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LOWER PALAEOZOIC ACRITARCHS AS PROXIES FOR THE RECONSTRUCTION OF PALAEOENVIRONMENTS

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Tyrannie heureuse que celle des passions, qui font les plaisirs de notre vie;
fâcheux empire que celui de la raison, s'il nous ôte les sentiments agréables
Charles de St Evremont (1616-1703)

Basic research is what I'm doing when I don't know what I'm doing
Wernher Von Braun (1912-1977)

Celestial navigation is based on the premise that the Earth is the center of the universe. The premise is wrong, but the navigation works. An incorrect model can be a useful tool
Kelvin Throop III

I don't have any solution, but I certainly admire the problem
Ashleigh Brilliant

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Pourquoi diable inclut-on les remerciements au début d'un travail alors que c'est ce qu'on écrit à la fin?
R. Holder

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RESUME

Le Paléozoïque Inférieur est marqué par une biodiversification importante d'un grand nombre d'organismes des milieux marins, où les représentants du phytoplancton (dont les acritarches) occupaient une place centrale en tant que producteurs primaires. Ces organismes microscopiques, aux affinités incertaines, sont très utiles pour la biostratigraphie et auraient un grand potentiel pour les reconstitutions paléogéographiques et paléoécologiques.

Une série d'études a été réalisée, dans les domaines de la taxonomie et de l'interprétation de la distribution spatio-temporelle des acritarches du Cambrien Supérieur, de l'Ordovicien et du Silurien Supérieur.

Tout d'abord, avant toute application, une taxonomie cohérente est nécessaire. Dans ce but, les statistiques multivariées ont permis 1) de proposer une classification alternative des acritarches galéates du Cambro-Ordovicien du Sahara Algérien et 2) de compléter la taxonomie usuelle du genre *Nellia* de la même succession d'Algérie.

Afin d'évaluer la biodiversité des acritarches ordoviciens, une analyse a été réalisée sur la base d'une révision complète de la littérature. Les résultats indiquent des schémas de diversité mieux exprimés au niveau régional qu'au niveau global.

En marge des études classiques en biostratigraphie et en paléogéographie, la suite de ce travail tente d'approfondir les aspects paléoécologiques des acritarches du Paléozoïque Inférieur. La relation entre la morphologie des acritarches galéates cambro-ordoviciens et certains paramètres environnementaux (tels que la salinité) a été analysée en comparaison avec les kystes de dinoflagéllés modernes. L'étude de la distribution des acritarches le long d'un transect latéral dans le Silurien supérieur de l'île de Gotland (Suède) a permis de proposer l'utilisation des acritarches en tant que marqueurs de paléoenvironnements. Dans le contexte des variations paléoclimatiques du Silurien supérieur, l'analyse de la distribution verticale des acritarches de la même région a montré que ces organismes étaient très sensibles aux changements environnementaux et pourraient être utiles aux modélisations paléoclimatiques dans le Paléozoïque Inférieur.

ABSTRACT

The Lower Palaeozoic is characterised by a major phytoplankton diversification. Organic-walled organisms (acritarchs) played an essential role in primary production. This group is very useful for biostratigraphy, but has also a high potential for palaeobiogeographical and palaeoecological reconstructions.

Late Cambrian, Ordovician and Late Silurian material was studied in order to analyse taxonomy, to review published data and to reconstruct palaeoenvironmental conditions and palaeoclimate . This research led to the publications of six articles attached to the present thesis.

Multivariate statistics on Cambro-Ordovician galeate acritarchs from the Algerian Sahara allow an alternative classification . The revision of the genus *Nellia* from the same succession is based on the combination of traditional taxonomy and statistical approach to demonstrate the high intraspecific variation.

For the evaluation of Ordovician acritarch biodiversity, a complete review of the literature has been carried out. The results reflect more regional trends and do not display global diversity patterns.

The relation between the morphology of the Cambro-Ordovician galeate acritarchs and environmental parameters (such as salinity) is analysed in comparison with modern dinoflagellate cysts. The acritarch distribution across certain facies boundaries has been investigated on a Late Silurian carbonate platform (Gotland, Sweden). Some acritarch taxa characterise specific palaeoenvironments. The detailed record of climatic changes in the Late Silurian is reflected by changes in the composition of acritarch assemblages from the Gotland succession. The sensitivity of acritarchs to environmental changes may represent an important tool for the reconstruction of the Lower Palaeozoic climate.

UTILISATION DES ACRITARCHES DU PALEOZOÏQUE INFERIEUR POUR LA RECONSTITUTION DES PALEOENVIRONNEMENTS - VERSION FRANÇAISE

I / Introduction - Que sont les acritarches?

Les acritarches constituent un groupe hétérogène de microfossiles représentant la grande majorité des microfossiles marins à paroi organique dans les sédiments protérozoïques et paléozoïques. Leur première occurrence remonte au Protérozoïque inférieur (Vidal, 1981) où les formes observées sont des microsphères dépourvues d'ornementation et peu diversifiées. Un développement majeur des acritarches a lieu au cours du Cambrien Inférieur (Vidal & Moczylowska-Vidal, 1997) avec l'apparition de formes inédites et abondantes dont certaines vont persister pendant tout le Paléozoïque, où la plus grande diversité semble être atteinte au cours de l'Ordovicien et du Silurien (Figure 1).

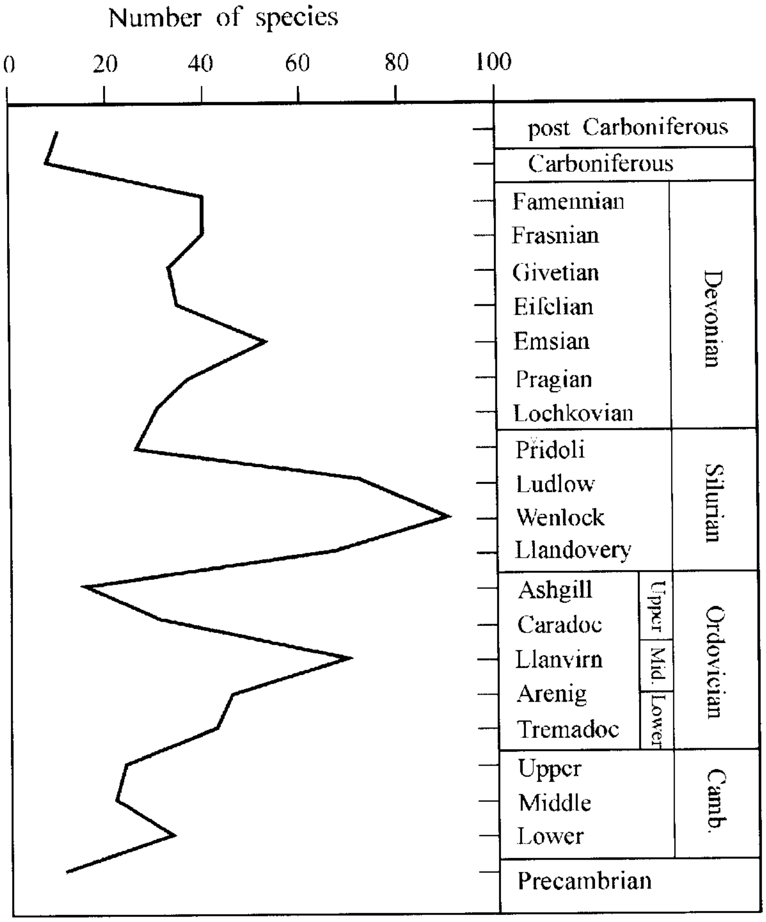

Figure 1 – Nombre d'espèces d'acritarches au cours du temps (Servais et al., 2004 ; modifié d'après Strother, 1996). La figure 2 présente une version corrigée de l'Ordovicien.

Par définition, ces microfossiles ("Acritarcha", du grec *akritos*, incertain, et *arche*, origine) sont à paroi organique et d'affinité biologique incertaine (Evitt, 1963). Toutefois, certains représentants du groupe ont été progressivement rapprochés ou regroupés avec d'autres palynomorphes dont la biologie et la classification sont mieux connus. Ainsi, bien que certains caractères restent manquants, la morphologie des acritarches les rapproche le plus souvent de certains dinoflagellés mésozoïques. Ce rapprochement s'appuie sur des recherches récentes (Moldowan et al., 1996; Moldowan & Talyzina, 1998) dans le domaine de la biogéochimie qui montrent que des dérivés de dinostéroïdes (substance commmune aux dinoflagellés) sont présents dans les sédiments paléozoïques et dans la paroi de certains acritarches du Cambrien, ce qui impliquerait la présence de (pré-)dinoflagellés avant le Trias. Certains acritarches (par ex. *Leiosphaeridia*) ont été re-attribués aux prasinophycées sur la base de critères morphologiques simples (Le Hérissé, 1989; Colbath & Grenfell, 1995; Mullins, 2001). Enfin, d'autres acritarches ont été classés hors du phytoplancton et regroupés avec les champignons (Pirozynski, 1976), les algues benthiques (Dorning, 1981) ou avec les spores alètes (par ex. *Virgatasporites*, voir Fensome et al., 1990). Dans l'ensemble, la majorité des acritarches paléozoïques sont associés aux sédiments marins et consituteraient des représentants du microphytoplancton (Martin, 1993; Colbath & Grenfell, 1995; Molyneux et al., 1996).

L'histoire de l'étude des acritarches a réellement débuté dans les années 1930 (par ex. Eisenack, 1931; Wetzel, 1933) alors que les acritarches étaient attribuées au groupe des "hystrichosphères" (du grec, *hystrichos*, porc-épic). Sur la base d'études sur des blocs erratiques de la région baltique, Eisenack jetait à cette époque les bases de la taxonomie usuelle des acritarches en décrivant quelques-uns des genres les plus communs. D'autres genres, comme *Micrhystridium* ou *Veryhachium*, ont été ensuite décrits par Deflandre (1937) et Deunff (1954) dans la même période.

Evitt (1963) scinde le groupe des hystrichosphères en attribuant une partie du groupe aux kystes de Dinoflagellés, le reste des représentants du groupe aux affinités non connues constituant alors, par défaut, les acritarches. Au cours des années suivantes, plusieurs grands travaux de systématique des acritarches furent menés pendant le développement de la palynologie du Paléozoïque dans plusieurs pays européens (par ex. en Angleterre: Downie, 1959; Espagne: Cramer, 1964, 1970; Belgique: Martin, 1969). De même, beaucoup de travaux significatifs sont effectués au cours de la même période en Amérique du Nord (Loeblich & Tappan, 1969) mais également en Amérique du Sud (ex. Brito, 1967, Pöthé de Baldis, 1975) et en Union Soviétique, où les travaux de Timofeev (1959) ont contribué à augmenter considérablement le nombre de genres et d'espèces décrits. Toutes ces recherches conduisirent à la définition des acritarches comme outil biostratigraphique de référence pour le Paléozoïque.

Parallèlement aux travaux de taxonomie et de biostratigraphie, Cramer était l'un des premiers à employer les acritarches pour la reconstitution paléogéographique à une échelle globale (Cramer, 1968, 1971; Cramer & Díez, 1972). Cependant, plusieurs auteurs ont critiqué l'emploi de ces provinces palynologiques à grande échelle (Le Hérissé & Gourvennec, 1995) puisque les assemblages d'acritarches semblaient plus influencés par des paramètres locaux et environnementaux que par un contrôle latitudinal. Néanmoins, de par leur occurrence, certains acritarches semblent endémiques à des zones climatiques bien définies alors que d'autres sont plus cosmopolites (Servais et al., 2003).

L'utilisation des acritarches en tant qu'outil biostratigraphique et paléogéographique à grande échelle est contrainte par leur extrême sensibilité aux variations locales des paléo-environnements. Les premières études relatives aux aspects écologiques des acritarches démarrent dans les années 1960 (Staplin, 1961) et s'étendent jusqu'à nos jours. D'une manière similaire aux observations sur la macrofaune (brachiopodes, trilobites), l'intérêt de ces recherches s'était orienté vers la reconstitution des variations du niveau marin et vers la distribution des espèces dans des transects latéraux (par ex. Jacobson, 1979; Dorning, 1981).

La majeure partie des travaux concernant les acritarches sont des études taxonomiques où les définitions d'espèces sont généralement fondées sur une approche phénétique à partir de l'analyse de quelques dizaines d'individus. La classification ainsi produite regroupe des unités arbitrairement appelées "espèces" ou "genres", qui ne correspondraient pas réellement à des entités biologiques, si on se réfère à l'écologie et au cycle de vie des dinoflagellés actuels. De plus, la classification adoptée par les différents chercheurs fait toujours l'objet d'un débat entre "splitters" et "lumpers". La classification induite par la phénétique a amené à la création d'un grand nombre d'espèces, produit par les "splitters". A l'inverse, le travail du "lumper" est une approche taxonomique consistant à regrouper un grand nombre d'espèces sous un seul taxon. Toutefois, seules les études détaillées semblent en mesure de faire la balance entre splitters et lumpers.

Cependant, comme le souligne Servais (1996), une approche biologique du problème de classification des acritarches requiert l'analyse de larges populations de manière à évaluer correctement l'ensemble du spectre de la variabilité morphologique. Les études détaillées relatives à la variabilité sont relativement récentes, demandant de nouvelles méthodes de traitement statistique afin de tester la validité de la taxonomie usuelle. De telles méthodes ont été employées ces trente dernières années mais sur des populations réduites, en ignorant le problème de ce que constitue un paramètre morphologique et de son évaluation. De fait, les statistiques s'avèrent-elles être un outil significatif pour comprendre la variabilité des acritarches, si on les applique à de grandes populations. Dans le premier chapître de notre travail, nous proposons d'approcher la variabilité du groupe abondant des acritarches "galéates" *via* les statistiques multivariées (Chap. II - A).

De même, une révision de la littérature du genre *Nellia* sera proposée en combinaison avec une approche statistique multivariée (Chap. II - B). Les conséquences qu'engendrent de telles approches sur ce genre restreint à quelques espèces seront exposées dans une seconde partie.

Le chapitre III présentera une réflexion sur la biodiversité des acritarches. Est-ce que le travail taxonomique usuel apporte une image globale sur la biodiversité des acritarches au cours de l'Ordovicien? Les signaux de biodiversité ne sont-ils pas influencés par d'autres paramètres?

Dans le quatrième chapitre, nous essayerons de mieux comprendre les aspects paléoécologiques des acritarches. La première approche (Chap. IV - A) discutera de la relation probable existant entre la morphologie des acritarches galéates et certains paramètres physico-chimiques de l'environnement telle que la salinité. Sur ce point, les acritarches galéates réagissent-ils de la même manière aux paramètres environnementaux que les kystes de dinoflagellés qui leur sont similaires par leur morphologie ?

Pour approfondir notre connaissance des aspects paléoécologiques, une étude a été menée dans le Silurien supérieur de l'île de Gotland sur la distribution latérale des acritarches au niveau local. En complément des études qualitatives antérieures sur la même période, que révèle l'approche quantitative de notre travail ? Les résultats et leurs interprétations sont présentés dans un second temps (Chap. IV - B).

De la même manière, quelques recherches antérieures discutent de l'éventuelle relation entre la distribution des acritarches et les paléoevironnements (par ex. Dorning & Bell, 1987). Dans le Silurien supérieur de l'île de Gotland, de profonds changements environnemetaux et climatiques sont indiqués par des excursions importantes d'isotopes stables. Notre dernière étude discute de la place des acritarches dans les modélisations des variations paléoclimatiques (Chap. IV - C).

II / Variabilité des acritarches

A – L'apport des statistiques à la classification des acritarches (Stricanne & Servais, 2002)

En paléontologie, l'application du concept d'espèce biologique est toujours problématique. La classification adoptée reflète le plus souvent une part de biais dans l'approche des caractères morphologiques qui constituent le seul paramètre disponible pour étudier la variabilité des organismes fossiles.

Classiquement, l'approche morphologique des acritarches est purement phénétique. La caractérisation biométrique constitue une part importante de la diagnose mais les mesures sont souvent relevées dans des populations assez réduites (de 10 à 100 spécimens). De plus, peu de critères définissent les acritarches, du fait de leur morphologie relativement simple. Les diagnoses sont donc souvent limitées à quelques mesures, arbitrairement considérées comme significatives pour un taxon étudié, alors que le reste des caractères n'est évalué que de manière subjective. Le plus souvent, les mesures se limitent à la taille de la vésicule (= coque) et à celle des processus (= épines). Suivant les auteurs, les diagnoses diffèrent aussi par plusieurs paramètres quantitatifs annexes tels que la taille globale (vésicule + processus), la structure ou le nombre de processus. De fait, la taxonomie des acritarches se révèle extrêmement confuse, ce qui conduit le plus souvent au recouvrement des diagnoses et à la multiplication des espèces dans la littérature.

Quelques études de traitement statistique ont été réalisées sur les acritarches. Toutefois, cette approche s'est révélée souvent limitée à l'emploi d'outils descriptifs simples (par ex. moyenne, écart-type) dans le cadre d'analyses bivariées (par ex. Brocke et al., 1997). D'autres outils statistiques, comme les tests de conformité du χ^2 (par ex. Kalvacheva & Chobanova, 1974; Vecoli et al., 1999) ont également été utilisés pour contraindre la variabilité entre différentes espèces. Les premières applications de statistique multivariée (par ex. Wauthoz & Gérard, 1999) ont rapidement montré le potentiel de ces méthodes pour approcher la variabilité. Cependant, seules quelques applications statistiques ont été tentées sur de petites populations alors que la variabilité des groupes étudiés demandait des outils plus performants pour maîtriser la variabilité sur de plus grands ensembles.

Une classification est rencontrée avec les acritarches "galéates" pour lesquels 83 espèces et quatre genres (*Caldariola*, *Cymatiogalea*, *Priscogalea*, *Stelliferidium*) ont été décrits. Cependant, un examen plus attentif montre qu'un continuum morphologique semble exister entre toutes les variantes généralement attribuées à des espèces ou des genres dans la littérature (Servais & Eiserhardt, 1995). Devant un tel "plexus", l'approche usuelle de révision taxonomique ("lumping") ne suffit pas pour résoudre le problème de classification, dans la mesure où l'importance de chaque caractère n'est pas ré-évaluée.

Dans le cas des acritarches galéates, notre travail propose d'employer les statistiques multivariées et la classification automatique afin de reclasser les individus d'une grande population fossile (564 spécimens) d'un sondage pétrolier nord-africain, indépendamment du statut taxonomique usuel. Onze critères morphologiques utiles à la classsification ont été retenus pour décrire les formes galéates. Ainsi, des critères tels que la couleur de la vésicule ou la taille du pylome n'ont pas été retenus dans la mesure où ils constituent des paramètres influencés secondairement par des processus taphonomiques. Les critères morphologiques ont été rangés dans trois catégories qui sont les paramètres continus (= quantitatifs), semi-quantitatifs et discrets (= qualitatifs). Les paramètres et les mesures des spécimens ont ensuite été traités par une analyse en composantes principales (ACP).

L'analyse des résultats indique que seuls cinq des onze paramètres morphologiques retenus sont utiles à la classification alors que les autres ne sont que des redondances. Les caractères les plus significatifs sont la longueur des processus, le diamètre de la vésicule, la présence/absence de ramification distale des processus, la présence/absence de membranes et la structuration ornementale (suite morphologique d'apparition de champs polygonaux dans le plexus). Dans le cadre de l'ACP, trois facteurs sont retenus et expliquent principalement la variabilité par les variations dans la longueur des processus et leur ramification. Un essai de classification automatique (Méthode des Nuées Dynamiques) a ensuite été réalisé et montre quatre "clusters" (unité de classification) où de nombreux spécimens attribués à des genres différents peuvent être réunis au sein des mêmes clusters.

Cette première approche statistique de la classification des acritarches galéates démontre que la taxonomie est biaisée par de nombreux points, dont le nombre et le "poids" statistique des caractères sont les plus importants. Notre travail montre que certains paramètres ont une importance surévaluée pour la classification. Quantifié par les statistiques, le continuum morphologique des galéates revèle également qu'une grande majorité des spécimens algériens pourraient éventuellement être regroupés dans une seule unité taxonomique puisqu'il est difficile de tracer une limite claire entre des clusters. Cette étude représente donc une étape supplémentaire vers l'utilisation des statistiques multivariées pour la compréhension de la classification des acritarches.

B – Révision du genre *Nellia* – stratigraphie et paléobiogéographie (Stricanne et al., accepted)

L'existence de continuums morphologiques chez les acritarches est également observé chez certains diacromorphes cambro-ordoviciens de la région nord-africaine, où le genre *Nellia* est retrouvé pour la première fois. Le genre *Nellia* présente des affinités avec un certain nombre de diacromorphes (acritarches présentant une bipolarité de la vésicule avec ou sans ornementation) dont les genres *Acanthodiacrodium*, *Buchinia*, *Calyxiella*, ainsi que quelques espèces des genres *Dasydiacrodium* et *Veryhachium*. Cette proximité morphologique indique qu'une révision taxonomique serait nécessaire afin de préciser les relations exactes qu'entretiennent les morphotypes des différents taxons.

Au niveau interspécifique, les quelques espèces de *Nellia* (*longiuscula*, *magna*, *sukatschevii*, *acifera*, ?*longispinata*) constituent également un plexus de formes où les variations sont continues entre chaque pôle morphologique. D'une manière similaire à la définition des espèces galéates, le choix des caractères utiles à la diagnose est fait arbitrairement par les différents auteurs, lesquels critères sont le nombre et la longueur des processus. Afin de caractériser les relations entre les morphotypes algériens de *Nellia*, une analyse statistique multivariée (AFC: analyse factorielle des correspondances) et une classification automatique (CHA: classification hiérarchique ascendante) ont été réalisées sur une population de 113 spécimens, caractérisés par 5 paramètres morphologiques. Les résultats montrent que la variabilité de la population peut être traduite par le nombre de processus antapicaux et, secondairement, par la hauteur de la vésicule et la longueur des processus apicaux. Ces résultats constituent une combinaison des deux schémas précédents adoptés pour la classification des espèces de *Nellia*, et indiquent de fait qu'un schéma de classification unique ne peut être réellement retenu si on ne tient compte que de la variation d'un paramètre.

Cependant, les deux clusters obtenus par classification automatique des spécimens algériens concordent avec le schéma de variabilité observé chez l'espèce *N. acifera* et *pro parte* chez *N. sukatschevii*, alors que l'espèce en nomenclature ouverte *N.* ?*longispinata* n'entre pas dans ce schéma. De manière provisoire, l'ensemble de la variation observée dans la population algérienne est attribuée à l'espèce *N. acifera*. L'analyse d'une plus grande population et de matériel d'autres régions semble nécessaire afin de mieux cerner le schéma de variabilité des morphotypes de *Nellia*, mais l'approche statistique démontre que ce schéma est déjà bien complexe au niveau local.

Les extensions stratigraphiques du genre *Nellia* sont généralement situées du Cambrien supérieur au Trémadocien inférieur. Les précédentes occurrences de *Nellia* combinées à cette découverte situent ce genre dans les hautes paléolatitudes et pourraient indiquer qu'il est associé à des assemblages d'acritarches caractéristiques des environnements marins froids.

III / Biodiversité des acritarches : exemple de l'Ordovicien (Servais, Li, Stricanne, Vecoli, Wicander, 2004)

La majeure partie des travaux relatifs aux acritarches concernent la taxonomie alors que peu d'études relatives aux affinités biologiques et aux aspects écologiques du groupe existent. Il est aujourd'hui reconnu que les acritarches constitueraient une partie du microphytoplancton durant le Paléozoïque. Dans le cadre de la biodiversification de la macrofaune au cours de l'Ordovicien, est-il possible de caractériser l'évolution du phytoplancton à paroi organique? Dans ce but, une révision des données de biodiversité a été proposée dans le cadre du PICG (Programme International de Corrélation Géologique) n° 410, intitulé "La Grande Biodiversification Ordovicienne". Cependant, en référence aux problèmes posés par la classification des acritarches, l'analyse de la biodiversité des acritarches à l'Ordovicien indique que les courbes de diversité doivent être interprétées avec précaution.

Les études de biodiversité précédentes (par ex. Tappan & Loeblich, 1973; Strother, 1996) ont montré que la diversité s'accroît du Précambrien au Silurien, puis décroît rapidement du Dévonien au Permien (cf. Figure 1).

La révision de la littérature sur l'Ordovicien proposée dans notre étude est fondée sur une revue des données de plusieurs centaines d'articles scientifiques. Bien que la couverture soit encore incomplète, les régions étudiées sont majoritairement situées en Europe et en Afrique du Nord, ainsi qu'en Chine et en Amérique du Nord. Afin d'établir une liste des espèces présentes, un recensement pour chaque région a été effectué, en incluant plusieurs informations dont l'extension stratigraphique.

La première information apportée par cette liste indique que la somme des espèces dans l'Ordovicien s'élève à plus de 1300. Cette quantité est principalement influencée par les espèces décrites pour les paléocontinents Baltica, Nord-Gondwana et Laurentia. En moyenne, la richesse spécifique s'élève globalement à toujours plus de 250 espèces par étage et indique une diminution du nombre d'espèces du Tremadoc à l'Ashgill. La distribution des acritarches ordoviciens est présentée dans la figure 2.

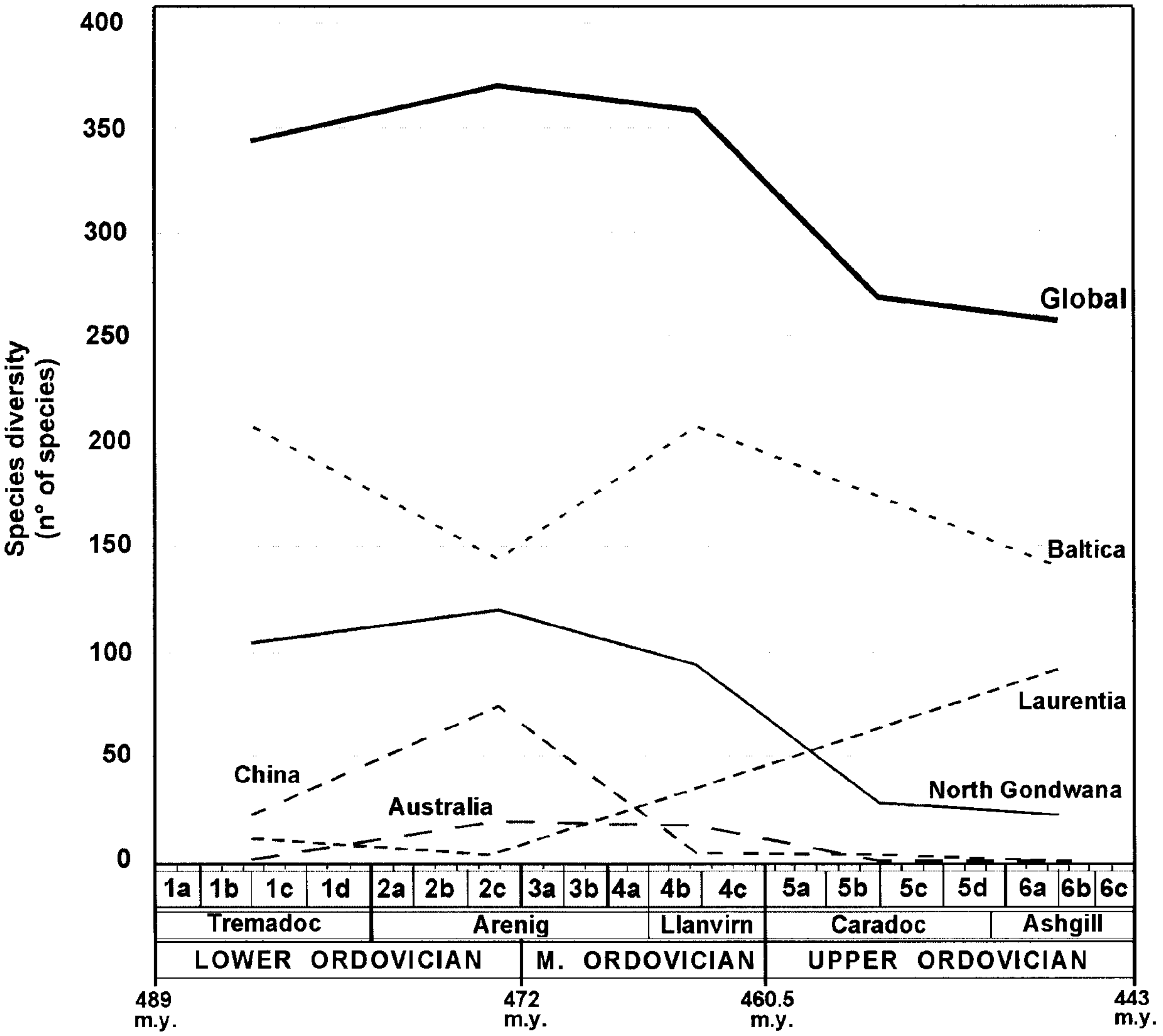

Figure 2 – Distribution des espèces d'acritarches au cours de l'Ordovicien (Stricanne et Servais, inédit). Les extensions stratigraphiques ne sont pas reportées.

