	13	15		16	26	
		singletons	0	0	2	2	0	2	1	0	0	0		0	17	2
		crossovers		4	7	24	34	20	11	11	11	13		16	12	
		origination		4	19	13	1	1	1	0	3	3		0	7	
		extinction		0	1	2	3	15	10	1	0	1		0	4	
		turnover		4	20	15	4	16	11	1	3	4		0	11	
		origination rate		0.5	5.4	2.2	0.4	0.5	0.2	0	1.8	1		0	3.3	
		extinction rate		0	0.3	0.3	1.2	6.8	2.3	0.3	0	0.3		0	1.9	
		turnover rate		0.5	5.7	2.5	1.6	7.3	2.6	0.3	1.8	1.3		0	5.2	
	studies per biozone		1	2	7	10	8	5	4	1	1	1		1	3	2

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Diversity by biozones

Geography	Taxonomy	Diversity index	*T. pedum*	*Stage 2*	*S. mickwitzi*	*Holmia*	*Protolenus*	*Ac. oelandicus*	*Pa. paradoxissimus*	*Pa. forchhammeri*	*Ag. pisiformis*	*Olenus*	*Pb. spinulosa*	*Leptoplastus*	*Peltura*	*Acerocare*
Gondwana	species	sampled-in-bin				11	13	11	45	16	7	26	27		63	49
		total				11	13	11	45	18	13	26	28		63	49
		total without singletons				3	4	9	16	14	13	18	26		49	37
		normalized					7.5	7	23	12	13	17	19		37	
		singletons				8	9	2	29	4	0	8	2		14	12
		crossovers					2	3	1	6	12	7	9		11	
		origination					1	6	7	6	1	5	14		26	
		extinction					1	0	8	2	0	6	3		12	
		turnover					2	6	15	8	1	11	17		38	
		origination rate					0.4	2.7	1.6	1.6	0.6	1.7	6.4		12	
		extinction rate					0.4	0	1.9	0.5	0	2	1.4		5.7	
		turnover rate					0.8	2.7	3.5	2.1	0.6	3.7	7.7		18	
	genera	sampled-in-bin				11	16	12	27	13	5	14	18		33	28
		total				11	18	17	28	18	16	20	22		33	28
		total without singletons				8	15	17	20	17	16	18	22		30	26
		normalized					12	14	18	15	16	17	18		25	
		singletons				3	3	0	8	1	0	2	0		3	2
		crossovers					6	11	8	11	15	13	14		17	
		origination					7	4	5	4	1	2	7		9	
		extinction					2	2	7	2	0	3	1		4	
		turnover					9	6	12	6	1	5	8		13	
		origination rate					2.8	1.8	1.2	1.1	0.6	0.7	3.2		4.3	
		extinction rate					0.8	0.9	1.6	0.5	0	1	0.5		1.9	
		turnover rate					3.6	2.7	2.8	1.6	0.6	1.7	3.6		6.2	
	studies per biozone					1	2	2	7	4	2	6	4		7	1

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Supplementary material S14

Spearman's r_s and probability value p for correlations between acritarch diversity indices and the number of studies per stage, and between global sampled-in-bin genus diversities of acritarchs and marine invertebrates (values for marine invertebrates were taken from the supporting information of Na and Kiessling, 2015).

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Correlation with studies per stratigraphic interval					
Stratigraphy	**Geography**	**Taxonomy**	**Diversity index**	**Spearman's *rho***	***p***
Stages	global	species	sampled-in-bin	0.96	0
			total	0.95	0
			normalized	0.93	0
			crossovers	0.18	0.625
			singletons	0.77	0.01
		genera	sampled-in-bin	0.89	0.001
			total	0.78	0.008
			normalized	0.52	0.121
			crossovers	0.16	0.651
			singletons	0.61	0.06
	Baltica	species	sampled-in-bin	0.85	0.004
			total	0.83	0.006
			normalized	0.82	0.024
			crossovers	0.27	0.563
			singletons	0.77	0.015
		genera	sampled-in-bin	0.86	0.003
			total	0.84	0.004
			normalized	0.73	0.064
			crossovers	0.2	0.667
			singletons	0.52	0.155
	Gondwana	species	sampled-in-bin	0.91	0.005
			total	0.91	0.005
			normalized	0.58	0.306
			crossovers	-0.31	0.617
			singletons	0.6	0.154
		genera	sampled-in-bin	0.64	0.124
			total	0.84	0.019
			normalized	0.37	0.541
			crossovers	-0.19	0.76
			singletons	0.38	0.401
Biozones	global	species	sampled-in-bin	0.87	0
			total	0.76	0.002
			normalized	0.57	0.032
			crossovers	0.03	0.908
			singletons	0.81	0
		genera	sampled-in-bin	0.85	0
			total	0.35	0.214
			normalized	-0.11	0.708
			crossovers	-0.31	0.275
			singletons	0.74	0.003
	Baltica	species	sampled-in-bin	0.87	0
			total	0.9	0
			normalized	0.88	0
			crossovers	0.56	0.072
			singletons	0.63	0.021
		genera	sampled-in-bin	0.88	0
			total	0.82	0.001
			normalized	0.83	0.002
			crossovers	0.38	0.249
			singletons	0.61	0.025
Biozones	Gondwana	species	sampled-in-bin	0.52	0.124
			total	0.55	0.098
			normalized	0.86	0.006
			crossovers	-0.02	0.954
			singletons	0.33	0.351
		genera	sampled-in-bin	0.45	0.19
			total	0.6	0.066
			normalized	0.83	0.01
			crossovers	0.22	0.605
			singletons	0.25	0.483
Correlation with marine invertebrates					
Stages	global	genera	sampled-in-bin	0.5515	0.0984