Cependant, les résultats montrés par la figure 2 doivent être interprétés avec beaucoup de précaution. Le processus de révision taxonomique met en évidence les synonymies potentielles de nombreuses espèces (Chapitre II). Certains morphotypes pourraient déjà avoir été décrits précédemment et introduisent de fait un biais. Ainsi que l'indiquent les résultats d'approches statistiques de la taxonomie, les continuums morphologiques communs à de nombreux groupes d'acritarches compliquent de manière conséquente l'évaluation de la biodiversité ainsi que l'approche taxonomique envisagée (par ex. un "splitter" utiliserait 83 taxons pour classer les acritarches galéates alors qu'un "lumper" tentera de réduire la variabilité observée jusqu'à un seul taxon). De plus, les résultats (Figure 2) montrent moins une image de diversité générale que l'état actuel de la description des acritarches. L'inégale répartition géographique des espèces décrites est également un facteur de biais dans cette évaluation. Ainsi, plusieurs centaines d'espèces ont été décrites dans l'Arenig de Baltica alors que très peu d'espèces sont décrites pour Laurentia pour la même période. Le principal résultat de notre étude est qu'il n'existe pour l'instant pas d'image complète de la diversification des acritarches à l'Ordovicien, bien que des tendances de diversité s'expriment au niveau local.

III / Acritarches et paléoenvironnements

A – Dynamique des populations : une nouvelle voie pour interpréter la distribution des acritarches ? (Servais et al., 2004)

Dans de nombreux groupes d'acritarches, l'existence de continuums morphologiques est reconnue mais l'interprétation de cette variabilité n'a été envisagée que rarement. Jusqu'alors, le but des recherches palynologiques a été la solution de nombreux problèmes de datation ou de corrélations biostratigraphiques. Toutefois, comme il l'a été montré dans les chapitres précédents, l'utilisation des acritarches en tant qu'outil biostratigraphique est contraint par la connaissance des aspects biologiques et écologiques du groupe. Or, ces aspects ont été ignorés le plus souvent, ce qui a engendré des classifications induites par le cadre stratigraphique régional où les acritarches étaient étudiés (par ex. Cramer, 1970). Nouvellement discutés, ces aspects nécessitent cependant un examen attentif afin de discerner correctement la part de variation morphologique qui peut être attribuée au génotype et celle qui revient au phénotype.

Dans le groupe des acritarches galéates, il a été montré que la variation morphologique du groupe était principalement traduite par la longueur des processus et par la complexité de leurs terminaisons (Chap. II - A). Afin de comprendre l'origine des variations observées chez les galéates, une étude complémentaire à l'analyse statistique multivariée a été menée sur la même population d'acritarches galéates du Sahara algérien. Plusieurs paramètres morphologiques ont été mesurés et leur évolution a été reportée dans une série stratigraphique transgressive à la transition cambro-ordovicienne. L'intérêt d'une telle étude est également de comparer le schéma de variation des acritarches galéates à celui des dinoflagellés, qui leur sont proches morphologiquement.

Les résultats indiquent que le développement des processus, ainsi que leur complexité (ramifications distales, striations basales), s'accroît progressivement des niveaux les plus bas (environnements "inshore") aux niveaux les plus hauts du sondage (environnements "offshore"). Parallèlement, la présence de membranes augmente alors que le nombre de spécimens sans ornementation diminue dans l'intervalle. Le diamètre de la vésicule ne montre pas de variations ni de tendances significatives. Ces variations progressives de l'ornementation sont corrélées entre elles dans le cadre de la transgression et entrent en contradiction avec le schéma taxonomique usuel dans lequel les quatre genres *Caldariola*, *Cymatiogalea*, *Priscogalea* et *Stelliferidium* ont été décrits.

Dans le cadre de cette étude, l'interprétation de la corrélation positive entre la croissance des processus et l'augmentation de leur complexité relève des caractéristiques morpho-fonctionnelles des processus. En effet, l'allongement de la longueur et le développement des ramifications des processus contraint leur structure à développer des striations basales pour une plus grande stabilité. Ceci confère moins d'importance en taxonomie aux stries dont l'utilisation en tant que caractère avait déjà été critiquée par Rasul (1974).

La croissance des processus est également observée chez les dinoflagellés dans des expérimentations en laboratoire (Kokinos & Anderson, 1995). Ainsi, un large spectre de variation morphologique est observé au sein d'une même espèce, notamment la croissance des processus chez les dinoflagellés actuels. La croissance est interprétée comme une dépendance de plusieurs paramètres environnementaux, dont la salinité constitue le plus important. Ces paramètres controleraient la rupture de la membrane des dinoflagellés et définiraient de fait la maturité atteinte par le kyste en formation. Constituant le dernier paramètre en formation, les processus sont donc le paramètre le plus variable de la morphologie des kystes de dinoflagellés, probablement en réponse aux variations de la salinité. Transposé aux acritarches galéates, de tels résultats permettent d'entrevoir de nouvelles explications de leur évolution morphologique et une vision alternative aux conceptions classiques de la taxonomie de ces organismes. La croissance et la ramification des processus feraient partie intégrante d'une réponse à des variations de paramètres environnementaux, ici supposées être celles de la salinité. Une telle assertion demande toutefois à être confirmée par des études complémentaires dans des cadres stratigraphiques où les paramètres environnementaux sont controlés.

B – Distribution latérale des acritarches : un exemple dans le Gorstien de Gotland (Stricanne et al., 2004)

L'île de Gotland (Suède) représente une région importante pour l'étude des environnements du paléocontinent Baltica au cours du Silurien. Protégés des déformations tectoniques et de l'enfouissement, les sédiments siluriens contiennent une grande quantité de palynomorphes fossiles très bien conservés. L'étude la plus détaillée relative aux acritarches de cette région est celle de Le Hérissé (1989) qui supputait l'influence des conditions environnementales sur les populations d'acritarches, en marge d'une large révision taxonomique. Plusieurs études corrolaires dans d'autres régions ou sur d'autres périodes ont tenté de reconstituer la distribution latérale des acritarches suivant des transects inshore-offshore (ou proximal-distal). Ces recherches qualitatives ont déterminé que la diversité des acritarches augmentait vers les milieux distaux mais également que la distribution de certains genres ou espèces était probablement corrélée aux faciès sédimentaires. Peu d'approches quantitatives ont été proposées pour appuyer ces modèles de distribution.

Dans notre travail, une telle approche (valeurs relatives et absolues) a été tentée pour mieux caractériser les signatures de la distribution latérale des acritarches dans les sédiments du Gorstien (Silurien supérieur) de l'île de Gotland. Un transect inshore-offshore isochrone a été suivi et huit localités ont été étudiées. Suite à des études géochimiques (par ex. Samtleben et al., 2000), les faciès sédimentaires de ce transect ont été attribués à une période climatique humide, caractérisée par un apport substantiel de sédiments terrigènes.

Les résultats se révèlent conformes aux études précédentes, avec une augmentation progressive de la quantité d'acritarches vers les milieux distaux alors que la proportion de sphéromorphes diminue. Les autres composants palynologiques (par ex. prasinophytes, chitinozoaires) ne montrent pas de tendance significative. Les quantités absolues d'acritarches (porteurs d'ornementation) augmentent progressivement vers les milieux offshore de même que leur diversité. A un niveau générique, les acritarches présentent des répartitions différentes. Parmi les genres les plus abondants, les proportions de *Micrhystridium* et *Dilatisphaera* sont plus représentés dans les milieux proximaux que dans les milieux distaux où les genres *Evittia* et *Percultisphaera* abondent. De même, les trois morphotypes (processus courts, *M. stellatum* s.l., longs processus ramifiés) du genre *Micrhystridium* présentent une répartition caractéristique. Alors que les morphotypes aux processus courts sont très fréquents en milieu proximal, leur proportion diminue progressivement vers les milieux distaux. A l'inverse, les morphotypes aux processus plus longs présentent des proportions plus grandes vers les milieux distaux, alors que les grandes proportions de *M. stellatum* s.l. ne montrent pas de tendance particulière.

Ces observations confirment l'ensemble des travaux antérieurs sur les distributions ordoviciennes et siluriennes en apportant quelques éléments complémentaires. La corrélation de l'occurrence des genres avec les environnements de dépôts est précisée mais ne caractérise pas spécifiquement un environnement par un assemblage d'acritarches bien défini (cf. Dorning & Bell, 1987). Dans notre étude, les assemblages à *Micrhystridium* sont caractérisés de manière informelle par la longueur des processus. L'observation d'un continuum morphologique entre toutes les espèces du genre indiquerait que des changements environnementaux (par ex. la salinité) continus influencaient probablement l'ornementation de ces organismes. Les résultats de ce travail induisent également l'utilisation des assemblages d'acritarches au niveau générique pour la reconstitution des paléoenvironnements.

C – Distribution temporelle et variations du climat : exemple dans le Silurien supérieur de Gotland (Stricanne et al., submitted)

Le Silurien a longtemps été considéré comme une période chaude et sans changements environnementaux majeurs, mais les recherches récentes apportent des preuves indiquant de profonds changements climatiques. La plupart de ces changements ont été mis en évidence par des pics récurrents d'excursions positives de $\delta^{13}C$ et le $\delta^{18}O$. Le $\delta^{13}C$ a été généralement rapporté aux changements de la bioproductivité alors que le $\delta^{18}O$ serait lié aux variations de la salinité et/ou de la température. Au cours du Silurien supérieur (Ludlow), la plus grande excursion isotopique du Phanérozoïque est représentée avec des valeurs atteignant 12 ‰ pour le $\delta^{13}C$ et jusqu'à 4 ‰ pour le $\delta^{18}O$. Selon Bickert et al. (1997), les faibles valeurs isotopiques sont attribuées à des périodes climatiques humides, les fortes valeurs à un climat plus aride aux basses latitudes. Dans les premiers stades des excursions isotopiques, de nombreux organismes benthiques (par ex. conodontes et trilobites) disparaissent alors que les organismes vivant dans les environnements pélagiques ou hémipélagiques sont affectés plus tardivement.

Toutefois, aucune approche quantitative n'a été entreprise sur les acritarches de cette période marquée par ces profonds changements environnementaux. Dans le Silurien inférieur de Gotland, Gelsthorpe (sous presse / in press) a quantifié en détail le declin progressif de la diversité des acritarches et a mis en lumière la sensibilité des acritarches aux variations climatiques. Dans la mesure où ces organismes vivraient dans les eaux de surface, une approche similaire permettrait de mieux saisir les mécanismes en œuvre lors de l'excursion isotopique. A cette fin, notre étude se concentre sur les variations quantitatives (relatives et absolues) des palynomorphes du Silurien supérieur de l'île de Gotland lors de l'excursion isotopique, interprétée comme une transition humide-aride.

La majeure partie des palynomorphes sont représentés par les acritarches et les sphéromorphes. Chez tous les palynomorphes, il n'y a pas de variations significatives sont observées à la fois pour les valeurs relatives et absolues lors de la période humide. Le développement de l'excursion isotopique correspond à l'élévation des quantités de spores et cryptospores alors que tous les palynomorphes marins montrent des proportions plus réduites. Dans les groupes d'acritarches, la réduction des quantités absolues se repercute principalement sur les acanthomorphes et les polygonomorphes. Au niveau générique, le même schéma de diminution des valeurs absolues se répète mais les proportions des genres se modifient profondément. Pendant la phase humide (valeurs isotopiques faibles), plusieurs genres d'acritarches à l'ornementation dévelopée (par ex. *Evittia*) sont très bien représentés. Lorsque les valeurs isotopiques s'élèvent pendant la phase aride, les assemblages se réduisent principalement aux genres *Micrhystridium*, *Veryhachium* et *Eupoikilofusa*. Lors de la transition humide-aride, une succession ordonnée de pics d'abondance de certains genres est observée. La distribution des morphotypes dans les plexus de *Michrystridium* et de *Veryhachium* est aussi très caractéristique, avec les formes à l'ornementation développée abondante pendant la phase humide et celle à l'ornementation réduite pendant la phase aride.

Le changement majeur des populations d'acritarches intervient pendant le développement de l'excursion isotopique. La diversité réduite observée dans les études antérieures s'accompagne d'une forte diminution des quantités absolues ainsi que d'un changement radical des groupes dominants dans les assemblages. Ces données indiquent une diminution de bioproductivité océanique pendant l'excursion isotopique et montre que l'excursion positive du $\delta^{13}C$ ne peut être la conséquence d'une productivité accrue. De fait, nos résultats confirment le modèle de Bicket et al. (1997) qui expliquent l'excursion isotopique plus par des changements de circulation océanique que par des variations de productivité. Cependant, selon Bickert et al. (1997), les périodes pendant lesquelles les valeurs isotopiques sont hautes peuvent être caractérisées par des salinités élevées. Pendant cette période, la réduction de l'ornementation observée dans les deux plexus de *Micrhystridium* et de *Veryhachium* pourrait compatible avec une forte augmentation de salinité, en comparaison avec de récentes études sur les dinoflagellés du Quaternaire (Ellegaard et al., 2002).

A tous niveaux, nos résultats confirment que les acritarches seraient sensibles aux changements environnementaux. Combinée aux autres palynomorphes, la distribution des acritarches pourrait constituer un argument de référence pour la définition des modèles de circulation océanique et climatique dans le Paléozoïque inférieur.

V / Conclusions et perspectives

Comme notre étude l'a montré, l'un des problémes récurrents relatif aux acritarches est que leur taxonomie nécessite encore une révision importante, dont l'ampleur est variable selon les groupes considérés. Dans ce contexte, les nouvelles méthodologies sont indispensables pour résoudre les problèmes taxonomiques. La classification par des techniques statistiques multivariées constitue de fait un élément intéressant, puisqu'elle fournit des supports quantitatifs à la révision taxonomique, comme dans le cas des acritarches galéates ou du genre *Nellia*.

Une taxonomie claire engendre toute une série d'applications en aval, telles que la biostratigraphie ou l'évaluation de la biodiversité. En cela, notre étude de l'approche de la biodiversité des acritarches à l'Ordovicien montre qu'il existe encore des biais majoritairement introduits par la taxonomie.

D'autres approches peuvent être proposées pour mieux comprendre les aspects biologiques des acritarches. Commune aux travaux en écologie, l'étude des populations d'acritarches (comme pour les galéates) représente l'une des voies porteuses à cette fin, notamment dans le cadre detransects inshore-offshore, où les populations d'acritarches montrent des schémas de distribution particuliers. Nos études dans le Silurien supérieur de l'île de Gotland ont constitué des études pilotes pour des approches similaires, dans la mesure où les schémas de distribution des acritarches doivent être bien connus avant l'utilisation de ces palynomorphes pour les recontitutions paléocéanographiques ou paléoclimatiques dans le Paléozoïque inférieur.

L'ensemble des articles présentés dans le cadre de ce travail démontre donc que les acritarches pourraient constituer un outil performant pour la reconstitution des paléo-environnements paléozoïques en dehors de leur utilisation en biostratigraphie classique ou en paléogéographie.

Pour les recherches futures, le prolongement des études des populations d'acritarches est important, notamment dans un contexte géologique où les conditions paléo-environnementales sont mieux contrôlées. Dans la mesure où les facteurs influençant la morphologie et la distribution des acritarches commencent à être mieux connus, de telles recherches pourraient apporter une réelle contribution aux modèles de circulation océanique et/ou climatique. L'autre apport de ces recherches serait une meilleure appréhension de la taxonomie des acritarches, pour laquelle les statistiques multivariées constituent déjà un outil adéquat en marge de la révision taxonomique traditionnelle.

Enfin, après la longue phase de première acquisition de l'information (qualitative), les prochaines recherches dans le domaine de la paléoécologie des acritarches vont réclamer toujours plus de quantification. Ceci pourrait être également mis en œuvre dans le cadre de comparaison de modèles de croissance de l'ornementation chez certains morphotypes d'acritarches sélectionnés et les dinoflagellés modernes (en culture de laboratoire) en fonction de paramètres physico-chimiques déterminés (température, salinité, etc...). En complément des études classiques de distribution, ces travaux constitueraient également un test sérieux pour mieux caractériser les aspects paléoécologiques des acritarches. Déjà pressenti dans les travaux actuels, le futur de la recherche des acritarches passe par une comparaison accrue avec le monde des dinoflagellés actuels et fossiles.

LOWER PALAEOZOIC ACRITARCHS AS PROXIES FOR THE RECONSTRUCTION OF PALAEOENVIRONMENTS – ENGLISH VERSION

I / Introduction – what are acritarchs?

Acritarchs are a heterogeneous group of microfossils representing the largest part of marine organic-walled microfossils in Proterozoic and Palaeozoic sediments. Their first occurrence is reported in the lower Proterozoic (Vidal, 1981) where most microfossils are devoid of any ornamentation and are of low diversity. A major biodiversification took place in the Lower Cambrian (Vidal & Moczylowska-Vidal, 1997) with the appearance of new and abundant forms that exist through all Palaeozoic times, where the greatest diversity seems to be reached during the Ordovician and the Silurian (Figure 1).

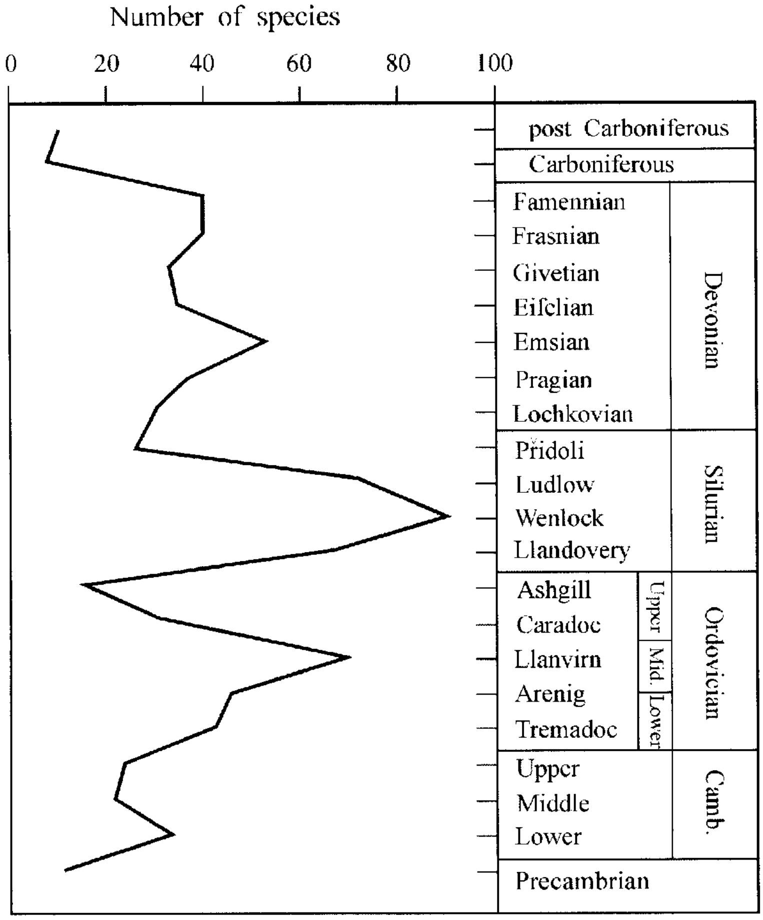

Figure 1 –Number of acritarch species versus time (Servais et al., 2004 ; modified after Strother, 1996). Figure 2 shows an updated version for the Ordovician.

According to their definition, acritarchs ("Acritarcha", from the Greek *akritos*, unknown, and *arche*, origin) are organic-walled microfossils of unknown biological affinities (Evitt, 1963). However, some acritarchs have been successively attributed to other palynomorphs of which the biological affinity and classification are better known. Although some features are missing, the morphology of many acritarchs can be compared to that of some Mesozoic dinoflagellates. This observation is supported by recent research on biogeochemistry showing that dinosteroids (Moldowan et al., 1996; Moldowan & Talyzina, 1998) are found in Palaeozoic sediments and in the walls of some Cambrian acritarchs. This implies that pre-dinoflagellates may be present before the Triassic. Some acritarchs (e.g., *Leiosphaeridia*) have been re-attributed to prasinophytes based on simple morphological criteria (Le Hérissé, 1989; Colbath & Grenfell, 1995; Mullins, 2001). Other acritarchs have been classified outside the phytoplankton and attributed to fungi (Pirozynski, 1976), benthic algae (Dorning, 1981) or alete spores (e.g., *Virgatasporites*, see Fensome et al., 1990). On the whole, the majority of Palaeozoic acritarchs associated with marine sediments and are considered to be part of the microphytoplankton (Martin, 1993; Colbath & Grenfell, 1995; Molyneux et al., 1996).

The history of acritarch study seriously starts in the beginning of the 1930s (e.g., Eisenack, 1931; Wetzel, 1933) when acritarchs were still attributed to the group of "hystrichospheres" (from the Greek *hystrichos*, hedgehog). On the basis of the study of erratic boulders of the Baltic area, Eisenack defined the bases of the usual taxonomy of acritarchs with the description of some of the most common genera. Other genera, such as *Micrhystridium* or *Veryhachium* have been described by Deflandre (1937) and Deunff (1954) in the same period of time.

Evitt (1963) splitted the group of the hystrichospheres attributing one part to dinoflagellate cysts, the other part of unknown affinity to the new group of the acritarchs. During the following years, several important systematical studies were published, contributing to the development of the Palaeozoic palynology in Europe (e.g., England: Downie, 1959; Spain: Cramer, 1964, 1970; Belgium: Martin, 1969). Similarly, other significant works were presented in North America (Loeblich & Tappan, 1969), South America (e.g. Brito, 1967, Pöthé de Baldis, 1975) and in the Soviet Union, where Timofeev

(1959) contributed to the increase of the number of taxa described in literature. These works helped the Palaeozoic acritarchs to become an accurate biostratigraphic tool.

In addition to taxonomical and biostratigraphical works, Cramer was one of the first to use acritarchs for palaeogeographical reconstructions on global scale (Cramer, 1968, 1971; Cramer & Díez, 1972). However, several authors criticized the use of Cramer's palynological provinces (Le Hérissé & Gourvennec, 1995) arguing that acritarch assemblages seem to be more influenced by local environmental parameters than by a latitudinal control. Nevertheless, some acritarchs seem to be restricted to specific climatic zones whereas some other are more widely distributed (Servais et al., 2003).

The use of acritarchs as a biostratigraphic and palaeogeographic tool on global scale is constrained by their extreme sensibility to local palaeoenvironmental variations. First studies on ecological aspects of acritarchs started in the early 1960s (Staplin, 1961) and extend nowadays. In a similar way to macrofaunal studies (brachiopods, trilobites), the interest turned to the reconstruction of sea level changes and to the species distribution according to lateral transects (e.g., Jacobson, 1979; Dorning, 1981).

The majority of works on acritarchs are taxonomic studies where the species definition is based on a phenetic approach from several tens of specimens. As such, the classification gathers units arbitrary called "species" or "genera" which do not really correspond to biological units, refering to the ecology of the life cycle of recent dinoflagellate cysts. Moreover, the classification concept is still subject to intense discussions between "splitters" and "lumpers". The phenetic approach of the classification led to the creation of a large number of species, produced by "splitters". On the contrary, the work of "lumpers"' consists in grouping a high number of species within a single taxon. However, detailed studies are necessary to find the right balance between splitters and lumpers.

Servais (1996) underlined that a biological approach of acritarch classification requires the analysis of large populations in order to better evaluate the spectrum of morphological variability. These detailed studies on variability need accurate statistical methods to test the validity of the current taxonomy of acritarchs. In the last thirty years, such methods have been tentatively used but mostly only on small populations, without an evaluation of the morphological criteria. The following question arises: are statistics a significant tool to understand acritarch variability, if applied to large populations? In the first chapter of our work, the variability of "galeate" acritarchs is investigated using multivariate statistics (Chap. VII-A).

Similarly, a review of the published works on the genus *Nellia* is proposed, combined with a multivariate statistic approach (Chap. VII-B). The consequences of this approach on the genus are exposed in the second part of this chapter.

Chapter VIII presents a reflexion about acritarch biodiversity. Does the current taxonomical knowledge provide us with a global picture of acritarch biodiversity in the Ordovician? Or are biodiversity signals influenced by other parameters?

In the chapter IX, we will try to better understand the palaeoecological aspects of the acritarchs. The first approach (Chap. IX-A) will discuss the probable relation between galeate acritarch morphology and some environmental parameters, such as salinity. May the galeate acritarchs be compared to the dinoflagellate cysts, regarding their morphological changes?

Approaching the palaeoecological aspects of the acritarchs, a study have been initiated in the upper Silurian of Gotland in order to understand the lateral distribution at a local scale. What reveals our quantitative approach in comparison to earlier qualitative studies in the same time slice? The results and their interpretations are presented in the second part (Chap. IX-B).

Some previous studies discussed the possible relation of acritarch distribution and palaeoenviroments (e.g., Dorning & Bell, 1987). In the Late Silurian of Goltand, strong environmental and climatic changes are indicated by strong excursions of stable isotopes. Our last investigation focuses on the acritarch distribution across the isotope excursion in order to test the most recent palaeoclimatic models (Chap. IX-C).

VII – Approach of the acritarch variability and new methodologies

A – Statistical approach of acritarch classification (Stricanne and Servais, 2002)

In palaeontology, the use of the biological species concept is problematic. The classification often mirrors a bias in the approach of morphological criteria, which are the only parameters available to investigate the variability of fossil organisms.

Usually, morphological studies use a phenetic approach. Biometric characterisation represents an important part of the diagnosis but measurements are often limited to small populations (10 to 100 specimens). Moreover, because of their simple morphology, only few morphological criteria define the acritarchs,. Thus, diagnoses are often limited to few measurements, considered to be relevant for the studied taxa, while other parameters are subjectively evaluated. Generally, the measurements are limited to the vesicle and processes (=spines) size. Following various authors, different diagnoses are produced and gather some other quantitative parameters, such as the overall size (vesicle + processes), the structure and the number of processes. All these different approaches often lead to the overlapping of diagnoses and a high number of species described in literature.

Some statistical studies have been conducted on acritarchs. However, most investigations were limited to the use of simple statistical tools (e.g., mean, standard deviation) in bivariate analyses (e.g., Brocke et al., 1997). Other statistical tools, such as χ^2 tests (e.g., Kalvacheva & Chobanova, 1974; Vecoli et al., 1999) have been used to constrain the variability in different species. First applications of multivariate statistics (e.g., Wauthoz and Gérard, 1999) have shown the great potential of these methods to approach acritarch variability. However, these few studies have been carried out on small populations while the variability of these groups necessitates modern tools to control acritarch variability at a larger scale.

"Galeate" acritarchs represent a large plexus in which 83 species and four genera (*Caldariola, Cymatiogalea, Priscogalea, Stelliferidium*) have been described. However, detailed observations have shown that a morphological transition exists between all morphotypes generally attributed to different species and genera in the current literature (Servais & Eiserhardt, 1995). The existence of such a plexus implies that the usual taxonomical review ("lumping") cannot solve this classification problem because the relevance of each morphological criteria is not evaluated.

Our study introduces the use of multivariate statistics and an automatic classification in order to re-classify galeate specimens from a large population (564 specimens) from a North-African borehole, independently from the usual taxonomical status. Eleven morphological criteria, have been used for the classification of galeate morphotypes. Some criteria, such as the vesicle colour or the pylome size, have not been retained because these criteria represent parameters influenced by taphonomical processes. The remaining morphological criteria have been classified into three categories: continuous (=quantitative), semi-continuous, and discrete (=qualitative) parameters. These parameters and the measurements were successively treated through a principal component analysis (PCA).

The results show that only five of the eleven morphological parameters retained in the analysis are really useful for the classification while the other parameters introduce redundancy. The most significant parameters are the process length, the vesicle diameter, the presence of distal ramifications, the presence of membranes and the ornamental structure (which traduces the progresssive apparition of polygonal fields in the plexus). The PCA shows also that three factors may be retained and mainly explain the galeate variability through the variations in process length and ramification. A tentative automatic classification (K-Mean Analysis) has been performed and shows four "clusters" (classification units) in which numerous specimens currently attributed to different genera may be grouped.

This first statistical approach of the galeate acritarch classification demonstrates that several problems results in a complex taxonomy, such as the number and the relevance of morphological criteria. Our study shows that some parameters have been overestimated for the classification. Quantified by statistics, the morphological continuum in galeate acritarchs reveals also that most Algerian specimens might be gathered into a single taxonomical unit as it is still difficult to put a clear limit between the clusters of the automatic classification. Thus this study represents a further step to the use of multivariate statistics to better understand acritarch classification.

B – Review of the genus *Nellia* – stratigraphic and palaeobiogeographic aspects (Stricanne, Servais, Talyzina, Vanguestaine, accepted)

Large morphological transitions are observed in some Cambro-Ordovician diacromorphs of the North African area, where the genus *Nellia* has been reported for the first time. *Nellia* shows affinities with numerous diacromorphs (acritarchs characterised by a bipolarity of the vesicle with or wothout ornamentation) including the genera *Acanthodiacrodium*, *Buchinia*, *Calyxiella*, but also some species of *Dasydiacrodium* and *Veryhachium*. This morphological resemblance lead to a taxonomical review in order to typify the relations of morphotypes in this plexus.

The species of *Nellia* (*longiuscula*, *magna*, *sukatschevii*, *acifera*, ?*longispinata*) represent a plexus of morphotypes in which morphological variability seems to be continuous between each morphological pole. In a similar way to the species definition for galeate acritarchs, the choice of morphological features used for classification is arbitrary. In order to characterise the relations between the Algerian morphotypes of *Nellia*, a multivariate statistical analysis (CFA: Correspondence Factor Analysis) and a cluster analysis have been preformed on a population of 113 specimens, each described by five morphological criteria. In this population, the results show that the variability can be explained by the number of antapical processes, and secondarily, by the height of the vesicle and the antapical process length. These results represent a combination of two previous classifications schemes of *Nellia* species, but also indicate that a unique classification cannot be obtained if only one parameter is taken into account.

However, the two clusters produced by the automatic classification are in agreement with the variability scheme previously observed for the species *N. acifera* and *N. sukatschevii pro parte*, but the species *N.* ?*longispinata* is not retained in these results. In our study, we decided to attribute all these morphotypes to the species *N. acifera*. The analysis of larger populations from other areas is necessary to better understand the whole scheme of variability of *Nellia* morphotypes, but the statistical approach of our work yet indicates that this scheme is really complex at a local scale.

The stratigraphical range of the genus *Nellia* embraces an interval spanning from the

Upper Cambrian to the lower Tremadocian. Combined to the present record of *Nellia* in North Africa, the previous occurrences indicate that the genus may be characteristic of high palaeolatitudes is are associated with cold-water acritarch assemblages.

VIII / Acritarch biodiversity: an example in the Ordovician (Servais, Li, Stricanne, Vecoli, Wicander, 2004)

Most of the works dealing with acritarchs are related to taxonomy, while very few is currently known about the biological and ecological aspects of these microfossils. Acritarchs are nowadays considered to be a part of Palaeozoic microphytoplankton. However, dealing with the major biodiversification events in the Ordovician, is it possible to characterise the evolution of the organic-walled phytoplankton? To this end, a review of biodiversity data has been proposed following a suggestion of the IGCP (International Geological Correlation Programme) n° 410 "The Great Ordovician Biodiversification Event". Due to the problems of acritarch classification the study of the Ordovician acritarch biodiversity show that diversity curves have to be interpreted with caution.

Previous biodiversity studies (Tappan & Loeblich, 1973; Strother, 1996) have shown that acritarch diversity increases from Precambrian to Silurian times, and then decreases significantly from Devonian to Permian times (Figure 1).

In our study, the literature review dealing with Ordovician acritarchs is based on several hundreds of scientific articles. Many regions have been investigated, such as Europa and North Africa, but also China and North America although all areas have not been studied. In order to establish a consistent species list, counts for each region have been made, including all available information (e.g., stratigraphical range).

The first results provided by the species list indicate that the species number is above 1,300. This quantity mainly results from the counts for Baltica, North-Gondwana and Laurentia palaeocontinents. The species richness rises up to more than 250 species per stage and indicates a decrease in acritarch species number at the end of the Ordovician. Figure 2 shows the distribution of acritarch species over time in the Ordovician.

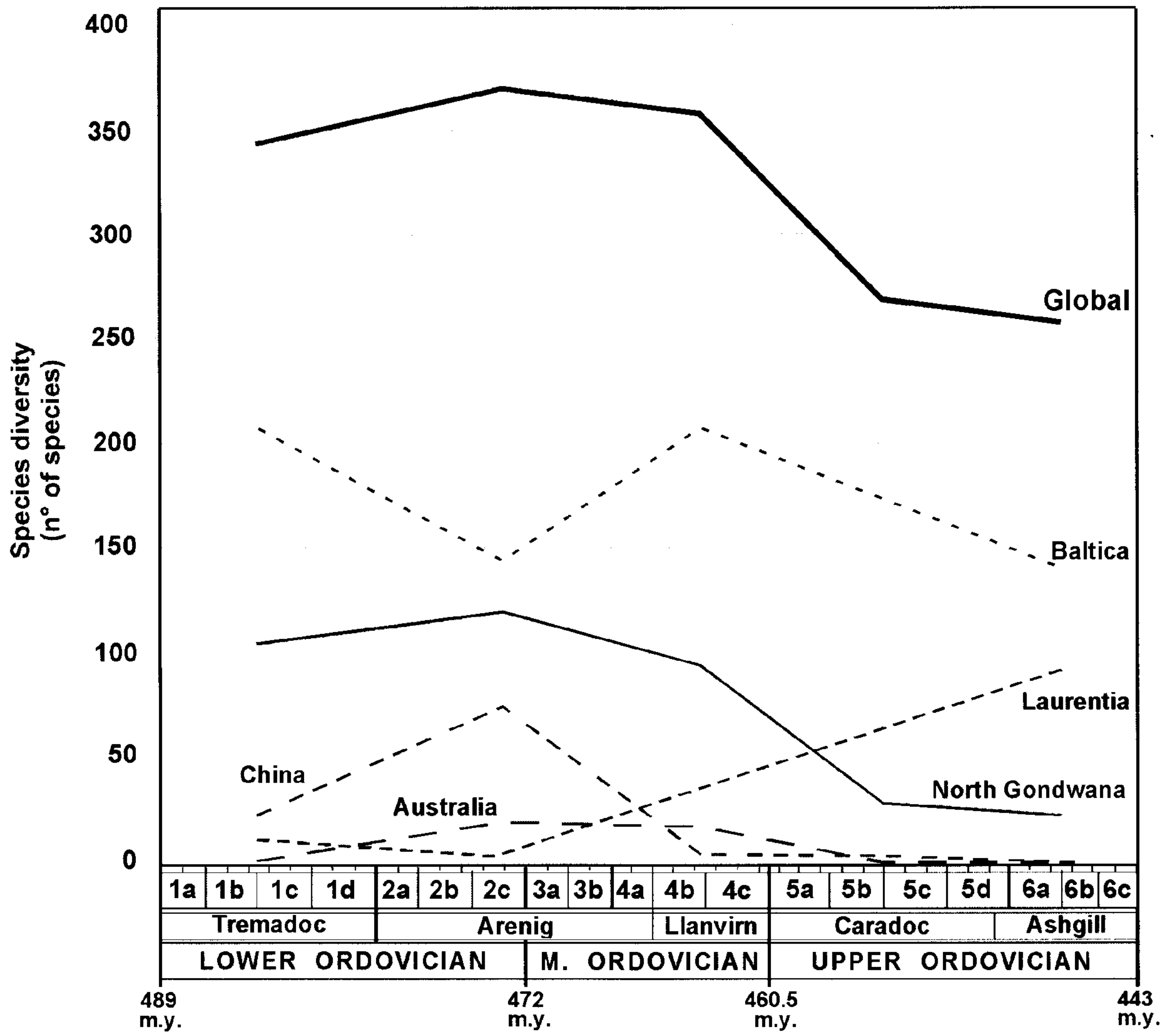

Figure 2 – Distribution of acritarch species in the Ordovician (Stricanne & Servais, unpublished). Stratigraphical ranges are not reported.

The results of Figure 2 should be interpreted with great caution. A critical view of the taxonomy indicates the possible synonymy of numerous acritarch species (see Chapter VII). Some morphotypes could have been already described and thus introduce a skew in the counts. As indicated above, many groups show a morphological continuum that complicate the evaluation of biodiversity (e.g., a "splitter" would use 83 taxa to classify galeate acritarchs while a "lumper" would reduce the variability observed to a single taxon). Accordingly, our results (Figure 2) show the status in the acritarch description rather than a real diversity picture. Another skew is caused by the unequal geographical repartition of the species described in the literature. For example, several hundreds of species have been erected from Arenig sediments of Baltica while very few species have been described for Laurentia during the same time interval. The main result of our study is that a global picture of the acritarch biodiversification in the Ordovician cannot be displayed so far, although at a regional scale biodiversity trends can clearly be observed.

IX/ Acritarchs and palaeoenvironments

A – Population dynamics : a new way to interpret acritarch distribution? (Servais, Stricanne, Montenari, Pross, 2004)

In many acritarch groups, morphological continuums have been previously reported but the interpretation of this variability has been rarely attempted. Up to now, dating sediments and establishing biostratigraphical correlations have been the main goals of acritarch research. However, as shown above, the use of acritarchs as biostratigraphical tools partly remains problematic because many biological and ecological aspects of acritarchs are still unknown. For a long time, these aspects have been mostly ignored and led to classifications influenced by the stratigraphical frame in which acritarchs were studied (e.g. Cramer, 1970). These aspects need to be approached with caution in order to determine the part of morphological variation attributable either to the genotype or to the phenotype.

In the galeate acritarch plexus, it has been shown that the morphological variability is mostly expressed by the process length and the complexity of their ramifications (Chap. VII-A). In order to better understand the origin of these variations, a complementary study to the statistical approach has been conducted on a galeate acritarch population of the Algerian Sahara. Several morphological parameters have been measured and their changes have been reported through the stratigraphical succession, that is characterised by a marine transgression crossing the Cambro-Ordovician boundary. The interest of our study is also to compare the variability of galeate acritarchs to that displayed by dinoflagellate cysts.

Our results show that the process length and the complexity of related features (distal ramifications, basal striae) increase progressively from the lower ("inshore" environments) to the higher levels of the borehole ("offshore" environments). Similarly, the presence of membranes increases while the number of specimens without ornamentation decreases in the succession. The vesicle diameter neither shows a significant variation nor a trend. In this transgressive section, the variations of the ornamentation are correlated to each other and contradict the usual taxonomical scheme in which the four genera *Caldariola*, *Cymatiogalea*, *Priscogalea* and *Stelliferidium* are described.

In this study, the positive correlation between process length and the increase of the ornamentation is interpreted as a morphofunctional character of the processes. Indeed, the progressive increase in process size probably lead to the development of basal striae to increase the process stability. This hypothesis would imply that the taxonomical relevance of striae is lower than previously thought, as underlined by Rasul (1974).

The growth of dinoflagellates processes has been observed in laboratory experiments (Kokinos & Anderson, 1995). A large spectrum of morphological variations is observed within a single species, especially the growth of modern dinoflagellate cyst processes is highly variable. The growth is thought to depend on several environmental parameters of which the most important seems to be salinity. These parameters probably control the breakdown of dinoflagellate membranes and the maturity reached by the dinoflagellate cyst during their formation. Processes are thus the most variable morphological parameter in dinoflagellate cysts, and probably at least partly in relation to salinity. Applied to galeate acritarchs, such a scheme would allow new interpretations of their morphological evolution and propose an alternative view to the classical taxonomy of these organisms. Process growth and ramifications probably represent a specific response to environmental changes, here thought to be salinity variations. However, such an hypothesis needs to be tested by further studies in stratigraphical frames with an accurate control of environmental parameters.

B – Lateral distribution of acritarchs : an example in the Gorstian of Gotland (Stricanne, Munnecke, Pross, Servais, in press)

The island of Gotland (Sweden) represents an important area for the study of Silurian palaeoenvironments of the palaeocontinent Baltica. Protected from tectonic stress and deep burial, Silurian sediments yield a great quantity of very well preserved fossil palynomorphs. The most detailed study concerning acritarchs of this area was carried out by Le Hérissé (1989) who evaluated the influence of palaeoenvironmental conditions on acritarch populations, together with a large taxonomical review. In other areas and time intervals other studies tried to reconstruct the lateral distribution of acritarchs along inshore-offshore (=proximal-distal) transects. These qualitative investigations determined that the genera and species diversity was probably correlated with sedimentary facies. However, few quantitative approaches were proposed to assess these models of distribution.

In the present study, such an approach (with absolute and relative values) has been tentatively introduced to better characterise the acritarch distribution in Gorstian sediments (upper Silurian) of Gotland. Eight localities have been investigated along an isochronous inshore-offshore transect. According to geochemical studies (e.g., Samtleben et al., 2000), the sedimentary facies of this transect have been deposited during a humid climate period, characterised by a significant input of terrigenous material.

Our results are in agreement with the observations of previous studies, showing a progressive increase of acritarch proportions towards distal facies while the percentages of sphaeromorphs decreases. The other palynological components (e.g., prasinophytes, chitinozoans) do not show any relevant trend. Process-bearing acritarchs also show an increase of the absolute values towards offshore environments, as well as an increase of the diversity. At the genus level, acritarchs show various distribution patterns. Among the most abundant genera, the percentages of *Micrhystridium* and *Dilatisphaera* are more important in proximal facies whereas *Evittia* and *Percultisphaera* are more represented in distal facies. Additionally, the three morphotypes of the genus *Micrhystridium* (short processes, *M. stellatum* s.l., long and ramified processes) show a specific distribution. The morphotypes with short processes show a larger abundance in proximal than in distal facies. The morphotypes with longer processes show an inverse scheme with higher percentages in distal than in proximal facies, whereas high percentages of *M. stellatum* s.l. are represented in the whole transect without any significant trend.

These results confirm those of previous studies on Ordovician and Silurian acritarch distribution. Although a correlation exists between the occurrence of some genera and the depositional environments, no attempt to characterise each palaeoenvironment with a set of given species is made (such as in Dorning & Bell, 1987). *Micrhystridium* assemblages are typified herein by the process length. A morphological continuum between all species of this genus would indicate that continuous palaeoenvironmental changes probably influence the ornamentation of these organisms. The potential use of acritarch assemblages, at the genus level, as a tool for the reconstruction of palaeoenvironments is thus confirmed.

C – Vertical distribution and climate variations : an example in the Late Silurian of Gotland (Stricanne, Munnecke, Pross, submitted)

The Silurian was considered for many years as a warm period without significant environmental changes, but recent studies brought new evidence of large climatic changes during this time. Most of these changes have been deduced from recurrent positive $\delta^{13}C$ and $\delta^{18}O$ excursions. The $\delta^{13}C$ values are generally interpreted as indices for bioproductivity changes while $\delta^{18}O$ values are probably linked to salinity and/or temperature variations. During the Ludlow (upper Silurian), the strongest positive isotope excursion of the whole Phanerozoic occurs with values for the $\delta^{13}C$ up to 12‰ and for $\delta^{18}O$ up to 4‰. According to Bickert et al., (1997) low isotope values are attributed to humid climatic periods, higher values to more arid climate at low latitudes. At the very beginning of the isotope excursions, a progressive turnover of numerous benthic organisms (e.g., conodonts, trilobites) occurs while pelagic or hemipelagic organisms are affected later.

However, in this time slice no investigation has been conducted on acritarchs, regarding these pronounced environmental changes. In the lower Silurian of Gotland, Gelsthorpe (in press) quantified the progressive turnover of acritarchs and highlighted that acritarchs are probably sensitive to climatic changes. As these organisms would live in surface waters, a quantitative approach (absolute and relative values) would allow to better understand the active mechanisms during the isotope excursion. Therefore, our study concentrates on quantitative variations of upper Silurian palynomorphs of Gotland across the excursion, interpreted as a transition from humid to arid conditions.

The major part of palynomorphs in this time interval is represented by process-bearing acritarchs and sphaeromorphs. In all palynomorph categories, no significant variations are observed in both absolute and relative values during the humid period. With the development of the isotope excursion, higher proportions of spores and cryptospores are represented while lower percentage values typify the development of marine palynomorphs. Within acritarch groups, the reduction in absolute values is mostly shown by acanthomorphs and polygonomorphs. At the genus level, the same pattern of reduction in absolute values is shown but several acritarch genera show significant differences in their percentages. During the humid period (low isotope values), several acritarch genera with prominent ornamentation (e.g., *Evittia*) are well represented. With the increase of the isotope values during the arid period, the assemblages are restricted to only a few number of genera, such as *Micrhystridium*, *Veryhachium* and *Eupoikilofusa*. At the humid-arid transition, an distinct succession of abundance peaks of several genera is observed. The morphotypes distribution in *Micrhystridium* and *Veryhachium* is also very particular, with abundant ornamented forms during the humid and less-ornamented forms better represented during the arid period.

The major changes in acritarch populations take place during the development of the isotope excursion. The decrease in diversity observed in previous studies accompanies the strong reduction in absolute values as well as the dramatic change in dominant groups in acritarch assemblages. These data indicate a reduction of ocean bioproductivity during the isotope excursion, and show that the positive $\delta^{13}C$ excursion cannot be the result of enhanced bioproductivity. Therefore, our results confirm the model of Bickert et al. (1997) who explain the excursion by changes in oceanic circulation rather than by productivity changes. However, according to Bickert et al., (1997) the time of high isotope values should be characterised by enhanced salinities. The observed reduction of ornamentation within the *Micrhystridium* and *Veryhachium* during this time may be compatible with a strong increase of salinity, when compared to recent studies on Quaternary dinoflagellates (Ellegaard et al., 2002).

In general, our results confirm that acritarchs may be sensitive to palaeoenvironmental changes. Combined with other palynomorphs, acritarch distribution would represent a powerful tool for the definition of Palaeozoic ocean circulation and climatic models.

X / Conclusions and perspectives

A recurrent problem for acritarchs is that the classification of many taxa still needs a significant review, of which the importance is different among the various groups. New methodologies are helpful to solve taxonomical problems. The classification *via* multivariate statistics is interesting because it provides a quantitative background to taxonomical reviews, as it has been shown for the galeate acritarchs and for the genus *Nellia*.

A clear taxonomy facilitates all further applications, such as biostratigraphy or biodiversity studies. However, our preliminary study on the acritarch biodiversity in the Ordovician shows that numerous problems still exist, mostly because of a lack of a consistent taxonomy.

Other approaches can be proposed in order to better understand biological apsects of acritarchs. Well known in modern ecology, the study of acritarch populations (as for galeate acritarchs) represents a promising new approach, especially in inshore-offshore transects, where acritarch populations show specific distribution patterns. Our studies in the upper Silurian of Gotland initiate further investigations because the distribution patterns of the acritarchs should be necessarily well known using these palynomorphs for palaeoceanographical or palaeoclimatical reconstructions in the Lower Palaeozoic.

The set of articles presented in this work demonstrates that acritarchs could represent an accurate tool for the reconstruction of Palaeozoic palaeoenvironments, in addition to the applications to the classical use of these microfossils for biostratigraphical purposes or for palaeogeographical reconstructions.

For future research the continuation of acritarch population studies in sections with a control of palaeoenvironmental conditions is important. As the factors influencing the acritarch morphology and their distribution are better known, such approaches may have a significant impact on oceanic circulation and/or climatic models. Another benefit of this research would be a better understanding of acritarch taxonomy, for which multivariate statistics yet represent an accurate tool together with the usual taxonomical review.

Hence, after the long period of qualitative works, the next turn of the research on palaeoecological aspects of acritarchs will probably need much more quantification. This could lead to a comparison between models of ornamentation growth in selected acritarch morphotypes and modern dinoflagellate in laboratory experiments where environmental parameters are controlled (e.g., salinity, temperature). Combined with classic studies on distribution, such works could also represent a significant test to better characterise palaeoecological aspects of acritarchs. The future of acritarch research necessarily needs a comparison with modern and fossil dinoflagellates.

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- **Stricanne, L.**, Servais, T., 2002. A statistical approach to classification of the Cambro-Ordovician galeate acritarch plexus. Review of Palaeobotany and Palynology, 118, 239-259.

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- Servais, T., **Stricanne, L.**, Montenari, M., Pross, J., 2004. Population dynamics of galeate acritarchs at the Cambro-Ordovician transition in the Algerian Sahara. Palaeontology, 47, 2, 395-414.

- **Stricanne, L.**, Munnecke, A., Pross J., Servais, T., in press. Acritarch distribution along an inshore-offshore transect in the Gorstian (lower Ludlow) of Gotland, Sweden. Review of Palaeobotany and Palynology.

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A statistical approach to classification of the Cambro–Ordovician galeate acritarch plexus

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Abstract

The investigation of large populations of galeate acritarchs recovered from the Late Cambrian to Early Ordovician of the Algerian Sahara allows the definition of 11 morphological criteria which may be useful for the differentiation of individual morphotypes. These parameters have been used for statistical analyses to understand better the classification of this important acritarch plexus. Following a critical evaluation of all parameters, five of them can be retained for multivariate and cluster analyses. The current taxonomic model, with a differentiation into the four genera *Caldariola*, *Cymatiogalea*, *Priscogalea* and *Stelliferidium*, cannot be maintained. The most important variables appear to be the process length and the presence/absence of ramifications of the distal end of the processes. A provisional four cluster model is proposed to classify the galeate acritarchs from the Algerian assemblages. This study is a first step in the process of investigating the potential use of multivariate statistics in galeate acritarch classification and may serve as a model for future studies to understand acritarch taxonomy.

Keywords: acritarchs; Cambrian; Ordovician; statistics; factor analysis; taxonomy

1. Introduction

The basis of classification in both the Linnaean system and the modern system of taxonomy is the species, which is the basic rank in both botanical and zoological nomenclature. Palaeontologists have difficulties applying the definition of a biospecies to fossils, as determination of genetic compatibility is no longer possible. The classification is therefore generally a parataxonomy based essentially on morphological criteria. The basic taxonomic unit in palaeontology is thus, in general, the morphospecies. However, genetic differences are not always expressed morphologically. On the other hand, a different morphology is not necessarily a signal of a genetic difference, but very often the result of changing ecological conditions (genotype versus phenotype).

Several classical examples of parataxonomy exist in palaeontology, and especially in palaeobotany and palynology, where the names of detached plant parts, such as leaves or cones, and the names of the micro- or megaspores are commonly different to the name of the whole plant.

Another special case in palaeontological nomenclature is that of the organic-walled micro-

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phytoplankton. For example, during the life-cycle of the dinoflagellates, involving sexual reproduction and cyst formation, a wide range of morphologies can be observed. However, in general, only the resting cyst can be fossilised. The thecate, motile cells are generally unknown as fossils. As recent cultural experiments have shown (e.g. Kokinos and Anderson, 1995), the level of morphological maturity of the encysting cell, and thus the morphology of the resting cysts which may be preserved in the sediment, primarily depends on how much development occurs before rupture of the expanding outer membrane during the life-cycle of the dinoflagellate. In addition, the resting cyst morphology is greatly influenced by parameters such as temperature and salinity (e.g. Dale, 1996; Ellegaard, 2000). A single dinoflagellate biospecies can thus produce a wide range of morphologies which might be attributed to a large number of taxonomic morphospecies. On the other hand, it is also possible to observe similar cyst morphologies from completely different species. A debated question in the classification of fossil phytoplankton is thus the species concept.

The group *Acritarcha* is generally interpreted as the major part of the microphytoplankton in late Precambrian and Palaeozoic oceans. Proposed originally (Evitt, 1963) as an informal, utilitarian category to group palynomorphs of unknown biological affinities, the acritarchs can be considered as a palaeontological 'catch-all' category of palynomorphs with unknown affinity, which probably include different protists such as the dinoflagellates or different divisions of the green algae, such as the Prasinophyta, Chlorophyta or Euglenophyta (Servais et al., 1997). Acritarch classification is generally purely phenetic. Acritarchs are grouped into different boxes by simple morphological comparisons. The criteria used as dividers for the generic, specific and infraspecific levels greatly vary from one author to another. The search for important characters to delimit individual taxa is still a debated question between acritarch workers (Servais, 1996).

Statistical techniques are potentially useful tools to evaluate the morphological criteria for acritarch classification. However, statistical analyses of acritarch morphology are rare in the literature. Pioneer studies were the publications of Deunff and Evitt (1968) and Gardiner and Vanguestaine (1971), who used bivariate analyses (measurement of the central body diameter and the process length (PL)) to explain the variability of morphotypes of *Tunisphaeridium* and *Micrhystridium dissimilare*, respectively. Such bivariate analyses have subsequently been used in several papers dealing with acritarch taxonomy, showing very often that previously separated morphotypes belong to a single entity, once they are observed in larger populations. Typical examples for such investigations are the studies on the genera *Frankea* (Servais, 1993) and *Dicrodiacrodium* (Servais et al., 1996).