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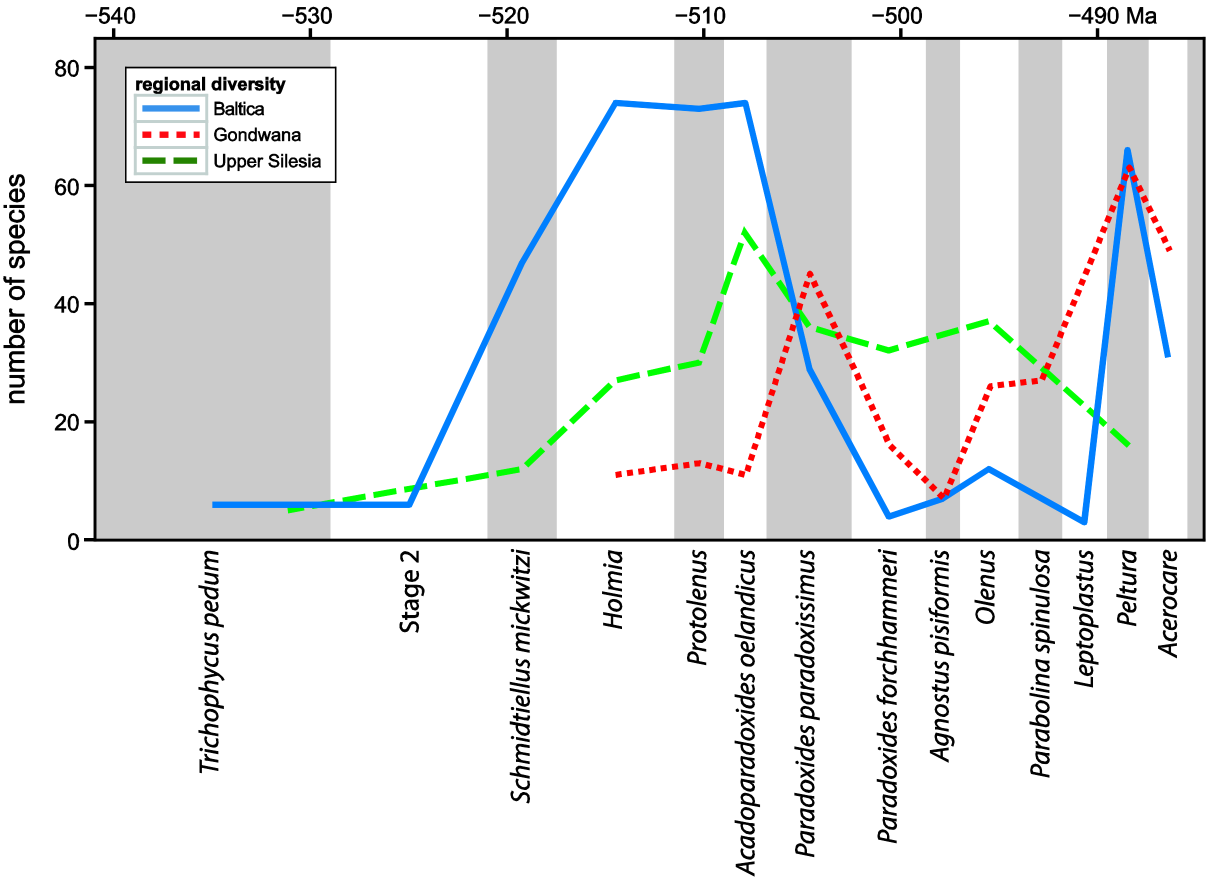
Supplementary material S15

Comparison of regional species diversities based on biozones; Baltica and Gondwana: this study, sampled-in-bin diversity; Upper Silesia: Moczydłowska (1998), total? diversity.



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