Kalvacheva and Chobanova (1974) were the first to attempt biometrics using histograms and χ^2 tests on a population of rectangular *Veryhachium*, with the main conclusion that all investigated specimens belong to the same unit. χ^2 tests, together with bivariate analyses and frequency histograms, were also used by Vecoli et al. (1999) to analyse *Frankea* populations from different localities. Molyneux and Leader (1997) introduced semi-quantitative values in their dataset. These authors used not only bivariate measurements, but also histograms of the frequency of concave, straight and convex sides to understand the morphotypes of *Coryphidium*. So far, the most complex attempt to support acritarch taxonomy with the help of statistical methods is the study of Wauthoz and Gérard (1999) who used principal component analysis, cluster analysis and discriminant analysis to classify 62 specimens of *Domasia*.

The aim of the present work is to understand, with the help of statistical analyses, the taxonomy of the galeate acritarch plexus. The investigations are based on large populations from the Algerian Sahara, from which the plexus was originally described. The galeate acritarchs are very important in the Late Cambrian and Early Ordovician at a world-wide level. However, their classification is confused so far.

The major objectives of this study are to evaluate critically all morphological criteria which can be considered to be useful for the classification of the galeates, and to try to find out if these param-

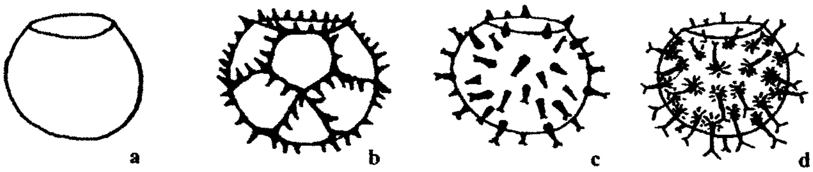

Fig. 1. Idealised line drawings of the four genera of galeate acritarchs. (a) *Caldariola*; (b) *Cymatiogalea*; (c) *Priscogalea*; (d) *Stelliferidium*. See text for explanation.

eters can be placed in a hierarchical order with the help of statistical methods. Of major interest for the palaeontologist is the question whether the galeate acritarch plexus can be divided by means of statistical analyses into individual morphotypes which may be used for biostratigraphical, palaeobiogeographical or palaeoecological purposes.

It is beyond the scope of the present paper to provide a stable classification scheme of the galeate acritarch plexus. This paper only tries to show that statistical methods may help to debate the question how highly variable acritarch morphotypes may be classified.

2. The galeate acritarchs

The term 'galeate' acritarchs was proposed by Servais and Eiserhardt (1995) for those Lower Palaezoic taxa characterised by a hemispherical vesicle outline and a large opening (pylome) closed by an operculum. The ornamentation of the vesicle can be by various means: processes, membranes, and/or sculptural elements. According to the distribution of these ornaments on the vesicle surface, four genera have been used to subdivide the galeate plexus (Fig. 1). The genus *Caldariola* Molyneux in Molyneux and Rushton (1988) shows no ornaments and, thus, represents the basic form: a smooth vesicle (Fig. 1a). *Cymatiogalea* Deunff, 1961 is characterised by a vesicle surface that is divided into polygonal fields, which may be interpreted as a para-tabulation (Fig. 1b). This second genus has been emended several times (Deunff, 1964; Deunff et al., 1974; Rasul, 1974). The third genus, *Priscogalea* Deunff, 1961, is a galeate taxon with processes distributed at random, but without polygonal fields and without membranes (Fig. 1c). This latter genus has been emended by Martin (1973) and by Rasul (1974). *Stelliferidium* Deunff et al., 1974 is characterised by striations that radiate away from the base of the processes (Fig. 1d).

As pointed out by Servais and Eiserhardt (1995), this classification scheme into four genera is not without problems. First of all, there are so many emendations by workers using different criteria that the taxonomic concept of the individual genera is no longer clear. At the specific level classification is even more complicated. A literature review shows that 83 species have been described so far (Table 1). Due to the confused state of the taxonomy at the generic level, it is presently possibly to assign some of these species to different genera. Many species have indeed been placed in two or more genera according to different interpretations of the hierarchy of the morphological criteria or due to different observation conditions. For example, some taxa, such as *Stelliferidium stelligerum* (Gorka, 1967) Deunff et al., 1974, show both polygonal fields and the striations radiating away from the process bases. Thus, the species could be placed in both *Stelliferidium* and *Cymatiogalea*. On the other hand, if the observation technique does not allow recognition of the striate ornamentation typical of *Stelliferidium*, such specimens could also be placed in *Priscogalea* (compare Servais and Eiserhardt, 1995, pl. 5, figs. 3 and 4).

In addition, it is possible to consider some taxa as representing extreme poles of the complete plexus of galeate forms, and it is imaginable to find all kinds of intermediates between these poles (Servais and Eiserhardt, 1995, Fig. 1). Several authors published the presence of 'intermediate passages' between individual species and even genera. Intermediates between smooth (*Caldariola*-type) and striate (*Stelliferidium*-type) galeate forms

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Table 1
List of galeate acritarch species described in the literature, including the authors of the original description and the name of the genus to which the species is presently attributed

Species	Author(s), Year	Actual position
alandicum	Tynni (1982)	*Stelliferidium*
ancora	Paris and Deunff (1970)	*Cymatiogalea*
anomalum	Di Milia et al. (1989)	*Stelliferidium*
apertum	Burmann (1970)	*Stelliferidium*
aspergilla	Martin and Dean (1988)	*Cymatiogalea*
barbara	Deunff (1961)	*Priscogalea*
bellicosa	Deunff (1961)	*Cymatiogalea*
bifurcata	Timofeev (1959)	*Cymatiogalea*
bouvardii	Martin (1973)	*Cymatiogalea*
brevipalmatum	Albani (1989)	*Stelliferidium*
carinatum	Vavrdová (1982)	*Stelliferidium*
catherinae	Paris and Deunff (1970)	*Cymatiogalea*
chevronensis	Vanguestaine (1974)	*Priscogalea*
cortinulamorphum	Paalits (1995)	*Stelliferidium*
cortinulum	Deunff (1961)	*Stelliferidium*
crassa	Umnova (1975)	*Cymatiogalea*
crassula	Vavrdová (1990)	*Cymatiogalea*
cristata	Downie (1958)	*Cymatiogalea*
cuvillierii	Deunff (1961)	*Cymatiogalea*
cuvillierii fucata	Martin (1973)	*Cymatiogalea*
cylindratum	Rasul (1974)	*Stelliferidium*
decora	Umnova (1971)	*Priscogalea*
dentalea	Paalits (1992)	*Cymatiogalea*
deunffii	Jardiné et al. (1974)	*Cymatiogalea*
distinctum	Rasul (1974)	*Stelliferidium*
diversita	Rasul (1974)	*Cymatiogalea*
echinata	Salujha et al. (1971)	*Priscogalea*
fascicularis	Yin (1985)	*Cymatiogalea*
fimbriata	Volkova (1990)	*Cymatiogalea*
fimbrium	Rasul (1974)	*Stelliferidium*
furcatum	Deunff (1961)	*Stelliferidium*
gautierii	Martin (1973)	*Stelliferidium*
gemmata	Vavrdová (1978)	*Cymatiogalea*
geometrica	Di Milia et al. (1989)	*Cymatiogalea*
glabra	Martin (1973)	*Caldariola*
gorkae	Rauscher (1974)	*Cymatiogalea*
granulata	Vavrdová (1966)	*Cymatiogalea*
grumosa	Aristova (1980)	*Priscogalea*
hunjiangensis	Yin (1985)	*Cymatiogalea*
ianischewskyi	Timofeev (1959)	*Cymatiogalea*
levis	Jardiné et al. (1974)	*Cymatiogalea*
margaritata	Deunff (1961)	*Cymatiogalea*
membrana	Rasul (1974)	*Cymatiogalea*
membranacea	Naumova (1950)	*Cymatiogalea*
membranispina	Deunff (1961)	*Cymatiogalea*
messaoudensis	Jardiné et al. (1974)	*Cymatiogalea*
minor	Timofeev (1959)	*Cymatiogalea*
modestum	Gorka (1967)	*Stelliferidium*
multarea	Deunff (1961)	*Cymatiogalea*
multiclaustra	Deunff (1961)	*Cymatiogalea*
operculata	Timofeev (1959)	*Priscogalea*
ornata	Pöthé de Baldis (1974)	*Priscogalea*

Table 1 (*Continued*)

Species	Author(s), Year	Actual position
paradoxa	Yin and Li (1978)	*Cymatiogalea*
parva	Vecoli (1996)	*Cymatiogalea*
parvivela	Di Milia (1991)	*Cymatiogalea*
perforata	Uutela (1989)	*Priscogalea*
philippotii	Henry (1966)	*Stelliferidium*
pingiculum	Martin and Dean (1988)	*Stelliferidium*
plenae	Fanderflit in Umnova and Fanderflit (1971)	*Priscogalea*
primordialis	Yin (1985)	*Priscogalea*
prisma	Martin (1973)	*Priscogalea*
procuvillierii	Paalits (1995)	*Cymatiogalea*
promptusa	Yin (1985)	*Priscogalea*
ramosa	Di Milia et al. (1989)	*Cymatiogalea*
redonensis	Paris and Deunff (1970)	*Stelliferidium*
regularis	Yin (1985)	*Cymatiogalea*
serrata	Naumova (1950)	*Priscogalea*
simplex	Deunff (1961)	*Stelliferidium*
spinata	Yin (1995)	*Cymatiogalea*
stelligerum	Gorka (1967)	*Stelliferidium*
striatulum	Vavrdová (1966)	*Stelliferidium*
stylifera	Umnova (1971)	*Cymatiogalea*
suecica	Eisenack (1959)	*Cymatiogalea*
testudinis	Yin and Li (1978)	*Cymatiogalea*
timofeevii	Deunff (1961)	*Stelliferidium*
trevisanii	Di Milia and Tongiorgi (1993)	*Cymatiogalea*
trifidum	Rasul (1974)	*Stelliferidium*
vanguestainei	Connery and Higgs (1999)	*Cymatiogalea*
velatum	Vecoli (1996)	*Stelliferidium*
velifera	Downie (1958)	*Cymatiogalea*
virgulta	Martin and Dean (1988)	*Cymatiogalea*
wironia	Paalits (1992)	*Cymatiogalea*
zagoriensis	Deunff (1977)	*Cymatiogalea*

have, for example, been discussed by Tongiorgi in Bagnoli et al. (1988). Servais and Molyneux (1997) illustrated the passage from smooth specimens to others with polygonal fields (*Cymatiogalea*-type). Such observations lead to various interpretations of the classification concept of the galeate plexus. In the original description of the two genera *Cymatiogalea* and *Priscogalea*, Deunff (1961) adopted the first concept by classifying all taxa from the Algerian Sahara into two units. By integrating further results from material of various localities, but mostly by considering new data from Poland and France, Deunff et al. (1974) proposed another subdivision of the plexus into two genera, *Cymatiogalea* and *Stelliferidium*, while *Priscogalea* became a junior synonym of *Cymatiogalea*. In this classification scheme the striate ornament was considered as an important criterion for classification at the generic level. At the same time, Rasul (1974), however, used but modified the two genera, considering striate ornaments to be of infrageneric significance. Subsequently, various concepts were used by individual workers without consistency (for a revision see Servais and Eiserhardt, 1995). Molyneux in Molyneux and Rushton (1988) first reviewed the problem and added *Caldariola* to the plexus. As noted by Servais and Eiserhardt (1995), the complete galeate plexus can thus be divided into four, three or two units, depending on the taxonomic ideas adopted. It is even possible to go further: the observation of large populations including all parameters used for the generic distinction suggests that the complete plexus belongs to a single entity, as all intermediates between individual morphotypes can be found. Considering this con-

Table 2
List of parameters commonly used in the literature

Quantitative parameters	Semi-quantitative parameters	Qualitative parameters
Vesicle	**Vesicle**	
Vesicle diameter$_1$	Vesicle surface texture$_2$	
Overall size$_{10}$	Vesicle colour$_2$	
Pylome		**Pylome**
Pylome diameter$_1$		Pylome outline geometry$_2$
Operculum		**Operculum**
Operculum diameter$_2$		Presence of the operculum$_2$
		Operculum outline geometry$_5$
Processes	**Processes**	**Processes**
Length of processes$_2$	Number of processes$_1$	Processes bifurcation$_1$
Thickness of processes$_6$	Process filled/hollow$_1$	
Length of pinnae$_8$	Number of processes/polyg. side$_2$	
'Antapical' Process length$_{11}$		
Distance between processes$_9$		
Membrane		**Membrane**
Membrane height$_2$		Membrane definition$_1$
Polygonal fields	**Polygonal fields**	**Polygonal fields**
Size of polygonal fields$_5$	Number of polygonal fields$_7$	Polygonal field definition$_1$
	Field geometry$_5$	
	Tabulation pattern$_6$	
		Striae
		Striae definition$_1$

References are given for the first use of each parameter. 1: Downie (1958); 2: Deunff (1961); 3: Henry (1966); 4: Vavrdová (1966); 5: Martin (1973); 6: Rasul (1974); 7: Vavrdová (1982); 8: Martin and Dean (1988); 9: Tongiorgi in Bagnoli et al. (1988); 10: Vavrdová (1990); 11: Vecoli (1996).

fused state of taxonomy, it seems evident that a stable classification scheme cannot yet be provided. However, for the above mentioned reasons it appears highly interesting to try to approach the classification of the group with statistical techniques.

It is evident that the 83 species described are palaeontological morphospecies, divided arbitrarily into four morphogenera. Most of these species are described on the basis of a limited number of specimens and many without a comparison with previously described morphotypes. It is therefore likely that many species are synonyms.

3. Geological setting, material and methods

The material used in this study comes from the Cambro–Ordovician transition in the borehole NI 2 of the Algerian Sahara. The borehole has been drilled in the area of Hassi-Rmel, some 400 km south of Alger. Galeate acritarchs have been measured from six samples from the borehole at the following depths: 3065.3 m, 3060.8 m, 3056.5 m, 3053.9 m, 3039.8 m and 3029.6 m. The precise location of the borehole, an introduction to the regional geology and to palynological studies can be found in previous publications, as this borehole and other drillings from this area have been extensively investigated for acritarchs since the late 1950s. One of the first publications on acritarchs from this area was Deunff's (1961) investigation, which included the description of the galeate taxa *Cymatiogalea* and *Priscogalea*. Therefore, this area can be considered as the type-locality of the galeates. Subsequent publications of the richly diversified and well preserved acritarch assemblages are the papers of Deunff (1964), Combaz (1967, 1968) and Jardiné et al. (1974). The borehole Nl 2 has recently been reinvestigated by Vecoli (1999). For a general understanding of the geology of the area, the reader is referred to Legrand, 1973, 1985 (and references therein).

Standard palynological techniques were used, including sieving with a 12 µm mesh. The material was observed using transmitted and reflected light on Zeiss Axioskop 2 and Zeiss Axioplan 2 microscopes. Microphotographs were taken on a Zeiss Axioplan 2 microscope with a Plan-Apochromat 63×/1.40 oil objective and on SEM. Image aquisition and measurements were all made in optical microscopy, partly using a Zeiss Axiovision 2.0 programme installed on a PC using a standard video camera. The material is housed in the collections of the Department of Palaeobotany and Palynology of Liège University.

4. Morphological criteria of galeates retained for statistical analyses

4.1. Parameters used for differentiation of galeate morphotypes in the literature

Before considering statistical analyses on the galeates, all parameters used for the description and distinction of morphotypes must be taken into consideration, including all criteria used for both specific and generic classification. As for all acritarchs, the criteria used are exclusively morphological characters. Table 2 indicates all parameters used in previous studies, with reference to the publications which they were first mentioned. These parameters can be divided into quantitative, semi-quantitative and qualitative criteria.

The two most frequently used parameters are quantitative: the vesicle diameter (VD) and the process length (PL). Fig. 2 illustrates a graph on

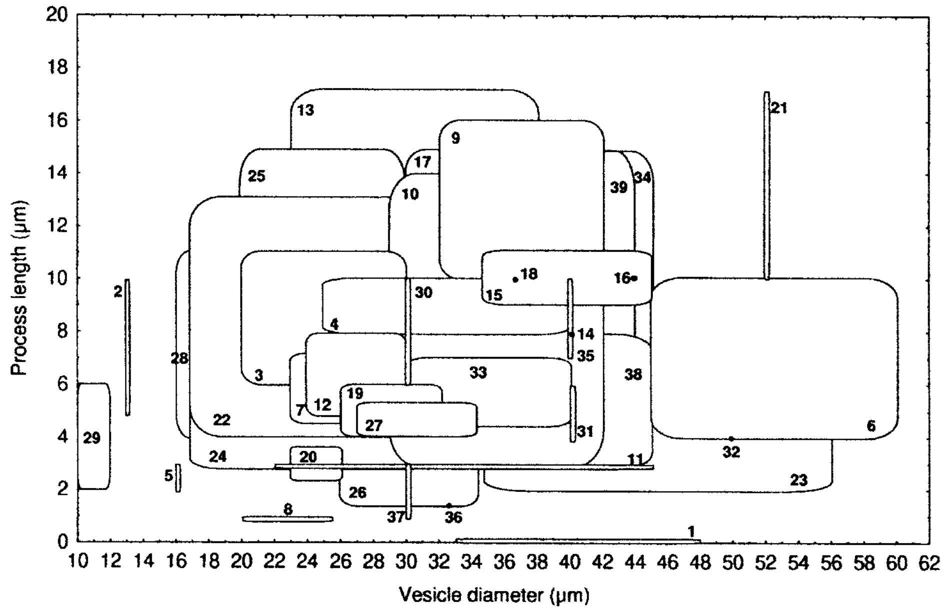

Fig. 2. Diagram showing the values of VD and PL of 39 species described in the literature. Plotted data are directly derived from the original descriptions or, if not available in the original definition, from other literature data. 1 – *Caldariola* morphotypes: *Caldariola glabra*. 2–24 – *Cymatiogalea* morphotypes: 2 – *C. ancora*; 3 – *C. aspergilla*; 4 – *C. bellicosa*; 5 – *C. catherinae*; 6 – *C. crassula*; 7 – *C. cristata*; 8 – *C. cuvillierii*; 9 – *C. deunffii*; 10 – *C. diversita*; 11 – *C. gemmata*; 12 – *C. gorkae*; 13 – *C. granulata*; 14 – *C. margaritata*; 15 – *C. membrana*; 16 – *C. membranispina*; 17 – *C. messaoudii*; 18 – *C. multarea*; 19 – *C. parva*; 20 – *C. parvivela*; 21 – *C. spinata*; 22 – *C. trevisanii*; 23 – *C. vanguestainei*; 24 – *C. virgulta*. 25–29 – *Priscogalea* morphotypes: 25 – *P. barbara*; 26 – *P. chevronensis*; 27 – *P. distincta*; 28 – *P. fera*; 29 – *P. perforata*. 30–39 – *Stelliferidium* morphotypes: 30 – *S. alandicum*; 31 – *S. apertum*; 32 – *S. carinatum*; 33 – *S. cortinulum*; 34 – *S. cylindratum*; 35 – *S. furcatum*; 36 – *S. modestum*; 37 – *S. redonensis*; 38 – *S. stelligerum*; 39 – *S. striatulum*.

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which these two parameters are plotted for 39 previously described species. The values plotted are those available from the original descriptions which include information on the VD and the PL. The graph illustrates that most of the galeate acritarchs have a VD between 20 and 45 μm, ranging from 10 to 60 μm. The PL varies generally from 2 to 15 μm, but ranges from smooth specimens (*Caldariola*) without outgrowths to processes with a length up to 17 μm. This graph clearly illustrates that there is a general overlap of the values, and it is almost impossible to distinguish separate morphotypes on the basis of these two parameters alone.

Other quantitative parameters used in the literature are the pylome and the operculum diameters. Besides total length, measurements of the processes include their thickness, the length of the terminal pinnae, and the distance between the bases of the processes. Additionally, some authors distinguished the length of 'antapical' processes or the length of processes around the pylome ('polar' processes). The height of the membrane and the diameter of the polygonal fields are other parameters frequently encountered in the literature.

Among the semi-quantitative parameters, vesicle surface texture and vesicle colour were introduced by Deunff (1961). The number of processes on the whole vesicle and along the side of a polygonal field can be counted. It has also been observed that some processes are hollow, while others are filled. The number of polygonal fields has been counted and some authors used the field geometry and the 'tabulation' pattern for classification purposes.

Qualitative parameters include the outline geometry of the pylome (polygonal, rounded, etc.) and operculum, as well as the presence/absence of the latter. The operculum may or may not be ornamented by concentric rings or other elements. Around the opening, a collar may be present, which may be striated or not. The distal termination of the processes has been used frequently to discern new taxa. The presence/absence of a membrane was considered to be important, as well as its morphology. Some articles also include a detailed description of the polygonal fields and of the striate ornamentation.

The literature review shows that the parameters are mostly used inconsistently. In addition, in some publications the importance of selected criteria has been exaggerated to allow new descriptions. It is likely that some of the parameters have a limited or no value for taxonomical investigations. Vesicle colour, for example, cannot constitute a taxonomic parameter, because the colouration of the organic matter in palynomorphs is a secondary phenomenon due to taphonomy and diagenesis of the sediments. The presence/absence of the operculum can also be a simple matter of preservation. Diagenesis and preservational aspects are very important. Many process terminations can be broken and most of the delicate membranes are generally destroyed in moderately or poorly preserved material. Microsculptural ornaments can also be modified by the depositional changes to the organic matter.

4.2. Parameters retained for statistical investigations

The aim of the present study is to approach all parameters of galeate morphology and to select those useful for classification, in order to understand and develop a hierarchy of characters with the help of statistical methods. Some parameters among those used in the literature cannot be used for statistical techniques. In addition, some values must be regarded critically, because their statistical analysis would lead to results which may be misinterpreted.

The selection in this study of some parameters is of course partly arbitrary. It is not always without problems and can surely be debated. It is important to consider that this study is a first approach, which can provide results which are valid for the investigated material, but which probably needs a revision when other galeate populations, displaying additional parameters, are investigated in detail.

In order to obtain reliable results from a statistical analysis, it is important to start with the distinction between continuous and discrete parameters and to control their relationship in order to avoid misinterpretations.

4.2.1. Continuous parameters

Although six classical quantitative morphological criteria can be measured (Fig. 3), only four of them can be used as continuous parameters in the statistical analysis. These four parameters used in this study are the VD, the PL, the ratio between PL and VD (PL/VD) and the total diameter (TD). The latter value is the sum of the VD and the PL (maximal value) of both sides of a specimen.

It is very important to remember that the VD measured (in most works in the literature and also in this study) is the diameter of the flattened specimen. As all specimens are no longer preserved in three dimensions, but flattened in more or less the same way (flattening of an almost spherical body), this parameter can be used for statistical analyses. However, the pylome diameter (PD) cannot be integrated in a statistical analysis, because practical measurements are not possible. Taphonomic aspects explain the difficulty of using this parameter: the galeate cysts can indeed show different positions in palynological slides. Only if the pylome is in polar view (view inside the vesicle) does the opening show its real dimension, which is identical to that of the operculum, if the latter is still attached or if it remains in the vesicle. However, if the flattened vesicle is laying in an oblique or in a perpendicular position to the plane of the palynological slide (lateral view of the vesicle), the pylome is crushed and may show a much larger value than that of the original dimension. In the material observed in this study, specimens which show the real dimension of the pylome (identical to the operculum size) represent less than 15% of the total number of measured specimens. For these reasons this parameter (PD) has not been used and all quantitative parameters related to the polar opening, such as the ratio PL/VD, cannot be employed. The values of 'antapical' and 'polar' (around the pylome) PLs were also not used here. In the present study, all processes were measured and an average of these values is used for the statistical dataset.

Other quantitative parameters used in the literature, such as the thickness of the processes, the length of pinnae, the membrane height, etc., have not been used in this study, because they are irrelevant for the material in this investigation and for most galeate acritarchs in general.

4.2.2. Discrete parameters

In addition to the quantitative values, some qualitative parameters can be selected for the statistical analysis (Fig. 3). Such parameters, used as bimodal values, are the absence/presence of polygonal fields (POL), the absence/presence of membranes (MBR), the absence/presence of striae (STR) and the absence/presence of ramifications at the distal ends of the processes (RAM). These discrete parameters were used as simplified bimodal (presence/absence) values, because it is difficult to recognise a clear order of differentiation within these criteria. For example, the membrane

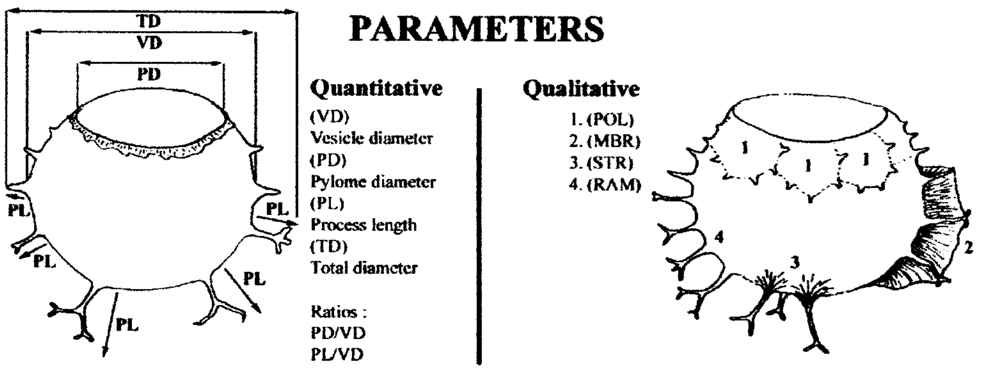

Fig. 3. Quantitative (continuous) and qualitative (discrete) parameters of galeate acritarch classification retained for the statistical analyses.

thickness and its morphology have been used commonly in the literature to distinguish individual morphotypes. However, it is difficult to include these values in a statistical analysis. On the other hand, the striae at the bases of the processes may show different microornamental elements, which are difficult to analyse statistically, as they are highly variable and generally impossible to qualify or quantify, not only on different specimens, but also on a same vesicle. The process ramifications also display great variability. Commonly used for the distinction of 'new' taxa in publications, including detailed descriptions of the morphology of the distal termination (bi-, tri-, or multifurcate, etc.), the ramifications may be highly variable within a single specimen and are difficult to place in a statistical dataset. In the present study, the morphology of the processes is thus simplified as a bimodal value: ramified or not. Although the absence/presence of polygonal fields has been introduced in the statistical database as a bimodal value, a further, semi-quantitative parameter related to the polygonal arrangement of the sculptural elements has been introduced.

4.2.3. Semi-quantitative parameter

The additional semi-quantitative parameter defined in this study is named ornamental structure (OS). As already discussed above, the galeate plexus often presents intermediate specimens between the different pre-defined morphotypes. For instance, Deunff (1961) defined *Cymatiogalea* as a morphotype with an "ornamentation constituted by processes (...) disposed according to polygonal areas on the surface of the vesicle". However, observation of the polygonal fields within the large populations of material from the Algerian Sahara leads to the conclusion that a continuous transition exists. This transition is not reflected by the current generic classification of galeates, which attributes morphotypes with polygonal fields to *Cymatiogalea* and those without the polygonal arrangement to *Priscogalea* or *Stelliferidium*. The transitional evolution of the OS is schematically presented in Fig. 4. According to this scheme, the appearance of the polygonal fields and their complexity can be coded according to an ordinal scale. The first level displays no processes and no ornament. The second level includes more or less distinguishable polygonal areas with a process at the corners of the fields. Additional steps may be observed with an increasing number of processes on the sides of the fields. Another level is represented by an irregular distribution of processes on the vesicle. As it is really difficult to define a graduate scale of growth for the polygonal fields, it has been attempted in this study to integrate this semi-quantitative parameter of OS in the statistical dataset in order to observe a possible signal. It is important to note that the OS closely related to the bimodal parameter of absence or presence of polygonal fields. This latter value has therefore been eliminated from future investigations.

The number of polygonal fields could be used as a further parameter. However, it is not employed here, because for most specimens it is not possible to count the total number of fields on a vesicle. The geometry of the polygonal fields was also not used because it may greatly vary from quadrangular to hexagonal on a single specimen, as indicated several times in the descriptions of *Cymatiogalea* morphotypes in the literature, as, for example, by Martin (1973) for the description of *Cymatiogalea cuvillierii fucata*.

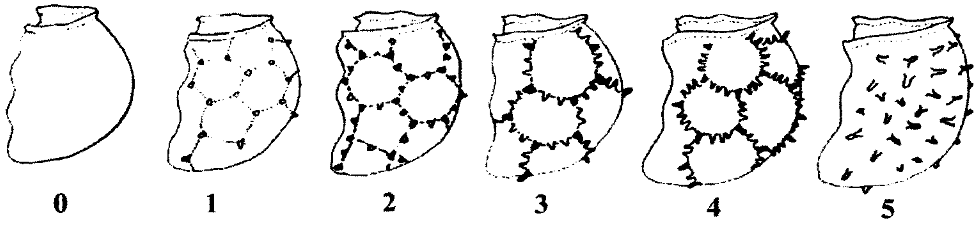

Fig. 4. Illustration of continuous variation of OS in galeate morphology.

Table 3
Spearman's rank correlation coefficient test

	VD	PL	PL/VD	TD
VD	1			
PL	0.141	1		
PL/VD	0.013	***0.9833***	1	
TD	**0.628**	***0.83***	**0.7386**	1

Table of r_s values, produced by the crossing of variables. Values indicated in bold and italics are those where distributions are the nearest. Values in bold are those where the distributions are partially correlated. The other values show only weak interrelationships.

5. Statistical analyses

5.1. Tests and methods used in this study

The six samples studied in this work all included high numbers of galeate acritarchs. Among them, the specimens which display all measurable parameters (perfectly flattened specimens without folds, presence of complete, unbroken processes, etc.) are used for the dataset. A total of 564 specimens were employed in the analyses, and for all of them the following 11 values were measured and/or coded: quantitative parameters: VD, PD, PL, TD, ratio PD/VD, ratio PL/VD; qualitative values: POL, MBR, STR, RAM; semi-quantitative value: OS.

As already mentioned above, the parameters related to the PD (PD and ratio PD/VD) are difficult to interpretate, and they were therefore excluded from the dataset. The presence/absence of polygonal fields has also been eliminated, as it is very close to the definition of the OS. It is possible that some of the other eight variables are linked. To avoid misinterpretations in the following multivariate analyses, non-parametric tests have been performed in order to detect whether these eight variables are really independent, and with the aim of establishing their degree of relation. Indeed, any repetitive information could deform the following multivariate analysis. The Spearman's rank correlation coefficient has been tested to control the quantitative data and χ^2 tests are used to verify the independence of the qualitative and the semi-quantitative parameters. A contingency coefficient has been calculated to understand the relations between two of the qualitative and one of the quantitative parameters.

The following statistical study was conducted in two steps. A factor analysis (principal component analysis method) was used to detect the structure in the relationships between variables, in order to classify and rank all variables and to define polarities. The second step is a K-mean analysis (dynamic cluster analysis) which was conducted to recognise structures in scatter plots, to minimise the variability within clusters and to maximise variability between clusters. Analysis of variance (ANOVA) test calculations (ratio of variances) were used to indicate the consistency between the variables (for more details on these methods, see also Wauthoz and Gérard, 1999).

5.2. Critical evaluation of statistical parameters

The most current rank correlation to determine the degree of linking between quantitative variables is the Spearman correlation rank coefficient ($-1 < r_s$ values < 1). If r_s is close to 1 (or -1), orderings become identical and the two variables are strongly correlated (inverse orderings if r_s is close to -1). If r_s is close to 0, orderings become uncertain and variables are independent.

Table 3 indicates the results of the Spearman's rank correlation coefficient of the four quantitative parameters VD, PL, PL/VD and TD. The distributions of the two variables PL and ratio PL/VD are very close and, thus, very probably related. For this reason, the parameter PL/VD has been eliminated and was not used for further

Table 4
Table of values of χ^2 calculated for every couple of qualitative variables

	OS	MBR	STR	RAM
OS	0			
MBR	2.9	0		
STR	6.685	2.848	0	
RAM	4.907	1.674	10.14	0

The value of χ^2 for the theoric distribution is 3.84 to the threshold of 5%. To the threshold of 5‰, it is 7.88.

Table 5
Values of χ^2 and contingency coefficient *C*, for the 2×2 tables crossing PL (two classes) and STR, as well as for PL and RAM

	PL vs STR	PL vs RAM
χ^2 values	58.64	104.45
C values	0.307	0.395

analyses. Another problematic parameter is the TD. As this variable is closely linked to both PL and VD, it is also best avoided for multivariate analyses. The two most valuable quantitative parameters for use in the following multivariate analyses are thus PL and VD.

As rank correlations cannot be used for qualitative variables, χ^2 tests have been performed to verify the assumption of linkages between these variables. Table 4 displays the χ^2 test performed on the semi-quantitative (OS) and the qualitative parameters (MBR, STR, RAM). The results indicate that a strong relationship exists between the presence/absence of the striae and the process ramification, but no relevant relation between the other parameters.

To compare the values of the quantitative parameters with those of the quantitative and the qualitative parameters, the contingency coefficient '*C*' has been calculated (Table 5). Although the χ^2 tests indicate that there is no correlation between PL and STR distributions (nor for the distributions of PL and RAM), the contingency coefficient $[C=\sqrt{\chi^2/(\chi^2+n)}]$ indicates a stronger relation between PL and STR than between PL and RAM. For this reason, the presence/absence of striae is not used in the following multivariate analyses.

Finally, a total of five parameters can be used for the multivariate methods: VD, PL, OS, RAM, and MBR.

Table 6
Multivariate analysis (factor analysis with principal component analysis)

	Factor 1	Factor 2	Factor 3
MBR	0.432	**−0.544**	**−0.487**
RAM	**0.792**	0.033	0.075
VD	0.230	**0.838**	−0.386
PL	**0.837**	−0.066	0.096
OS	0.693	0.103	**0.684**
Variance percentage	41%	20.33%	17.42%

Table showing the eigenvalues for each parameter.

5.3. *Multivariate analysis*

The multivariate analysis (factor analysis with principal component analysis extraction) indicates that three factors can be selected as they hold the most important part of the information, 78.75% of the total variance. As illustrated in Table 6, each factor can be interpreted as follows:

– factor 1 is best explained by the variables PL and RAM. Along this axis, morphotypes without processes are opposed to those with long and ramified processes and a large overall size;

– factor 2 is mainly explained by the variables VD and MBR. The two poles are represented by morphotypes with large vesicles without a membrane for the first pole and by specimens with a small vesicle and a large membrane at the other end of the axis;

– factor 3 is explained by the variables OS and MBR. This axis essentially opposes morphotypes with large membranes and no structural ornamentation to those with complex polygonal fields but without membranes.

Factor 1 is by far the most important, with 41% of the total variance. Factors 2 and 3 follow with 20.33 and 17.42%, respectively. The most important parameter to approach the variability of the 564 specimens observed in the six samples of the Algerian Sahara appears to be the PL.

Table 7
ANOVA test indicating the *P* values for each model of grouping

	2	3	*4*	*5*	6	7	8	9
MBR	1.3×10^{-3}	6×10^{-8}	1.5×10^{-9}	2.3×10^{-8}	1.5×10^{-7}	5.8×10^{-6}	1.8×10^{-6}	7.6×10^{-6}
RAM	0	0	*0*	*0*	0	0	0	0
VD	4.1×10^{-2}	1.4×10^{-7}	*0*	*0*	0	0	0	0
PL	0	0	*0*	*0*	0	0	0	0
OS	0	0	*0*	*0*	0	0	0	0

Table 8
Main parameters of the four cluster model from the K-mean analysis

	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Number of specimens	154	93	187	130
VD mean value	32.7	37.6	34.1	30.4
VD min–max	19 to 47.6	32.9 to 50.4	24 to 44.1	21 to 36.4
PL mean value	1.9	3.6	7.7	2.5
PL min–max	0 to 8	0.7 to 6	5.4 to 12.5	0.5 to 6.5
OS mean value	1	4	3	5
OS min–max	0 to 3	3 to 5	2 to 5	4 to 5

All means and range values (except for OS) in μm.

5.4. Dynamic cluster (K-mean) analysis

A K-mean (dynamic cluster) analysis was conducted to identify structures in scatter plots. This analysis is based on the same five parameters used for the factor analysis. Table 7 shows the results of the ANOVA test, where different clustering models (from 2 to 9) are evaluated. This analysis retains a four cluster model which provides an optimal grouping of all specimens observed in the six samples. The second best model is a distribution model into five clusters.

The specimens of the Algerian Sahara can thus be attributed to four morphological groups, which are defined by the statistical analysis using five of the 11 originally selected variables. Between these four groups it is possible to find some hinge elements. Table 8 indicates the attribution of the measured specimens into the four clusters and the boundaries of the latter. The four groups show no overlap and all specimens are attributed to one of the four clusters. Fig. 5 illustrates the four cluster model according to the different factors. The first graph illustrates the distribution of all specimens in the four clusters according to factors 1 and 2, while the second graph illustrates the same specimens distributed according to factors 1 and 3.

6. Interpretation

6.1. Interpretation of the clustering

Based on the 564 specimens from the six samples investigated, the results of the statistical analyses show that a classification scheme into four units (clusters) can be proposed. This is one of the possible models of classification, but other distributions into three or five clusters could also be considered.

The four clusters are defined by the data indicated in Table 8, using the five parameters that had been retained. The most important parameters appear to be PL and the absence/presence of ramifications at the distal end of the processes, but all other parameters also have their importance. Some groups of specimens seem to be related to others, as continuous variation between morphotypes can be observed. Such transitions indicate that these morphotypes cannot easily be differentiated and that they should not be attributed to different taxonomic units (genera or species). On the other hand, four clusters have been defined by the K-mean analysis. The clusters represent major separate units, which could be proposed as groupings, which may represent entities in a classical taxonomical scheme. It is interesting to compare this classification scheme into four groups with the classical palaeontological classification models of the galeates into up to four genera and into 83 species.

Cluster 1 includes 154 specimens. Processes are generally short and the structural ornamentation is limited to the levels 0–3 according to Fig. 4 (compare Table 8). Many of these specimens can be attributed to previously described species of the genera *Caldariola*, *Cymatiogalea* and *Stelliferidium*. Although the first two genera are generally used as separate entities in the classical classification schemes, it has been shown that transitions exist (Servais and Eiserhardt, 1995; Servais and

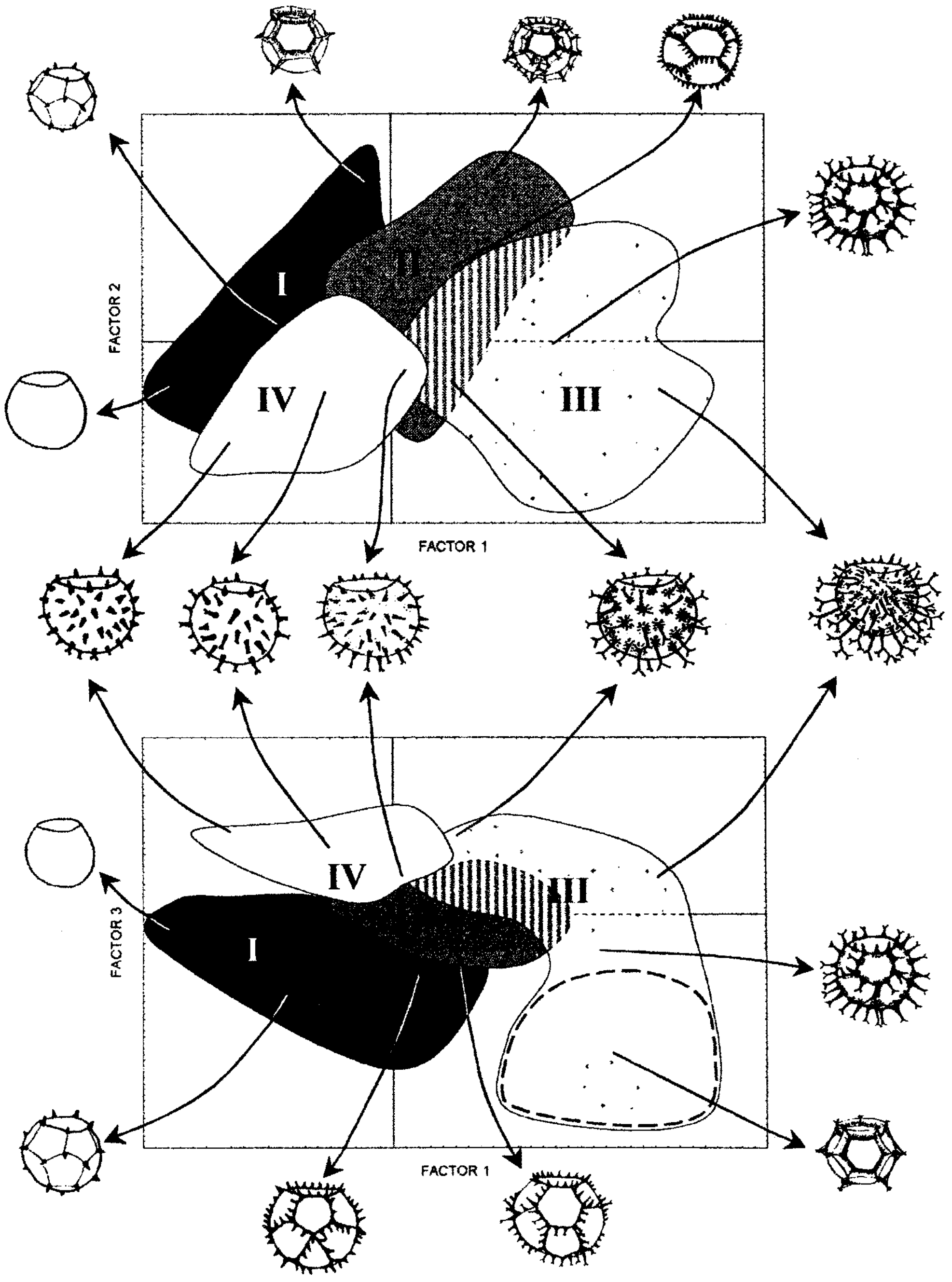

Fig. 5. Figure illustrating the four cluster model. A distinction of a fifth cluster is possible in cluster III.

Molyneux, 1997). In addition, it is well known that transitions between specimens with very short to somewhat longer processes may exist, as Rasul (1974), for example, mentioned in the description of his specimens of *Cymatiogalea cuvillierii* (Deunff, 1961) Deunff, 1964: 'all gradations exist between granules to short processes'. Many of the specimens in this study can indeed be attributed to *Caldariola glabra* (Martin, 1973) Molyneux in Molyneux and Rushton, 1988 (e.g. Plate I, panel

1). Other specimens show a transitional development of the polygonal fields and a progressive elongation of the processes (e.g. Plate I, panels 2–5). These morphotypes could be attributed to the following species described in the literature: *C. cuvillierii* Deunff, 1961 pro parte (subsp. *cuvillierii* autonym and subsp. *fucata* Martin, 1973), *Cymatiogalea ancora* Paris and Deunff, 1970, *Cymatiogalea dentalea* Paalits, 1992, *Cymatiogalea procuvillierii* Paalits, 1995, *Cymatiogalea vanguestainei* Connery and Higgs, 1999, and *Cymatiogalea levis* Jardiné et al., 1974. On the other hand, specimens without any structured distribution of the ornaments could be attributed to the following species: *Priscogalea barbara* Deunff, 1961, *Priscogalea perforata* Uutela, 1989, or, when striate ornaments at the bases of the processes are visible, *Stelliferidium modestum* Gorka, 1967, and *Stelliferidium redonensis* Paris and Deunff, 1970.

Cluster II includes some 93 specimens recognised in the populations of the six samples. Processes are generally longer than in cluster I (compare Table 8). Several of them could be attributed to the following species described in the literature: *Cymatiogalea cuvillierii* Deunff, 1961 pro parte, *Cymatiogalea virgulta* Martin in Martin and Dean, 1988, *Priscogalea prisma* Martin, 1973, and *Stelliferidium carinatum* Vavrdová, 1982.

The largest number of specimens (187) is attributed to cluster III which includes numerous specimens with the longest processes. These morphotypes can be attributed to species of *Cymatiogalea*, such as *Cymatiogalea aspergilla* Martin in Martin and Dean, 1988, *Cymatiogalea cristata* Downie, 1958 pro parte, *Cymatiogalea deunffii* Jardiné et al., 1974, *Cymatiogalea gorkae* Rauscher, 1974, *Cymatiogalea margaritata* Deunff, 1961, *Cymatiogalea membranispina* Deunff, 1961, *Cymatiogalea messaoudensis* Jardiné et al., 1974 pro parte, *Cymatiogalea multarea* Deunff, 1961, *Cymatiogalea multiclaustra* Deunff, 1961 pro parte, *Cymatiogalea spinata* Yin, 1995, and *Cymatiogalea velifera* Downie, 1958, or to species of *Stelliferidium*, such as *Stelliferidium alandicum* Tynni, 1982, *Stelliferidium furcatum* Deunff, 1961, *Stelliferidium simplex* Deunff, 1961, *Stelliferidium stelligerum* Gorka, 1967 and *Stelliferidium striatulum* Vavrdová, 1966.

Finally, cluster IV includes specimens with generally shorter and unramified processes, and a well developed OS (levels 4 and 5 of Fig. 4), including specimens close to *Cymatiogalea cuvillierii* Deunff, 1961 pro parte, *Cymatiogalea cristata* Downie, 1958 pro parte, *Cymatiogalea membranispina* Deunff, 1961 pro parte, *Cymatiogalea parva* Vecoli, 1996 and *Cymatiogalea parvivela* Di Milia, 1991 pro parte, *Stelliferidium cortinulum* Deunff, 1961, and *Stelliferidium velatum* Vecoli, 1996.

6.2. The impact of statistical analyses on galeate classification

The association in a same cluster of specimens which classically would be attributed to different galeate genera, as well as the observation of intermediate passages between previously distinguished morphotypes suggest that a complete revision of the taxonomy of the galeates is required.

In the classical method of galeate classification and in the classical way of describing new galeate taxa, the importance of individual parameters useful for the distinction of a morphotype is generally exaggerated. Some of the parameters selected by the authors have no or only limited weight, according to the statistical analyses realised in this work. These parameters should therefore possibly be avoided for the distinction of morphotypes. On the other hand, descriptions of galeate acritarchs that attempt to introduce all available parameters are rare. However, in order to understand the importance and independence of a selected taxon, it is important to consider all morphological criteria. Otherwise, only the morphological extremes will be described as separate taxa.

As only a part of the galeate plexus is usually present in an assemblage, not all the characters useful for classification are present in the dataset of an individual worker. This is the reason why discussion about the selection of morphological criteria still exists. The statistical analyses of the Algerian material show useful insights for a pos-


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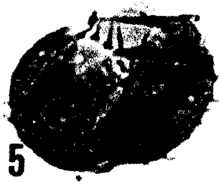
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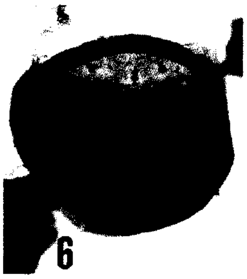
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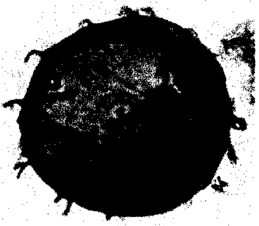
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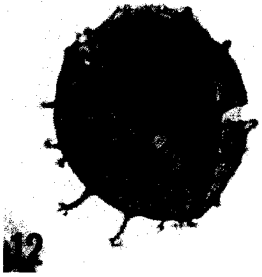
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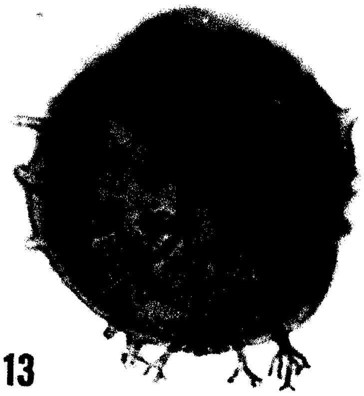
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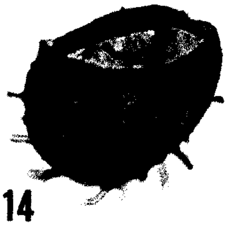
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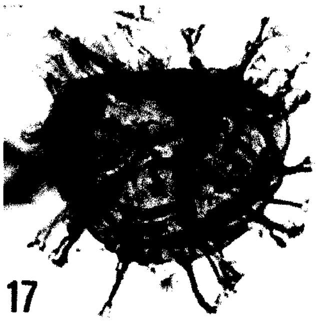
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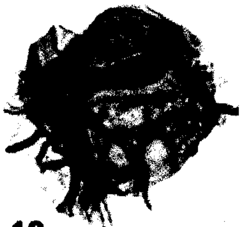
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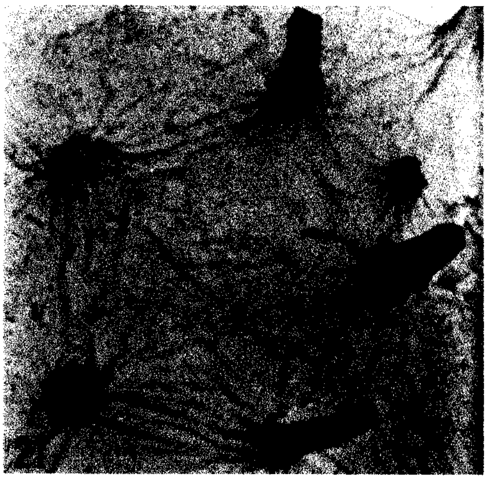

sible future classification scheme. However, it is important to note that the statistical analyses in this study are valid for the galeate material of the Algerian Sahara, but not necessarily for assemblages from other localities of the same or of a different age. It is evident that some criteria, which may be very important for the understanding of the complete plexus of galeate acritarchs, have not been introduced in the dataset used in this study, because some parameters are not relevant for the Algerian material. On the other hand, some parameters which may have a substantial importance have not been selected for the statistical methods. This shows clearly that the statistical techniques may help to understand the classification of the galeates, but that the methods are also limited, because of an arbitrary selection of the criteria. In future studies, all useful parameters for the description of galeate morphology must be critically evaluated, which may result in a modification of the galeate (para-) taxonomy.

Nevertheless, a series of important conclusions can be drawn following this preliminary work on a selected assemblage. First of all, it appears evident that a separation into four distinctive genera is not necessarily justified. All intermediates exist between the four genera as defined so far. *Caldariola* should be considered a synonym of *Cymatiogalea* and/or *Stelliferidium*.

Another important conclusion concerns the striate ornament. Are *Priscogalea* and *Stelliferidium* distinct units or do they belong to the same entity? The parameter of the striate ornamentation has been used by some authors as an important criterion for the distinction at a generic level (Deunff et al., 1974), while other authors limited this importance to the specific level (Rasul, 1974). It is important to note that striate forms occur more frequently when the PL is increasing. In addition, the correlation tests indicated that the presence of the striae on the vesicle surface can be correlated with the process ramification. The process illustrated in Plate I, panel 20, for example, clearly shows a complex ramification and a striation which extends up to the process stem. This relation between striate ornament, PL and process ramification implies that, during the formation of the cyst, these parameters are very probably linked and are related to the process

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Plate I. Galeate acritarchs from the Late Cambrian to Early Ordovician of the Algerian Sahara. All magnifications approximately ×725, except for panel 13, approximately ×1150, panel 20, approximately ×17000, panel 21, approximately ×8000.

1. specimen with a smooth vesicle attributable to *Caldariola* – slide no. 55141 (depth 3039.8 m) – England Finder Graticule Coordinates (EF):V 45.
2. specimen attributable to *Cymatiogalea cuvillierii* – 55141 (3039.8 m) – EF:W 34-3.
3. specimen attributable to *Cymatiogalea cuvillierii* – 55141 (3039.8 m) – EF:T 54.
4. specimen attributable to *Cymatiogalea cuvillierii* – 55141 (3039.8 m) – EF:R 38-4.
5. specimen attributable to *Cymatiogalea cuvillierii* – 55117 (3029.6 m) – EF:S 34-4.
6. intermediate specimen between *Caldariola* and *Priscogalea* – 55117 (3029.6 m) – EF:R 45.
7. specimen attributable to *Priscogalea* – 55141 (3039.8 m) – EF:S 35.
8. specimen attributable to *Cymatiogalea* sp. – 55117 (3029.6 m) – EF:K 39-4.
9. intermediate specimen between *Cymatiogalea* and *Stelliferidium* – 54512 (3056.5 m) – EF:E 36.
10. specimen attributable to *Cymatiogalea* – 55117 (3029.6 m) – EF:K 40-3.
11. specimen attributable to *Cymatiogalea* – 55117 (3029.6 m) – EF:Q 45-4.
12. specimen attributable to *Priscogalea* – 55141 (3039.8 m) – EF:V 37-1.
13. specimen attributable to *Stelliferidium* – 54512 (3056.5 m) – EF:F 42-3.
14. specimen attributable to *Stelliferidium* – 55117 (3029.6 m) – EF:L 44-2.
15. specimen attributable to *Stelliferidium* – 55141 (3039.8 m) – EF:X 43.
16. specimen attributable to *Priscogalea* – 55117 (3029.6 m) – EF:S 33-4.
17. specimen attributable to *Stelliferidium* – 55117 (3029.6 m) – EF:M 40.
18. specimen attributable to *Priscogalea* – 55117 (3029.6 m) – EF:W 65-4.
19. specimen attributable to *Stelliferidium* – 55141 (3039.8 m) – EF:V 53.
20. multifurcated process with pinnae ramification – depth 3053.9 m.
21. polygonal field with the characteristic striation at the base of each process – depth 3053.9 m.

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construction. This confirms the idea that the striae are not only an ornamentative element, but that they have a functional purpose related to pressure in the water column (Montenari and Servais, 2000).

A further question is the distinction or not of the two genera *Cymatiogalea* and *Stelliferidium*. Arguments that both units cannot be distinguished come from both the statistical analysis and from the observation on the microscope. The statistical analysis integrates specimens from both units into the same clusters. The observation on the Algerian material indicates in addition that numerous morphotypes commonly show processes which are disposed along the sides of polygonal fields and which show radial striations at the base of each process. A clear illustration for this kind of structure is indicated in a SEM microphotograph in Plate I, panel 21. Such structures have been described in *Stelliferidium modestum* (Gorka, 1967), *Stelliferidium carinatum* Vavrdová, 1982, *Cymatiogalea dentalea* Paalits, 1992, *Cymatiogalea procuvillierii* Paalits, 1995, *Cymatiogalea wironia* Paalits, 1992, and are probably also present in *Cymatiogalea vanguestainei* Connery and Higgs, 1999. Rauscher (1974) also illustrated a schematical model to indicate that the striate ornament of *Stelliferidum stelligerum* (Gorka, 1967) Deunff et al., 1974 may create a polygonal network all over the vesicle. The taxonomic value of the striae is thus debatable. It should not be neglected, but its significance at the generic level is maybe overstated. Their importance should be at least infrageneric, as proposed by Rasul (1974). The presence of the striae is very probably related to the process construction, which is very probably linked to ecological parameters (Montenari and Servais, 2000).

These arguments show that a distinction of the four galeate taxa can be debated. Intermediates exist between all genera and possibly all these forms belong to a same biospecies. However, it is at present impossible to make this statement, as the biological affinity of the galeate organism is unknown, although the recovered microfossils indicate many similarities in morphology and in spatial distribution to fossil and modern dinoflagellates.

7. Conclusions

Although the statistical methods have their limitations, it appears evident that the techniques are very useful and that they provide interesting insights in the classification of extremely variable organisms such as the galeate acritarchs.

The most important result from the observation of large populations of galeates from the Cambro–Ordovician boundary beds of the Algerian Sahara and their integration in a statistical analysis is the conclusion that the four galeate acritarch genera *Caldariola*, *Cymatiogalea*, *Priscogalea* and *Stelliferidium* should be debated. It is not evident to maintain the four units as separate taxa, as all intermediates exist.

As shown by factor analysis, the PL appears to be the most significant morphological parameter in the Algerian assemblages. The branching of the processes appears to be associated with PL, as is the presence of striate ornament at the base of each process. The second most important explanation of variability is characterised by the presence of membranes and the VD. Finally, a combination of the presence of membranes and development of the OS constitutes the third order.

It is well known that dinoflagellate species are very sensitive to environmental factors such as salinity or temperature, and the variations are very often reflecting process size and ramification (e.g. Kokinos and Anderson, 1995; Ellegaard, 2000). It is obvious that, during the life of the galeate organism, environmental conditions have affected some morphological features more than others. However, it is very difficult to attribute the variability of a given parameter to a selected environmental factor. It is therefore impossible to understand if the morphological differences in the galeates are expressions of genetic changes or are ecological variants (genotype versus phenotype). So far, no answer can be given using the multivariate analyses, as no accurate and independent data (e.g. geochemistry, indicating information on the palaeosalinity, palaeotemperature) are associated with the dataset.

The four cluster model proposed here can be regarded as a first outline of variability in the galeate plexus of the Algerian assemblages. On the basis of this model and with the help of additional statistical studies, the classical taxonomy used for the galeate plexus should be revised. In future analyses, it is necessary to approach the galeate variability with additional parameters (e.g. distance between processes for density indication, ratio between 'polar' and 'antapical' PL). Additional multivariate analyses (correspondence and discriminant analyses) may also help to better understand this fairly complex plexus of acritarchs.

Finally, it appears evident that a classification model that can reach a consensus will probably integrate both classical phenetics and modern statistical methods.

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Article II

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Article II – *"Reevaluation of the Upper Cambrian-Lower Ordovician acritarch Nellia acifera Golub & Volkova", accepted for publication in Neues Jahrbuch für Geologie und Paläontologie, Stuttgart, Germany*

Reevaluation of the Upper Cambrian-Lower Ordovician acritarch *Nellia acifera* GOLUB & VOLKOVA

Ludovic Stricanne, Tübingen, **Thomas Servais**, Villeneuve d'Ascq, **Nina Talyzina**, Villeneuve d'Ascq, and **Michel Vanguestaine**, Liège

with 3 figures, 1 Plate, 2 Tables

STRICANNE, L., SERVAIS, T., TALYZINA, N. & VANGUESTAINE, M. (200X): Reevaluation of the Upper Cambrian-Lower Ordovician acritarch *Nellia acifera.* [Auswertung des oberkambrischen-unterordovizischen Acritarchen *Nellia acifera*]. N. Jb. Geol. Paläont., 200x: xx-xx; Stuttgart.

Abstract

The acritarch genus *Nellia* GOLUB & VOLKOVA in VOLKOVA & GOLUB, 1985, is reported for the first time from the Cambrian/Ordovician of North Africa. Multivariate statistical analyses demonstrate the presence of a continuous morphologic variability between the species of *Nellia.* The relation of the genus *Nellia* to the other diacrodian acritarch genera is shortly discussed. The stratigraphical and palaeogeographical distribution of *Nellia* is summarized: the genus and its species are so far found in latest Cambrian and earliest Ordovician sections of Baltica, Avalonia and Gondwana, from localities in high latitudes (> 60°S) in the southern hemisphere.

Article II – *"Reevaluation of the Upper Cambrian-Lower Ordovician acritarch Nellia acifera Golub & Volkova", accepted for publication in Neues Jahrbuch für Geologie und Paläontologie, Stuttgart, Germany*

Zusammenfassung

Das Vorkommen der Acritarchengattung *Nellia* GOLUB & VOLKOVA in VOLKOVA & GOLUB, 1985, wird hier zum ersten Mal im Kambrium-Ordovizium Nordafrikas nachgewiesen. Multivariate statistische Analysen belegen eine durchgehende morphologische Variabilität zwischen den Arten der Gattung. Die Verbindungen zu anderen diakromorphen Acritarchen werden diskutiert. Die stratigraphische und paläogeographische Verbreitung zeigt, dass die Gattung *Nellia* und deren Arten bisher in Abfolgen des Oberen Kambriums und des Unteren Ordovizium von Baltica, Avalonia und Gondwana in Lokalitäten angetroffen wurden, die sich in hohen Breitengraden (> 60°S) der südlichen Erdhalbkugel befanden.

Résumé

Le genre d'acritarches *Nellia* GOLUB & VOLKOVA in VOLKOVA & GOLUB, 1985, a été retrouvé pour la première fois dans le Cambro-Ordovicien de l'Afrique du Nord. Des analyses statistiques multivariées démontrent l'existence d'une variabilité morphologique continue entre les espèces de *Nellia.* Les relations avec les autres acritarches diacrodiens sont discutées et les distributions stratigraphique et paléogéographique du genre *Nellia* sont résumées : le genre et ses espèces sont trouvés jusque maintenant uniquement dans le Cambrien Supérieur et l'Ordovicien Inférieur dans des séquences de Baltica, Avalonia et Gondwana, dans des localités qui se trouvaient à haute latitude (> 60°S) dans l'hemisphère sud.

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Introduction

The species is the key systematic unit for biology. However, in palaeontology direct biological affinities are not always easy to follow and palaeontologists therefore use the morphospecies, that is based essentially on morphological criteria, as the basic classification unit. By definition, acritarchs are microfossils that can not be firmly assigned to any group of living organisms (EVITT, 1963). Acritarchs are commonly described as species and genera, but in acritarch investigations, a "species" must be considered rather as a "morphotype" because the classification is purely based on morphology. Which characters are the most relevant for a differentiation of acritarch taxa is a subject of a continuous debate. Gross morphology, wall ornamentation, shape, excystment structure and size are criteria that have been commonly taken into account (e.g., LE HÉRISSÉ, 1989; SERVAIS, 1996).

Today it is widely accepted that most Palaeozoic acritarch morphotypes probably represented cysts of organisms that constituted the organic-walled microphytoplankton in the Palaeozoic oceans. Acritarch morphotypes may include dinoflagellates, prasinophycean, chlorophycean and zygnemaphycean algae, crustacean eggs and exoskeletal remains, spores, fungal palynomorphs, tintinnomorphs or remains of cyanobacteria (SERVAIS et al., 1997). Recently, the presence of dinoflagellate related taxa among Early Cambrian acritarchs has been estimated, but not yet proved, using combined morphological and biogeochemical (biomarker) analysis (MOLDOWAN & TALYZINA, 1998; TALYZINA et al., 2000).

Recent studies on modern phytoplankton, particularly on dinoflagellates, show that gross morphology and especially the size of dinoflagellate cyst processes may vary considerably inside one species (e.g., KOKINOS & ANDERSON, 1995; ELLEGAARD, 2000). The variation depends on several factors of which the level of morphological maturity of a cyst during its formation may represent the most relevant factor (KOKINOS & ANDERSON, 1995, p. 155). The difference in the process ornamentation of dinoflagellate cysts can also be caused by environmental factors. It has been demonstrated that in conditions of a higher salinity morphotypes of the same species have processes that are shorter, thicker and/or more membranous (ELLEGAARD, 2000).

The analysis of acritarch variability requires not only a great number of specimens and a good preservation of the palynomorphs, but includes necessarily the comparison with similar morphotypes from other areas and/or stratigraphical levels. However, most acritarch species and genera were originally described on the basis of a limited number of specimens and without considerations of morphological variability. This led to overlaps of diagnoses and to an enormous amount of species, some of which having a confusing taxonomy. The variability of several significant acritarch morphotypes was investigated in the last years by using bivariate or multivariate statistical analyses and the taxonomy of the investigated taxa has been reviewed. SERVAIS (1993), SERVAIS et al. (1996), BROCKE et al. (1998) and FATKA & BROCKE (1999) used bivariate analyses to discuss the taxonomomy of the Ordovician genera *Frankea*, *Dicrodiacrodium*, *Aureotesta* and *Arbusculidium*, respectively, while statistical tests and multivariate analyses were used by VECOLI et al. (1999), WAUTHOZ & GERARD (1999), STRICANNE & SERVAIS (2002) and WAUTHOZ et al. (2003) to better understand the variability of *Frankea*, *Deunffia-Domasia*, and the galeate acritarchs (*Caldariola*, *Cymatiogalea*, *Priscogalea*, and *Stelliferidium*), and *Crassiangulina* respectively.

In the present study, the Cambrian/Ordovician acritarch genus *Nellia* is analysed.

Morphotypes belonging to this genus are here reported for the first time from the Tremadocian of North Africa, from a sample in the borehole Nl 2 near Hassi-Messaoud in the Algerian Sahara. The investigation of the population allows a discussion of the relationships between *Nellia* and other members of the diacrodian acritarch plexus, such as *Veryhachium dumontii* VANGUESTAINE 1973, or *Dasydiacrodium caudatum* VANGUESTAINE 1973.

A multivariate statistical analysis gives new insights on the intraspecific variability of *Nellia.* Most of the specimens recovered in the Algerian assemblage are attributable to *N. acifera* (UMNOVA in UMNOVA & VANDERFLIT 1971) VOLKOVA 1990. A large variability and numerous intermediate specimens are also observed indicating possible relationships between *N. acifera* and *N. sukatschevii* (TIMOFEEV 1959) VOLKOVA 1990.

Material and Methods

The specimens investigated in this study come from the borehole Nl 2 at Bordj Nili, near Hassi-Messaoud in the Algerian Sahara (Fig. 1). For detailed descriptions of the geology of the area the reader is refered to LEGRAND (1973, 1985). The acritarch assemblages of the Cambrian-Ordovician of this area and from this borehole were previsouly investigated by COMBAZ (1967) and JARDINÉ et al. (1974) and more recently by VECOLI and coworkers (for full references see VECOLI, 1999 and PARIS et al., 2000). The sedimentary succession of the Upper Cambrian in the Nl 2 borehole is represented by quartzites with "tigillites" in the lower part, which intercalate with green shales higher in the succession. This succession is attributed to the lithostratigraphic unit "Grès de Miribel". The upper part of the Upper Cambrian rocks includes interbedded quartzitic sandstones and black shales of the lithostratigraphic unit "Grès de Bordj Nili" (LEGRAND 1973). On the basis of the occurrence of individual acritarch taxa VECOLI et al. (1995) suggested a Cambrian-Ordovician boundary in the overlying interbedded shales and fine-grained chloritic sandstones of the "Grès de Bordj Nili" unit (-3048 m).

The specimens of *Nellia* GOLUB & VOLKOVA in VOLKOVA & GOLUB, 1985, discussed in the present paper come from a sample taken at the depth of -3029.3 m, some meters above the Cambro-Tremadocian boundary as defined by VECOLI et al. (1995). The "Grès de Bordj Nili" sediments are overlain by the interbedded shales and grey-green siltstones of the lithostratigraphic unit "Argiles d'El Gassi". An early Tremadocian (Early Ordovician) age for this unit has been suggested on the basis of to the presence of graptolites belonging to *Rhabdinopora flabelliformis* s.l. (LEGRAND, 1973).

Microfossils were extracted from the rock applying standard palynological techniques by using HCl and HF acids and filtering with 12 μm meshes. The mounting medium "Euparal" by Chroma-Gesellschaft was used for the palynological preparations. The examination of palynomorphs was carried out under transmitting light using a Carl Zeiss Axioskop II microscope with Plan-Neofluar objectives. For the measurements, the image acquisation and analysing system Carl Zeiss Axiovision 2.0 was used. The sediments

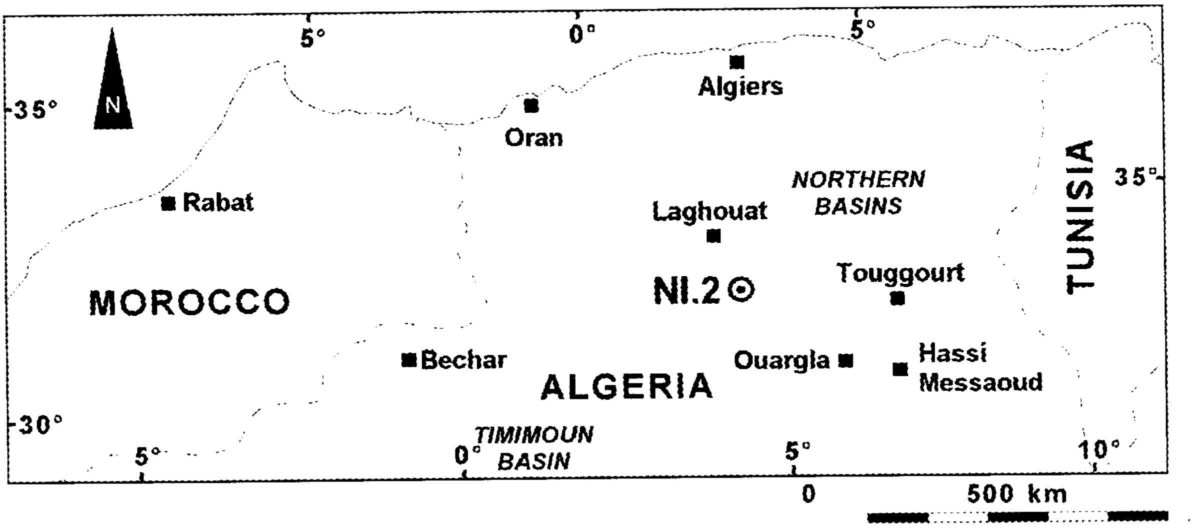

Figure 1: Localisation of the borehole Nl 2 in the Algerian Sahara.

of the investigated section are extremely rich in palynomorphs as previous studies already indicated (e.g., VECOLI et al., 1995, VECOLI, 1999, STRICANNE & SERVAIS, 2002). The studied microfossils are well preserved, yellow to amber in colour, which roughly corresponds to a thermal alteration index (TAI) 2 (HAYES et al., 1983). A total of 113 specimens belonging to the genus *Nellia* are recovered from the palynological slides n° 54509 and n° 54510. The preparations are stored in the micropalaeontological collection at Liège University and have a reference abbreviation 54509 Algérie NL2-3029.3 and 54510 Algérie NL2-3029.3, respectively.

The statistical approach used to characterise the relations between the morphotypes is a multivariate analysis. A correspondence factor analysis (CFA) is used to take into account both quantitative and qualitative data and in order to understand non-linear relationships between variables. Subsequently, the specimens are classified by hierarchic ascendant classification on the basis of the coordinates of each specimen in the scatterplot drawn up with the CFA method. To perform such automatic classification, Ward's method (WARD, 1963) has been used for minimal loss of the total inertia during the processing. To improve the classification accuracy, the n-clusters models provided by the automatic classification have been tested by a discriminant analysis.

The genus *Nellia* and its species

The genus *Nellia*

The genus *Nellia* was erected by GOLUB and VOLKOVA in VOLKOVA & GOLUB (1985) for diacromorph acritarchs, that are also named diacrodian acritarchs, with a rectangular to heteropolar vesicle with one pole showing few short, wide conical processes and the other bearing long spiny processes, that are parallel to the vesicle and thus form a rectangular outline of this pole. Anastomosing features and membranes were described to be present in some cases at the second pole.

According to its original diagnosis (see a translation in Appendix 1), the genus *Nellia* clearly belongs to the diacrodians. The relation and differences with some of the constituents of the Late Cambrian to Tremadocian diacrodians is summarised in Fig. 2. *Nellia* is comparable to other diacrodian genera by having a vesicle outline bearing two poles. The basic differences with some other diacrodians are as follows (Fig. 2): *Dasydiacrodium* Timofeev 1959, ex Deflandre & Deflandre-Rigaud 1962 (Fig. 2f-h) may show a similar vesicle outline, but it never presents a membrane at one of the poles. *Arbusculidium* Deunff 1968, emend. Welsch 1986, emend. Fatka & Brocke 1999 (Fig. 2j-l) bears processes that branch at one of the poles, but also has no membranes. The genus *Stephanodiacrodium* Vavrdová 1986 also has sharp-tipped processes, but with an irregular net at one pole. *Calyxiella* Golub & Volkova in Volkova & Golub, 1985, emend. Di Milia et al. 1989 (Fig. 2n) possesses a bunch of filaments, sometimes connected by a net or a membrane. Overlapping of this genus with *Nellia* is thus possible. *Barakella* Cramer & Diez 1977 (Fig.2o) possess few processes with a bunch of hairy processes at one pole. The genus *Buchinia* Volkova 1990 (Fig. 2p; translation of the diagnosis in Appendix 1) displays numerous hair-like processes at one of the poles, that may also show a membrane or anastomosing hairs (for a translation of the original diagnosis see the appendix). *Ladogella* Golub & Volkova in Volkova & Golub, 1985 (Fig. 2q-s; translation of the diagnosis in Appendix 1) is also characterised by a bunch of hairy processes. However, these smaller outgrowths are always surrounded by larger processes. *Acanthodiacrodium* Timofeev 1959, emend. Deflandre & Deflandre-Rigaud 1962 (fig. 2m),

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Figure 2: a – *Nellia? longispinata* Parsons & Anderson 2000 ; b – *Nellia acifera* (Umnova in Umnova & Vanderflit 1971) Volkova, 1990 ; c – *Nellia sukatschevii* (Timofeev 1959) Volkova, 1990 ; d – *Nellia magna* Volkova 1990 ; e – *Nellia longiuscula* Golub and Volkova in Volkova & Golub, 1985 ; f – *Dasydiacrodium* sp.; g – *Dasydiacrodium glabrum* Combaz 1967; h – *Dasydiacrodium tumidum* (Deunff 1961) Tongiorgi in Bagnoli et al. 1988; i – *Veryhachium dumontii* Vanguestaine 1973 ; j to l – *Arbusculidium filamentosum* (Vavrdová 1965) Vavrdová 1972, Fatka & Brocke 1999 emend.; m – *Acanthodiacrodium angustum* (Downie 1958) Combaz 1967; n – *Calyxiella izhoriensis* Volkova & Golub 1985; o – *Barakella fortunata* Cramer & Díez 1977; p – *Buchinia* Volkova 1990 ; q – *Ladogella rotundiformis* Volkova & Golub 1985; r – *Ladogella volkovae* Di Milia in Di Milia, Ribecai & Tongiorgi , 1989 ; s – *Ladogella filifera* Di Milia in Di Milia, Ribecai & Tongiorgi, 1989.

a genus that has been emended numerous times (see PAALITS & HEUSE, 2000), and to which several hundreds of species have been assigned, is always bipolar (two identical poles) and shows no membranes.

Although the differences between *Nellia* and the genera cited above have been considered to be evident in taxonomical conceptions published in literature, the boundaries between the different taxa are not always clear. For example, specimens that can taxonomically be attributed to *Nellia longiuscula* (Fig. 2e) and *Nellia magna* (Fig. 2d) are indeed morphologically very close to species of the genera *Buchinia* (Fig. 2p) and *Calyxiella* (Fig. 2n). Attributions to other taxa and misinterpretations can easily be made. This is based on the fact that the taxonomical status of some diacrodian genera, that were established by different authors, is highly problematical so far. The plexus of diacromorph acritarchs surely needs a detailed revision on the basis of a literature review and of a revision of large populations, including those from the Baltica continent. Such a complete review is not the objective of the present paper, that is limited to a revision of the constituent species of the genus *Nellia.*

History and current status of the species of *Nellia*

The first species, *Nellia sukatschevii*, was first described by TIMOFEEV (1959, p. 76) as a species of *Acanthodiacrodium* among 51 other *Acanthodiacrodium* species (see a translation of the original diagnosis in Appendix 1). The specimen drawn by TIMOFEEV (1959, pl. 4, fig. 36) is unique, showing a quadrangular vesicle with four long and acute processes with stiff processes at one side (left side of the figured specimen) and the ends of the processes at the other pole are curved in order that their tips are turned towards each other. TIMOFEEV indicated the size of this species comprised between 36 and 40 μm (54-69 μm with processes comprised).

UMNOVA in UMNOVA & VANDERFLIT (1971) created the new species *Acanthodiacrodium bucerum* (pl. 1, figs 18, 19) and the variety *A. bucerum* var. *aciferum* (plate 1: figs 20, 21) later attributed respectively to *Nellia sukatschevii* and *N. acifera* by VOLKOVA (1990). The original illustration of *A. bucerum* consists of drawings of two specimens also figured as pictures in UMNOVA (1975, pl. 12, figs 21, 22). Shorter apical and longer curved antapical processes are discernable. A fifth possible smaller additional antapical process is present on the paratype. UMNOVA (1975, pl. 12, figs 23, 24) also figured two specimens of *A. bucerum* var. *aciferum* bearing a single apical and 4-5 antapical processes.

GOLUB & VOLKOVA in VOLKOVA & GOLUB (1985) designated the species *Nellia longiuscula* as the type species of their new genus. This type species (see a translation of the original diagnosis in Appendix 1) was described as being retangular in outline with one pole bearing 4 to 6 short (2-5 μm) conical processes and the other pole with numerous longer (14-20 μm) processes that form a tight bunch that may also show membranes between the long processes.

Subsequently, VOLKOVA (1990) described one additional species, *Nellia magna* and transfered the species *A. buciferum* and its variety *aciferum* to the genus *Nellia*: *N. sukatschevii* (TIMOFEEV 1959) VOLKOVA 1990 and *N. acifera* (UMNOVA in UMNOVA & VANDERFLIT 1971) VOLKOVA 1990. *Nellia magna* (see a translation of the original diagnosis in Appendix 1) has its first pole decorated with 2 to 4 short processes (3 to 12 μm in length) and the other pole with long processes (25 to 40 μm) connected by a membrane. *Nellia acifera* (see a translation of the diagnosis in Appendix 1) was described as bearing a rectangular to rounded vesicle. The first pole bears one to three simple processes that are 3 to 13 μm long, while the other pole shows 3-6 processes of a length between 7 to 15 μm, that are connected by a membrane, that is often not visible, however, according to the original diagnosis (possibly due to preservational problems). *Nellia sukatschevii* (see a translation of the diagnoses in Appendix 1) presents a similar body shape and on most specimens with two processes, more rarely up to five processes, at one pole. These processes are between 9 to 16 μm long, according to this diagnosis. Two processes are also present at the other pole and they are connected by a membrane. One or two additional processes may be present at this second pole. However, this diagnosis does not fit with the original specimen figured by TIMOFEEV (1959, pl. VI, fig. 36).

More recently, a further new species was questionably attributed to the genus: *Nellia? longispinata* PARSONS & ANDERSON (2000). Thus PARSONS & ANDERSON (2000) described this new species with one prominent process at the first pole. They questionably attributed this species to *Nellia* because they did not clearly observe a membrane at the second pole, that would be necessary for the attribution to the genus.

Five species are therefore currently attributed to the genus, of which one attribution remains questionable. Similarly to the somewhat confused taxonomical status of the genus, the distinction of the species does also not appear to be without problems, as possible overlaps exist between the five species following their original descriptions. The main diagnostic features retained for the specific recognition are the number and the lengths of the processes which are two parameters known to be highly variable in acritarch morphotypes (as in dinoflagellate cysts). The taxonomical status of these five species therefore appears somewhat uncertain and the observation of larger population may be useful for a better understanding of the relation between the different species.

In summary, all five species show a first pole with fewer and smaller processes following the observation of TIMOFEEV (1959). This pole was generally named, for convenience, the "apical" pole. The processes are in number of one or two, and may rarely reach the number of six. Their length varies from a few μm to up to about 15 μm. The other pole, named "antapical" pole, usually has a higher number of longer (up to 40 μm) processes that are often bent towards each other and may show a membrane.

Nellia morphotypes in Algeria

A continuous morphological variability can be recognized in the population of *Nellia* observed in the acritarch assemblage investigated in the present work. The morphological variability was observed on both poles of the specimens of *Nellia*, but it is particularly well expressed on the "apical" pole. A selection of specimens are illustrated in Figure 4.

Among the 113 well-preserved specimens of *Nellia* from the Algerian Sahara, 86 specimens possess one process on the apical side of the central body. 18 specimens display two or three apical processes and three specimens have four processes. Six specimens did not have processes on the apical pole, or the number of processes was not possible to define because of preservational conditions.

On the "antapical" pole, commonly two or three processes, more rarely four processes were observed. These processes usually have a similar length. In a few specimens the processes branch at the basis. The processes, and particularily their tips often bend towards each other, which feature also guides the attribution of the specimens to the genus *Nellia.* A delicate membrane connecting processes of the "antapical" pole was observed in some specimens. However, in many other specimens the membrane was absent, probably due to degradation, as it was also described by VOLKOVA (1990).

Among the *Nellia* specimens observed, one of the antapical processes seems shorter and is situated slightly higher than the other processes at this pole, which may be due to the flattening during sedimentation, diagenesis, or the processing of the samples. Two additional processes situated in the middle part of a specimen have also been recorded. Such processes were mentioned in the diagnosis of *Nellia acifera* by VOLKOVA (1990). It is important to note that the majority of the Algerian specimens do not possess a complete membrane between the antapical processes. The attribution to *Nellia* is therefore limited to the gross morphology. A simple split opening was observed in some specimens in a meridian position between the apical and antapical poles.

Statistical investigation

Because of the simple morphology of *Nellia* morphotypes, five parameters have been considered for the multivariate analysis of which four were retained for a statistical description (Tab. 1). The following dimensions have been measured: the vesicle height VH (i.e. the distance between base of the apical process an the middle of the line between antapical processes), the length of the apical APL and antapical processes ATPL, the distance between the antapical processes DBATP.

	VH	**DBATP**	**APL**	**ATPL**
Minimal value	11	4	0	0
Maximal value	37	25	14.5	23
Mean	23.7	16.3	1,9	5.8
Standard deviation	4.3	3.7	2.7	3.9
Variance	18.7	14.1	7.2	15.7

Table 1: Descriptive statistics of the five morphological parameters. Minimal, maximal and mean values in µm.

The number of antapical processes has been added to the database as a discrete parameter. However, as the two/three antapical processes are undistinguishable in length one from the others, we considered the addition of the lengths of the antapical processes as a single continuous morphological feature.

The results of the CFA are interpreted through different factors of which a relevant selection is taken. Fig. 3-A displays the distribution of specimens in the first plane (Factor 1 - Factor 2) in which more than 26 % of total inertia (i.e. variability) can be recovered. Fig. 3-A presents the results of the cluster analysis in a hierarchic tree. Fig. 3-B illustrates also the results of the cluster analysis with the outlines of two clusters where some specimens are indicated (at the contact between the clusters and in some extreme parts). Table 2 shows the results of the discriminant analysis. The values of the "Wilks Lambda" index support the model with two clusters which corresponds to the best partition of morphotypes. Such interpretation is corroborated by the total reallocation provided by the analysis, while other models propose lower rates of reallocations.

The best discriminant parameter on Factor 1 (Fig. 3-B) is obviously the number of antapical processes which divides the scatterplot in two areas with strong relationships: an area with specimens having two antapical processes (negative values of F1) and the other one with specimens having three antapical processes (mostly, positive values of F1). The factor 1 also shows a complete gradation in length of antapical processes. This variation represents the main scheme of continuous variation in the Algerian population but does not, however, allow any discrimination between morphotypes having shorter and longer antapical processes.

The Factor 2 is best explained by the body height and the length of the apical process. It presents the distribution of morphotypes having a low body height and a small

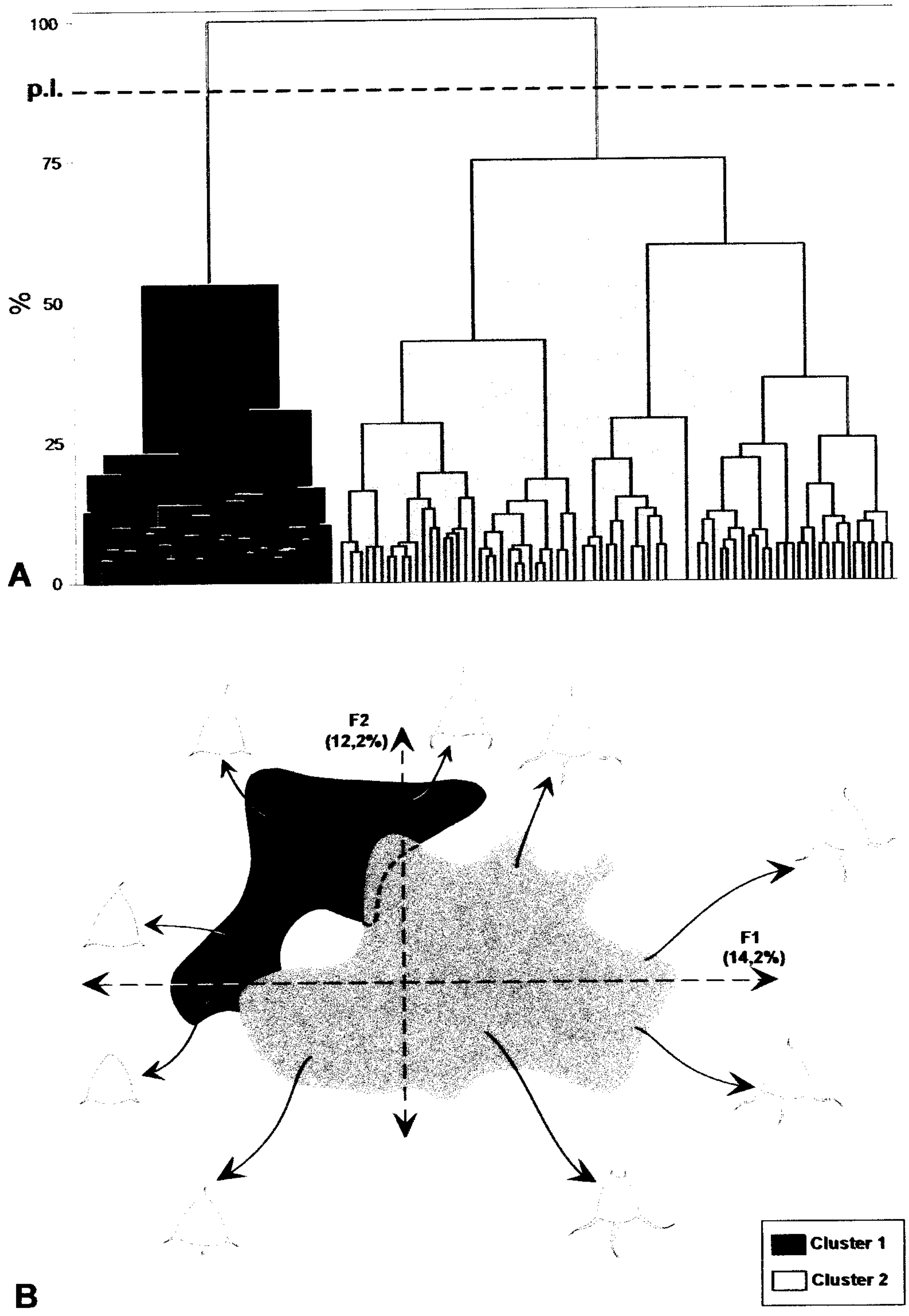

Figure 3: A – Cluster analysis of the Algerian specimens of *Nellia*, retaining two clusters. X-Axis: specimens of the study; Y-Axis: relative distance in percent. In black: cluster 1; in grey: cluster 2; p.l: phenon line. Vertical scale of the Y-Axis converted in percent distances to the total agregation distance. B – Figure illustrating the first plane of the Correspondence Factor Analysis. The two clusters are indicated following the results of the cluster analysis and the discriminant analysis.

	2 clusters	**3 clusters**	**4 clusters**
Wilks Lambda	0.00239	0.82558	0.75183
% Correct reallocation	100%	66%	53%

Table 2: Results of the discriminant analysis. Values of the Wilks Lambda show a great consistency (minimal value) for a model with 2 clusters, rather than three or four as proposed by the cluster analysis. Respective correct reallocation is also provided for each model.

apical process (negative values of F2) and the other forms are represented by morphotypes with a greater body height and a longer apical process (positive values of F2).

Questionable specific attributions

In previous works, two ways of classification have been suggested for the morphotypes included in the genus *Nellia.* The first, by VOLKOVA (1990), is based on the number of antapical processes covered by a membrane, i.e. *Nellia longiuscula* GOLUB and VOLKOVA in VOLKOVA & GOLUB, 1985, *N. acifera* (UMNOVA in UMNOVA & VANDERFLIT 1971) VOLKOVA 1990, *N. magna* VOLKOVA 1990, *N. sukatschevii* (TIMOFEEV 1959) VOLKOVA 1990. A second classification is based on the number and prominance of the apical process(es) whereas body shape is considered to be variable (PARSONS & ANDERSON 2000), i.e. *Nellia? longispinata* PARSONS & ANDERSON 1996. These two morphological classification schemes overlap in some cases. For instance, the specimen of *N. acifera* illustrated by VOLKOVA (1990: pl. 24, fig. 12) fits partly into the definition of *Nellia? longispinata* PARSONS & ANDERSON 2000.

Within the Algerian population, the two clusters drawn up with the automatic classification are partly in accordance with the usual taxonomy of the species in *Nellia.* The automatic classification (Fig. 3-A) gives further details on the way the partition is realised. Morphotypes from cluster I (32 specimens) may be attributed to *N. sukatschevii* after VOLKOVA (1999) and PARSONS & ANDERSON (2000), with specimens having two antapical and one single apical processes. Although rare, the occurrence of specimens with numerous (up to four) or without any apical process is recorded (for negative values of F1 and low values of F2). Extreme morphologies are also recorded for less discriminant criteria. For high values of Factor 2, morphotypes having a large (high) vesicule and longer processes are present.

Links with cluster II are carried out by morphotypes with both short antapical and apical processes and a smaller vesicle. The cluster II (81 specimens) is characterised by morphotypes with a large variability in apical/antapical processes lengths. Two other extreme mophologies are recorded. The first extreme shows a longer apical process with a large (high) vesicle, the second is characterised by shorter apical process(es) and longer antapical processes. These morphotypes fit also in the descriptions of *N. acifera* from the East European Platform (VOLKOVA, 1990, 1999).

Cluster II includes also some morphotypes which may be attributed to *N. longiuscula* (for negative values of F2 and low positive values of F1). The morphotypes show some more variability on the apical pole, where two apical processes are frequent, althought there are still three antapical processes. In *N. longiuscula*, the variability indicated by GOLUB and VOLKOVA in VOLKOVA & GOLUB (1985) is well expressed on both poles with four to six processes, which is a higher number of processes in comparison with the Algerian specimens of our study. For this reason, it is problematic to assign without difficulties some morphotypes from cluster II to *N. longiuscula*, as these morphotypes are not well separated by the multivariate analysis.

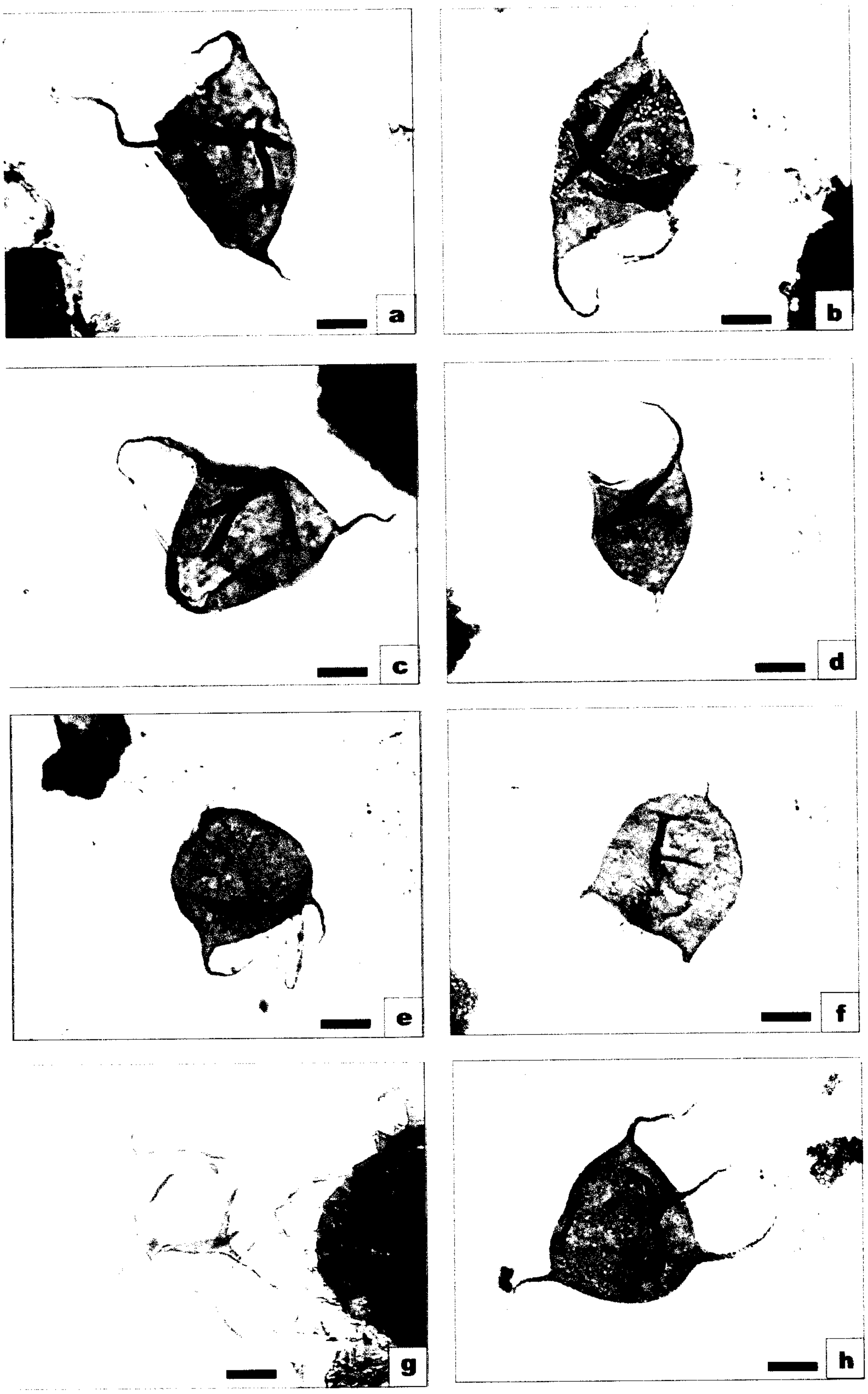

Figure 4: For all microphotographs, scale bars: 10 µm. a-d: specimens attributable to *N. sukatschevii*; e: specimen attributable to *N. acifera*, with the antipical membrane; f-g: specimen attributable to *N. acifera*; h: specimen attributable to *N. longispinata*.

Some of the morphotypes from the two clusters correspond to the specimens figured as *N. sukatschevii* by VOLKOVA (1999) and PARSONS & ANDERSON (2000). However, both works do not demonstrate that the specimens with two antapical processes constitute a pole of the population of the quadrispinosed *N. sukatschevii* morphotypes as shown by TIMOFEEV (1959). We therefore exclude herein their specimens from the species *N. sukatschevii* and attribute the trispinosed-quadrispinosed morphotypes of our study to *N. acifera,* according to the diagnosis of this species proposed by VOLKOVA (1990), which describes such kind of morphological features (Appendix 1). Moreover, the multivariate analysis and the automatic classification both indicate that the pattern of morphological variation does not allow an optimal discrimination between the clusters. The pattern of variation of the apical process length recognized by PARSONS & ANDERSON 2000 for the definition of *N.? longispinata* is not considered here as valid because no significant step in the analysis has been recognized for this parameter. As the Algerian plexus of *Nellia* seems to be a complex unit of morphotypes with a large morphologic variability, we suggest the attribution of the whole Algerian population to the species *N. acifera.*

Discussion

The classification of *Nellia,* used in previous works, did not fully include the morphological variation expressed in the populations. In the Algerian material investigated here, two morphotypes are present, which are attributed to *N. acifera,* based on the statistical analysis showing possible connections between the populations as seen between cluster I and II (Fig. 3). These morphotypes are characterised by specimens having a trispinosed-quadrispinosed triangular to rounded-quadrangular vesicle with measurements indicated on Table 1.

Such morphotypes were not figured by TIMOFEEV (1959) who illustrated only one large specimen of *N. sukatschevii* with bispinosed apical and antapical poles, without any membrane. Comparable morphotypes from the Moscow area were presented by UMNOVA & VANDERFLIT (1971, pl. 1, fig. 18) and UMNOVA (1975, pl. 22, fig. 21) as *Acanthodiacrodium bucerum* and *Dasydiacrodium bucerum*, respectively. Other morphotypes with more antapical processes but only one single apical process are also shown in both works (UMNOVA & VANDERFLIT, 1971: pl. 1, figs 19, 20, 21; UMNOVA, 1975: pl. 22, figs 22, 23, 24). In other acritarch populations from the Leningrad district, VOLKOVA (1990) illustrated some specimens of *N. sukatschevii* with two apical processes (pl. 24, figs 5-8). In this area, these morphotypes seem to be more common, apart from some specimens with more processes on the two poles. In the diagnoses of *N. sukatschevii* and *N. acifera*, VOLKOVA (1990) mentions the presence of a membrane. In the Leningrad district, VOLKOVA (1999) presented also some acritarch assemblages where morphotypes attributed to *N. sukatschevii* (pl. 2; figs 4-5) are less abundant than *N. acifera.* These *sukatschevii* morphotypes are characterized by one or two apical processes and two antapical processes, while *N. acifera* is represented by specimens with single short apical process and three antapical processes, similar to the specimens figured by UMNOVA & VANDERFLIT (1971) and UMNOVA (1975). The material from Newfoundland figured by PARSONS & ANDERSON (2000) is mostly represented by morphotypes having a single apical and 2-5 antapical processes. Their measurements show that the apical process is on an average longer in *N. sukatschevii* and *N.? longispinata* than in *N. acifera.* A large variation in the apical process length characterises the specimens that they illustrated as *N.? longispinata*. Comparable morphotypes are represented in the Algerian population. In our material, the specimens with a single apical process are predominant and 2-3 antapical processes are present. Furthermore, the variation in size of the apical process follow nearly the same pattern of variation but it is more expressed in specimens having three antapical processes (cluster II) which represent the most frequent morphotype.

Considering the whole population of *Nellia* from different areas, the Algerian material comprises morphotypes comparable with those of Newfoundland and partly with those from Russia. Nevertheless, any comparison with other areas should be limited as local environmental influences may imply large differences in the morphology of *Nellia* specimens. Moreover, our interpretations are limited to material from the Algerian Sahara and do not include detailed variability studies on material from Russia or Newfoundland. For these reasons, we make no formal taxonomical proposal in this study.

The statistical investigations of the specimens of *Nellia* from the Algerian material allow also a comparison with other genera. The material figured in this study is characterised by morphotypes having a morphological variability centered on triangular to pyramidal vesicle outlines, with one or several processes at the apical pole while the antapical pole always has more processes. This morphological feature is shared with some other diacrodians. The distinctive feature is represented by the antapical membrane which is only present in *Nellia*, while other genera rather present, with few antapical processes, either a bunch of thin hairy processes (i.e. *Barakella*, *Buchinia*, *Calyxiella*, *Ladogella*) either a reticule (i.e. *Arbusculidium*) or numerous processes without any additional structure (i.e. *Acanthodiacrodium*). The nearest forms from the Algerian morphotypes of *Nellia* are represented by morphotypes in *Dasydiacrodium* and *Veryhachium*. Some *Nellia*-like morphotypes of both genera have been attributed to different species such as *Dasydiacrodium caudatum* and *Veryhachium dumontii* by Vanguestaine (1973). After its original diagnosis, *D. caudatum* presents a triangular to oval granulate vesicle with one apical process (sometimes two) and 6 to 14 antapical processes. The diagnosis of *V. dumontii* also describes a granulate triangular vesicle with three main processes (with one inflated pole, defining the apex) and usually additional processes at the antapex. Considering the large variation observed in *Nellia*, it is possible that some specimens of Algeria may constitute intermediate morphologies with morphotypes of *D. caudatum* and *V. dumontii.* Some specimens previously published in the literature are morphologically close to *Nellia.* For instance, we consider that the specimens of *D. caudatum* figured by Vecoli (1999; pl. 6, figs. 3-4) are very close to those attributed to *Nellia* in this study. However, the present study remains limited to the genus *Nellia* and its interspecific variability and further investigations on *Dasydiacrodium* and *Veryhachium* are still necessary to understand the relations between these three genera.

Stratigraphy and palaeobiogeography

The genus *Nellia* is known from several localities in Russia and Newfoundland, but it is recorded as *Nellia* in the Algerian Sahara for the first time. GOLUB and VOLKOVA in VOLKOVA & GOLUB (1985) defined *Nellia* and its type species *N. longiuscula* from Upper Cambrian sediments of the Leningrad district in Russia. VOLKOVA (1990, 1999) recorded previously the presence of the four species *N. acifera*, *N. longiuscula*, *N. magna* and *N. sukatschevii* in the Upper Cambrian of the Yaroslav'l region from Russia. In the acritarch assemblages of the East European Platform, PAALITS (in HEINSALU et al. 1991, in MENS et al. 1993) and OLARU (2000) noted also the occurrence of *Nellia longiuscula* in the Upper Cambrian of north-eastern Estonia and Romania, respectively.

In Newfoundland, the species *Nellia acifera*, *N. sukatschevii* and *N.? longispinata* were recovered in the the biozones Ra 9 to Ra10b, the latter being attributed to the Tremadocian (Parsons & Anderson, 2000, tab. 1). However, the definition of these biozones by using the *Nellia* species remains problematical. The morphologic variations observed in the species of *Nellia* in Algeria show the need of a revision of the status of these biozones, which were defined partly by *N. acifera* (and *Ooidium rossicum*) for the biozone Ra9, and by both *N. sukatschevii* and *N.? longispinata* for the biozone Ra10a.

In Algeria, the sample of our study is situated in the range attributed to the lower Tremadocian by Vecoli et al. (1995) and Vecoli (1999), where the occurrence of *Nellia* has never been reported in previous studies. Thus the range of the genus *Nellia* is so far known from the Upper Cambrian to the lower Tremadocian.

Regarding the palaeogeography during the Early Ordovician (see for example Bassett et al. 2002; fig. 1-B), the occurrences of *Nellia* cited above are distributed in localities situated on Avalonia, Baltica and the northern margin of Gondwana. All these localities are close to palaeolatitudes of 60° S or higher. These areas at high palaeolatitudes are related to cold water areas and may imply that *Nellia* was palaeogeographically limited to the high latitudes of the southern hemisphere and possibly to cold marine environments.

Conclusions

The genus *Nellia* is recorded in the Algerian Sahara for the first time. It is apparently distinguishable from *Acanthodiacrodium*, *Arbusculidium*, *Buchinia*, *Calyxiella*, *Dasydiacrodium*, *Ladogella* and *Veryhachium*. However, due to the large variability and different preservational conditions, the *Nellia* specimens may be confused with some of these genera and some of their species (e.g. *Dasydiacrodium caudatum*; *Veryhachium dumontii*). Further investigations are necessary to clarify the exact relations and boundaries between these taxa.

The morphological variability between morphotypes formerly attributed to the species *N. acifera*, *N.? longispinata* and *N. sukatchevii* implies that all of them may correspond to one and the same unit, of which the status still needs to be clarified. Indeed, many intermediate specimens are recorded in the Algerian material and the statistical analysis has shown that the differences between these morphotypes are not enough relevant to support any attribution to the different species described in the usual literature. In our study, the morphological differences observed on the specimens currently attributable to *N.? longispinata* PARSONS & ANDERSON 2000 is of a low level of statistical significance. Thus, these specimens are included in the species *N. acifera*. Similarly, the morphological differences between the species *N. sukatschevii* and *N. acifera* does not allow a clear discrimination and all Algerian specimens currently related to the two species are also attributed to the species *N. acifera*. However, further investigations from other localities are still needed before a definitive taxonomical statement can be made. Such examinations should similarly clarify the position of some morphotypes currently described in open nomenclature.

According to the previous studies, the stratigraphical range is shown to be within the Upper Cambrian-lower Tremadocian. Palaeogeographically, the genus *Nellia* is so far limited to high latitudes of the southern hemisphere, but more research is necessary to provide the evidence that *Nellia* is part of a cold-water assemblage.

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Appendix 1

Translation of diagnoses of some taxa (from Russian)

Buchinia VOLKOVA in VOLKOVA (1990), p. 59.

The vesicle is quadrangular in outline, heteropolar. Ornamentation is concentrated at poles. At one pole there are 1-3 simple processes. At the other, there are 1-5 simple processes, 1-3 of which can be significantly longer than others. At this pole a bunch of thin hairs is situated. The last can be connected by anastamoses or a membrane. Hollow bases of pocesses at both poles freely communicate with the vesicle cavity. The surface of vesicle and processes is smooth or has a very weak ornamentation.

Ladogella GOLUB & VOLKOVA in VOLKOVA & GOLUB (1985), p. 95.

The vesicle is rounded, rounded-rectangular or irregular rounded multi-angular in outline. The wall is relatively thick. The wall surface is smooth or shagreen and bears processes of two types. Processes of the first type are distributed more or less evenly on the vesicle surface. They are simple, non-branching with conical hollow basis, which later transforms into a thin solid spine of a middle size. The top of the last is sharpened and can be slightly widened. The spine surface is smooth, granulated or covered with small spines. Processes of the second type are grouped in a small bunch on antapical pole (for the antapical is taken a pole with structure) and is a bunch of thin hairy-like processes, with basis thickened in a shape of grain or small hillock.

Nellia GOLUB & VOLKOVA in VOLKOVA & GOLUB (1985), p. 96.

Vesicle is rectangular, heteropolar in outline. Ornamentation is concentrated at poles. One of the poles possess few short wide conical processes, the other has long spiny processes. The last are parallel to the longitudinal axis of the vesicle, and compose the rectangular outline of this pole. The spiny processes can be connected by anastamoses or membrane. Hollow basis of processes on both poles freely communicates with the vesicle cavity. The surface of the equatorial zone and processes is smooth and shagreen.

Nellia acifera (UMNOVA in UMNOVA & VANDERFLIT 1971) VOLKOVA 1990 in VOLKOVA (1990), p. 73.

Vesicle shape is rectangular-rounded. The wall is thin, the wall surface is microgranulate shagreen and smooth. 1-3 spine-looking processes of 3-13 µm long are developed on one pole. On the other pole, there are 3-6 spine-looking processes of 7-15 µm long, which are connected by a membrane all along the processes, including their top. Commonly, ends of processes are bent towards the center of the vesicle. The membrane is often not preserved, but the bending of tips of processes is almost always observed. In the middle part of vesicles of some samples 1-2 processes without membrane are often observed. Processes on both poles are hollow, with inner cavity freely communicating with the vesicle cavity, tips are blunt. Vesicle length including processes 30-50 µm, width 15-24 µm. Measured 18 specimens.

Nellia longiuscula GOLUB & VOLKOVA in VOLKOVA & GOLUB (1985), p. 96.

The vesicle is rectangular in outline. One pole possesses 4-6 weekly developed wide conical processes of 2-5 µm. The other pole is ornamented with multiple long spine-like processes, basis of which is situated one and the same level. All along, processes are connected by anastomoses, between which a membrane can be present. Processes compose a tight bunch, parallel to the longitudinal axis of the vesicle. The surface of the wall and the processes is smooth. Size (in µm) : length of vesicle (including processes) 25-45, width 15-24 (holotype 20-36), length of bunch of spine-looking processes 14-20 (holotype 18).

Nellia magna Volkova in Volkova (1990), p. 74.

The vesicle is rectangular in outline. One pole possess 2-4 small processes with wide conical basis, 3-12 µm (in holotype 4 µm) long. On the other pole, there are long hollow spine-looking processes, which are connected with each other by a membrane all along the processes. Ends of processes are slightly bent inside the vesicle. The wall of vesicle and processes is thin, the surface is smooth or shagreen. The vesicle length including processes is 55-75 µm (holotype 58 µm), width 20-28 µm (holotype 25 µm), length of the bunch of spine-looking processes is 25-40 µm (holotype 38 µm).

Nellia sukatschevii as *Acanthodiacrodium sukatschevii* in Timofeev (1959), p. 76.

Vesicles are rectangular in outline, solid; each corner possesses one sharpended, long spine. The length of each spine is _ of the vesicle diagonal. At one of the poles, spines are bent so that they are turned with the sharp ends towards each other. The sculptural background is shagreen. The colour is light yellow-grey.

Nellia sukatschevii (Timofeev 1959) Volkova in Volkova (1990), p. 74-75.

The vesicle outline is rounded-rectangular, which sometimes reminds trapezium. The vesicle wall is thin; the surface is microgranulate, less commonly smooth. One pole possess 2, seldomly 1 to 5 spiny hollow processes 3-14 µm long. Two spiny processes are situated at corners of the opposite pole. Processes are hollow, 9-16 µm and bent towards each other. They are connected by a membrane all along, sometimes excluding tips. Seldomly, this pole possess 1-2 additional processes, but the membrane is absent from these processes. Cavities of processes freely communicate with the vesicle cavity, ends are blunt. Membrane between processes is often not preserved, but bending of processes towards each other is usually observed. Total length of the vesicle with processes is 33-35 µm; width is 17-22 µm. 12 specimens measured.

Appendix 2

List of citations of *Nellia* species in literature

TIMOFEEV (1959):	*Acanthodiacrodium sukatschevii*
TIMOFEEV (1966):	*Acanthodiacrodium sukatschevii*
UMNOVA & VANDERFLIT (1971):	*Acanthodiacrodium bucerum* (UMNOVA) var. *aciferum*
UMNOVA (1975):	*Dasydiacrodium bucerum* var. *aciferum*
VOLKOVA & GOLUB (1984):	*Nellia longiuscula*
VOLKOVA & GOLUB (1985):	*Nellia longiuscula*

VOLKOVA (1990):	*Nellia acifera* *Nellia magna* *Nellia sukatschevii*
HEINSALU et al. (1991):	*Nellia longiuscula*
MENS et al. (1993):	*Nellia longiuscula*
VOLKOVA (1995):	*Nellia longiuscula* *Nellia magna*
VOLKOVA & KIR'YANOV (1995):	*Nellia longiuscula* *Nellia magna*
PARSONS & ANDERSON (1996):	*Nellia acifera* *Nellia sukatschevii*
VOLKOVA (1997):	*Nellia magna*
VOLKOVA (1999):	*Nellia acifera* *Nellia longiuscula* *Nellia magna* *Nellia sukatschevii*
OLARU (2000):	*Nellia longiuscula*
PARSONS & ANDERSON (2000):	*Nellia acifera* *Nellia? longispinata* *Nellia sukatschevii*

Article II – *"Reevaluation of the Upper Cambrian-Lower Ordovician acritarch Nellia acifera Golub & Volkova", accepted for publication in Neues Jahrbuch für Geologie und Paläontologie, Stuttgart, Germany*

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Article II – *"Reevaluation of the Upper Cambrian-Lower Ordovician acritarch Nellia acifera Golub & Volkova", accepted for publication in Neues Jahrbuch für Geologie und Paläontologie, Stuttgart, Germany*

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Article III

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Acritarchs

Thomas Servais, Jun Li, Ludovic Stricanne,
Marco Vecoli, and Reed Wicander

The organisms that produced the acritarchs are thought to have been the major component of the organic-walled microphytoplankton in Proterozoic and Paleozoic oceans. As the primary producers, these organisms represent the base of the food chain in the Proterozoic and Paleozoic marine ecosystem. In order to understand the functioning and evolution of the Paleozoic marine ecosystem, it is essential to understand the marine phytoplankton. An interesting question discussed by such authors as Strother et al. (1996b) is whether Phanerozoic phytoplankton diversity and invertebrate diversity are linked or decoupled from each other.

Is biodiversification of the major Ordovician fossil groups related to the evolution of the microphytoplankton, for example, acritarchs? This chapter discusses some of the problems in producing an Ordovician phytoplankton (acritarch) diversity curve and whether biodiversification, speciation, and radiation events can be identified, as they seemingly have for the major macrofossil groups.

■ The Group "Acritarcha" (TS, RW)

Definition and Interpretation

During the early 1960s, palynologists were able to attribute most Mesozoic "hystrichospheres" (organic-walled microfossils with a "spherical" body and "spines") to the dinoflagellates (a class of the Pyrrhophyta). However, there remained a large number of predominantly Proterozoic and Paleozoic organic-walled microfossils whose biologic affinities were still uncertain. Evitt (1963) thus proposed the term "Acritarcha" to include all organic-walled microfossils of variable shape and size and of unknown biologic affinity. Etymologically, *acritarch* means "of uncertain origin" (from the Greek: *akritos,* uncertain, confused; and *arche,* origin). Acritarchs are, therefore, by definition, an informal polyphyletic group of organic-walled *incertae sedis* microfossils without any nomenclatural rank or status and must be considered a palynological catchall category. For a detailed review of subsequent definitions and a discussion on the value and meaning of the term *acritarch,* see Servais et al. (1997).

The interpretation of what acritarchs are tries to answer the question about their biological affinities, that is, to which biologic entities can the different acritarch morphotypes be assigned? A consensus exists today that most acritarchs are probably the cysts of diverse marine microphytoplankton groups and that most of them were probably "pre-dinoflagellates." Although microfossils displaying the morphological criteria of dinoflagellate cysts (e.g., the presence of an "archeopyle" excystment opening and paratabulation) first appear in the Middle Triassic, there is now sufficient ultrastructural and molecular phylogenetic evidence to indicate that the dinoflagellates,

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together with other groups of the alveolate lineage, such as the ciliates and apicomplexans, possibly diverged as early as the Proterozoic (Fensome et al. 1996). Additionally, geochemical (biomarker) studies (Moldowan et al. 1996) suggest that some Early Paleozoic acritarchs, particularly acanthomorphic acritarchs, may belong to the dinoflagellates (Talyzina et al. 2000).

Many acritarchs display openings that can be compared with excystment structures, thus strengthening the belief that they probably represent cysts of unicellular algae belonging to the Dinophyceae. Some morphotypes are, however, undoubtedly phycomata of unicellular prasinophycean green algae (Colbath and Grenfell 1995), while others can likely be attributed to chlorophycean algae (Brenner and Foster 1994), the Chlorococcales (families Hydrodictyacea and Scenedesmaceae), and Zygnematales (family Zygnemataceae) (Wood and Miller 1996).

There are also those acritarch morphotypes that probably do not belong to the microphytoplankton but are related to miospores (reproductive elements of plants), the exoskeletal remains of higher organisms (Fatka and Konzalova 1995), or even egg cases of meroplanktonic zooplankton (Van Waveren and Marcus 1993). However, the number of Ordovician acritarch species that belong to these latter groups is probably quite limited.

As stated earlier, acritarchs are generally interpreted as marine organisms. Most taxa certainly lived in marine environments based on their association with various known marine fossils. A few taxa, however, indicate probable brackish or even freshwater environments, and a small number of nonmarine acritarchs are known from both modern and ancient oceans (Riding and Duxbury 1993).

Despite the problems of attributing biologic affinity, most authors today agree that acritarch morphotypes represent, in most cases, cysts of various marine phytoplanktonic organisms. Therefore, acritarch diversity changes during the Paleozoic do not reflect the evolution of a single biologic group but rather the whole organic-walled phytoplankton (even if one includes the very limited number of taxa that may possibly be related to nonalgal groups). An analysis of Ordovician acritarch diversity thus attempts to understand the biodiversification, including radiations and extinctions, of the cyst-forming organic-walled microorganisms that formed the major part of the marine microphytoplankton and thus the evolution of the principal primary producers of the Ordovician oceans.

History and Methods

Alfred Eisenack, a pioneer worker on Paleozoic organic-walled microfossils, first published on Ordovician acritarchs, as well as chitinozoans and melanosclerites, during the early 1930s. However, stratigraphic palynological research did not seriously develop until the 1950s, when the oil industry recognized the value of palynomorphs for dating and correlation. Since that time, acritarch investigations have greatly increased in number. A review of the literature on Ordovician acritarchs (Servais 1998) shows that since the early 1960s between 10 and 20 papers have been published every year, versus less than 43 papers per year before 1960. Compared with most Ordovician macrofossil groups, the study of acritarchs is still in its infancy.

In analyzing acritarchs, the enclosing rock matrix often determines the method of study. In most cases, standard palynological preparation techniques involving dissolution of the rock with hydrochloric (HCl) and hydrofluoric acid (HF) are employed (Wood et al. 1996). The liberated specimens can then be studied by light or scanning electron microscopy.

In low-grade metamorphic rocks, where they are often the only fossils still present and typically are poorly preserved, acritarchs can be studied only by means of petrographic thin sections. This is because palynological extraction using acids yields only fragments of organic matter that can no longer be identified. The technique of polished sections (Munnecke and Servais 1996) is very useful for the observation of specimens in situ, that is, inside the rock matrix. However, neither of these techniques is suitable for routine biostratigraphic studies.

Acritarchs, as silt-sized particles, normally occur in mudstones, but they may also occur in low numbers in limestones and fine-grained sandstones. They are less frequent and generally absent in coarse sandstones because they have been washed out or destroyed by taphonomic processes. Acritarchs are typically completely flattened in clastic sediments, but they may, in some limestones, be three-dimensionally preserved.

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Acritarchs generally range in size between 20 and 100 micrometers (microns). Some forms, however, are smaller (less than 10 microns) but remain almost totally undescribed because the filters used in palynological preparation are typically 10-micron mesh size and usually only the fraction greater than this size is analyzed. Although some Proterozoic acritarchs are as large as several hundred microns in diameter, most Ordovician acritarchs described are between 20 and 50 microns, while morphotypes in most post-Devonian rocks are small (typically less than 20 microns) and display a very simple morphology (Molyneux et al. 1996).

The number of acritarch specimens in Lower Paleozoic sediments is commonly between 20 and 100 individuals per gram of rock but can easily reach 10,000 specimens in well-preserved material. Dorning (1999) noted that the Tremadocian Shineton Shales of the Welsh Borderland contained many samples with more than 100,000 acritarchs per gram. The large number of individuals available for study constitutes both advantages and problems for the group. Highly diverse acritarch assemblages with abundant specimens provide a large database with a high potential for meaningful biostratigraphic, paleoecologic, and paleobiogeographic interpretations. However, the complete description of all constituents in a large set of samples can easily take many years to complete.

Biostratigraphic, Paleoecologic, and Paleobiogeographic Distribution

Just as for the dinoflagellates in Mesozoic and Cenozoic sediments, acritarchs have a high biostratigraphic potential that is not yet realized. Published Ordovician stratigraphic schemes integrate acritarch zones with a duration of about 2 million years (Cooper et al. 1995). Because of a pronounced provincialism that is also observed in most other Ordovician fossil groups, the publication of a global acritarch zonation appears at this time to be unrealistic. Although the exact stratigraphic range of many acritarchs remains to be determined, the first-appearance datum (FAD) of some selected species with a restricted stratigraphic range is now known (Brocke et al. 1995) and should be very useful for the definition of biohorizons.

It is noteworthy that the last-appearance datum (LAD) is difficult to establish, as small palynomorphs can commonly be recycled into younger rocks. In the peri-Gondwanan area, which includes not only the British Isles but also southern China, the formal definition of a succession of biohorizons, based on the FAD of selected taxa, should soon be possible for the Tremadocian (Dorning 1999), as well as other parts of the Lower and Middle Ordovician (Li et al. 2002a). The duration of these zones should be about 2 million years, perhaps even shorter. For some regions and some age intervals it is reasonable to expect zones of about a 1-million-year duration.

In terms of paleogeography, two widely accepted "provinces" have been defined on the basis of the occurrence of certain taxa. Volkova (1997) defined a "warm-water" province that is characterized by the presence of the genera *Athabascaella*, *Aryballomorpha*, and *Lua* in the Tremadocian of Baltica, Laurentia, Australia, and North China. Li (1989) redefined the "Mediterranean" province on the presence of such taxa as *Arbusculidium filamentosum*, *Coryphidium*, and *Striatotheca*. This latter geographic assemblage, also named "peri-Gondwanan" province, occurs from high to low latitudes in many localities along the border of Gondwana (Li and Servais 2002) during the Early and Mid Ordovician. Although taxa from both provinces are present on Baltica, a clear distinction between the assemblages of peri-Gondwana and Baltica can be drawn (Servais and Fatka 1997).

Modern and fossil dinoflagellates reflect not only a latitudinal (climatic) signal but also a coastal-neritic signal, that is, a nearshore-offshore trend, as well as a salinity signal. They are therefore very useful for paleoceanographic reconstructions (Dale 1996). Similar to the dinoflagellates, the composition of an acritarch assemblage results from a combination of environmental parameters. These include such factors as temperature, light, nutrient supply, water chemistry, salinity, pH, water depth, surface currents, and turbidity.

The potential of acritarchs for Paleozoic paleoecologic interpretations has yet to be realized. Various studies have demonstrated nearshore to offshore trends (Staplin 1961; Dorning 1981; Wicander and Wood 1997; Vecoli 2000) and that the highest diversity of acritarchs occurs at intermediate depths. Future detailed studies are needed to better understand the influence of fluctuating sea levels on the composition of acritarch assemblages. Thus far, only a few such studies have been done, and these concern the

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Late Ordovician of Laurentia (Jacobson 1979; Colbath 1980).

As with all fossil groups, taphonomy must be considered when reconstructing the phytoplankton biocoenosis. In terms of fossilization potential, it is interesting to note that only 17 percent of modern dinoflagellate species produce resting cysts (Head 1996). Furthermore, it is well known that oxygenation, burial diagenesis, and metamorphism can damage or destroy the organic matter contained in the sediments. This is the reason why many originally palyniferous sediments have proved to be barren after laboratory processing. Nevertheless, it is important to remember that the extremely resistant acritarchs have often been the only fossils found in otherwise unfossiliferous sediments. Furthermore, acritarchs have proved to be extremely useful for understanding the geology of ancient basins and orogenesis as well as being biostratigraphically useful in mildly metamorphosed sediments, such as phyllites (Montenari et al. 2000).

Previous Compilations

Some 40 years after Eisenack's first investigations, Tappan and Loeblich (1973) summarized the status of acritarch research. They counted more than 400 species described from the Ordovician, making it the system with the highest recorded number of species. Six years later, Cramer and Díez (1979) compiled an index listing the diagnoses and stratigraphic ranges of all known Paleozoic acritarch genera.

During the ensuing years, the data set of acritarchs increased, and thanks to a consortium of oil companies that brought together their databases, Fensome et al. (1990) published the first complete catalog of acritarch species for all geologic epochs, including a species index listing almost all species described to 1989.

The important data set of Fensome et al. (1990) was used by Strother (1996) to establish distribution curves of genera through time. The latter author incorporated the age information provided by Fensome et al. (1990) for the holotype of each taxon to plot the number of all validly published genera over time by normalizing the values per million years. This confirmed the general temporal trend inferred by Tappan and Loeblich (1973). After a continuous increase in acritarch diversity from the Precambrian to the Devonian, a rapid decrease occurred near the end of the Devonian. This decline led to a "phytoplankton-blackout" during the Carboniferous and Permian (Riegel 1996:133) and was followed by the replacement of acritarchs by dinoflagellates in the Middle Triassic.

Strother (1996) also used Downie's (1984) review of Paleozoic British acritarchs to compile summary charts showing the stratigraphic distribution of selected acritarchs from the Cambrian through the Devonian. Strother (1996), in applying the data sets of Downie (1984) and Fensome et al. (1990), was the first to plot the distribution of acritarchs for the Paleozoic since Tappan and Loeblich (1973).

Downie's (1984) data set was based on his own investigations during the previous 25 years and on the Ph.D. research of seven of his students, four of whom investigated the British Ordovician. In Downie's (1984) compilation, the ranges of 57 Cambrian, 131 Ordovician, 122 Silurian, and 104 Devonian species were given for the British series and stages. The indicated ranges included both the distribution of the aforementioned species in the British Isles and their ranges elsewhere in the world.

We also use Downie's (1984) data set in this study (figure 32.1). However, we also include the data available from the Llanvirn with reference to British stratigraphic nomenclature (Fortey et al. 2000). The plotted results (figure 32.1) provide a biodiversity curve for the Cambrian through Devonian for the British Isles, that is, the eastern part of Avalonia. Because the British sequence is by far the best studied of all global sections, and because only a few new species have been described since the mid-1980s, the distribution curve given in figure 32.1 provides the most up-to-date information about the biodiversity of Paleozoic acritarchs, at least for Britain and other parts of Avalonia. According to these data, acritarch diversity increased from the Late Cambrian to the Tremadocian and Arenig (more than 40 species present), reaching a peak in the Llanvirn (about 70 species). A rapid decrease in the number of species can be observed in the Caradoc, and this trend is even more accentuated in the Ashgill. This does not necessarily reflect a decrease in diversity but the fact that, at this time, almost no acritarch studies had been conducted on Caradoc and Ashgill assemblages of the British Isles and other areas.

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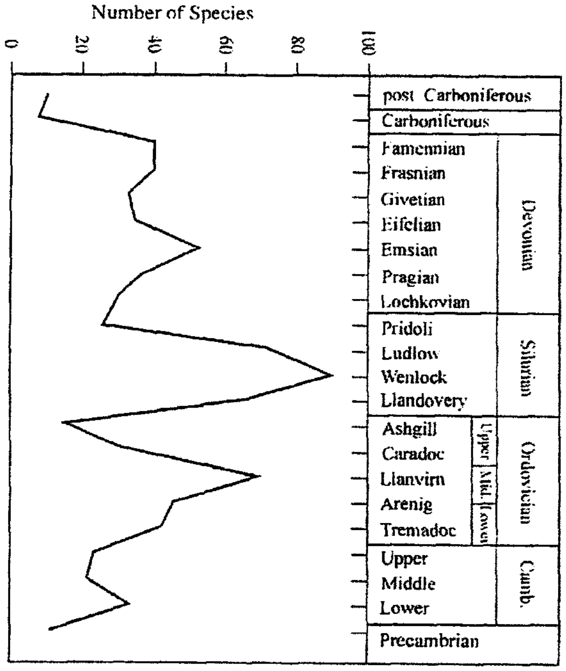

FIGURE 32.1. Number of acritarch species from the Precambrian to immediately post Carboniferous, based on Downie's (1984) data set from the British Isles (following Strother 1996).

■ The Data Set (TS, LS)

A marked contrast exists between the Proterozoic and Cambrian acritarch biodiversity patterns of speciation and extinctions, and the total number of species never exceeds 100, according to Vidal and Moczydłowska-Vidal (1997). The situation in the Ordovician appears to be more complex, with a developing provincialism and much greater diversity, making a general overview more difficult.

Following a suggestion from the International Geological Correlation Programme (IGCP) no. 410, "The Great Ordovician Biodiversification Event," Ordovician acritarch workers formed an acritarch clade group with the objective of assembling all data to establish a global biodiversity curve for Ordovician acritarchs. Accordingly, all the known Ordovician acritarch literature was first compiled (Servais 1998) into a complete bibliographic index with more than 700 references, including theses and abstracts, and listings of more than 250 acritarch genera from the Ordovician.

The compilation of published papers updated to 2001 is plotted on a paleogeographic map (figure 32.2) to document the current status of Ordovician acritarch research. Most studies (several hundred papers) have been concentrated in Europe (Baltica, Avalonia, and peri-Gondwana) and North Africa. The documentation from other regions comprises 50 papers from China (about 40 from the Yangtze Platform alone), 25 papers from North America, about 10 articles from South America, and 4 papers from Australia (2 that only included detailed descriptions of taxa). Some paleocontinents still have no coverage.

The next step for the acritarch clade team was to establish a complete database of Ordovician species (Servais and Stricanne 2001). The team compiled files that included for each species (1) its current generic attribution, (2) the year of its description, (3) the author(s), (4) the age of the type material, and (5), where possible, the stratigraphic range of the species. Compilation is now in the final stage and includes almost all species (more than 1,300). Together with the other taxa that have been described from older or younger sediments, the number of species known to have existed during the Ordovician currently exceeds 1,500.

The exact stratigraphic range for most species is not known. Whereas many Ordovician taxa have been described in monographic works in which the biostratigraphy was not the first objective, others have come from samples of sediments lacking independent age control. Many acritarch investigations had as their prime objective the dating of otherwise unfossiliferous rocks, commonly from areas with a complex geologic history, involving orogenesis and metamorphism (Albani 1989). Thus, for many of the 1,300 known species from the Ordovician, the age of the holotype has not been satisfactorily established.

Another problem is that for many species the holotype was neither well illustrated nor described, leading to numerous potential synonymies. Thus, the real number of Ordovician species is probably lower than documented. Nevertheless, many species from well-investigated sequences are currently well known and are extremely useful in the biostratigraphy of some areas (especially in the Lower and Middle Ordovician of Baltica and peri-Gondwana, including South China).

The compilation of a catalog of Ordovician acritarch species indicates that for most species a taxonomic revision is needed and precise stratigraphic

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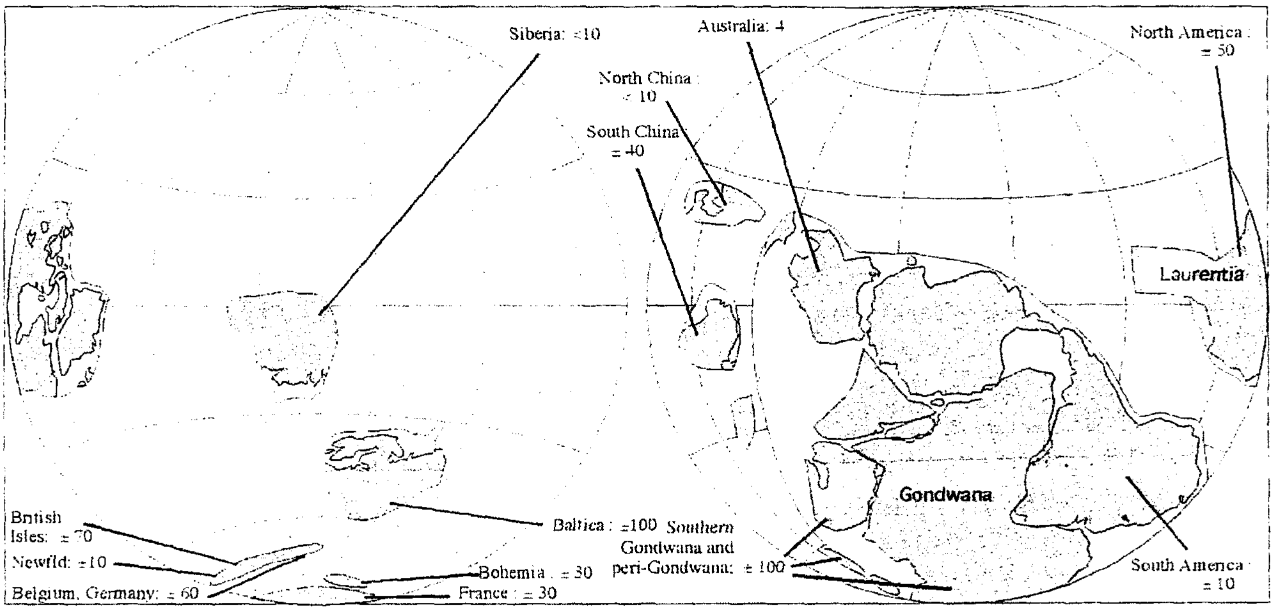

FIGURE 32.2. Number of articles on Ordovician acritarch research plotted on a paleogeographic reconstruction of Li and Servais (2002) for the Arenig (~ 480 Ma), based on the literature compilation of Servais (1998). Data from Avalonia are from Newfoundland, the British Isles, Belgium, and Germany. The area of "southern Gondwana and peri-Gondwana" includes the data from Iran, Pakistan, Saudi Arabia, Jordan, and northern Africa.

ranges must be established before attempting to draw diversity curves.

The counting of all new Ordovician species indicates that many species were described from the Baltica continent, including parts of the former Soviet Union, with 150 to 200 species for each of the British series. In the investigations of Ordovician acritarchs from southern Europe and North Africa, more than 100 new species were described in both the Tremadocian and Arenig, more than 80 species in the Llanvirn, but fewer than 40 species in both the Caradoc and Ashgill. New species from the Lower and Middle Ordovician of Laurentia are few in number. However, more than 100 species are described in the Upper Ordovician of this continent. Only a few species are described from Australia, and Chinese Ordovician acritarchs are mostly described from the Arenig (more than 70 species for this interval).

The data set also provides the first estimation of the total number of species in the Ordovician. Although this number never exceeds 100 and generally lies between 30 and 60, compared with the Cambrian (Vidal and Moczydłowska-Vidal 1997), the Ordovician appears to have a much higher diversity, with possibly more than 200 species being present worldwide during all time intervals of this period.

In view of this information, it is premature to propose a global biodiversity curve. However, the revision of regional diversity trends of areas that have been investigated in more detail provides some useful insights, as shown in the next section.

■ Local and Regional Diversity Trends

Some research projects have included investigations of acritarch assemblages from continuous sections with excellent independent biostratigraphic control. These include monographs that depict local or regional biodiversity trends. Summarized in the following paragraphs are results from Baltica and a reevaluation of publications from three other areas, the aim being to document those regional biodiversity trends possibly in relation to geologic events.

Baltica

The acritarch data set from Baltica is the largest compared with other areas in terms of the number

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of described taxa. However, it is difficult to provide an overview for this region because different authors have tended to adopt different taxonomic concepts. Many monographic articles include a large number of new species, but most lack definitive biostratigraphic control.

Because of the possibility of large numbers of synonymous species, it is difficult to establish acritarch diversity trends for Baltica. Nevertheless, the detailed study of one section in Estonia provides very useful information (Uutela and Tynni 1991). This section, the Rapla borehole (some 60 km south of Tallinn), is biostratigraphically well documented, and the diversity patterns of the acritarchs were compared not only with those of the chitinozoans but also with the changing lithofacies (Kaljo et al. 1996). A major result was recognition of regularly alternating acritarch and chitinozoan peaks (high acritarch diversity corresponding to low chitinozoan diversity and vice versa), except at the beginning of the Llanvirn, when both groups radiated strongly. The extinction curves of both groups are similar, with major extinctions occurring during the late Caradoc (Keila) and late Ashgill (Pirgu), the latter reflecting the Late Ordovician extinction event.

North America (RW)

The current Ordovician acritarch data set indicates that 103 genera and 337 species that are reported in the literature occur in North American Ordovician strata. Of these, 26 genera and 153 species were originally described as new.

Despite what appears to be a reasonably large data set for North American Ordovician acritarchs, many of the papers only describe one or a few acritarch species and do not include the entire acritarch assemblage. Furthermore, several of the described assemblages are based on only one or a few samples from a single locality and do not represent an entire formation. Most of the reported occurrences are not from continuous sections. Moreover, the sampling did not include several formations and lithotopes; nor did it cross series or stage boundaries. This makes it difficult to determine precise stratigraphic ranges for many species and to compare assemblages. Additionally, some of the illustrations and original descriptions of species are inadequate for positive attribution in subsequent studies, resulting in new species being created and a consequently higher diversity than actually existed. Furthermore, numerous species have been erected on the basis of only a few specimens, potentially leading to a large number of synonymies.

Reported occurrences of Lower Ordovician (Tremadocian and Arenig) acritarchs from North America are sparse (Dean and Martin 1978, 1982; Martin and Dean 1981; Martin 1984, 1992; Barker and Miller 1990). The acritarch assemblages described by Dean and Martin (1978) and Martin and Dean (1981) are from sections in eastern Newfoundland, Canada (part of Avalonia), and have little in common with the Laurentian assemblages discussed in the following paragraphs.

Lower Ordovician Laurentian acritarch assemblages have been described by Dean and Martin (1982), Martin (1984, 1992), and Barker and Miller (1990). Dean and Martin (1982) and Martin (1984, 1992) reported on Tremadocian and Arenig acritarch assemblages from Wilcox Pass, Alberta, Canada. At this locality, assemblages were reported from the Survey Peak Formation (Tremadocian) and the Outram and Skoki formations (Arenig). Twenty-four species were recorded (six new) from these three formations, the majority from the Survey Peak Formation. Important taxa include *Aryballomorpha grootaertii, Athabascaella playfordii, A. rossi,* and *Lua erdaopuziana,* which are also found in northeastern China (Martin and Yin 1988).

Barker and Miller (1990) reported a Tremadocian acritarch assemblage recovered from a stratigraphic test well in Terrell County, Texas. The assemblage was dominated by sphaeromorphic and acanthomorphic acritarchs, including representatives of the genera *Aryballomorpha, Athabascaella,* and *Lua.*

The genera *Aryballomorpha, Athabascaella,* and *Lua* have been reported from Laurentia, northeastern China, Australia, and Öland, Sweden. This association is considered by some authors to be characteristic of a warm-water province (Barker and Miller 1990; Servais and Fatka 1997; Volkova 1997). Except for Öland, the aforementioned locations all were located at low latitudes during the Tremadocian, and Öland (part of Baltica) was located in intermediate latitudes, between the warm- and cold-water assemblages.

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There are no Middle Ordovician acritarch assemblages reported from North America. Loeblich and Tappan (1978 and authors quoted therein) did, however, describe numerous new acritarch species from the Mountain Lake Member of the "Middle Ordovician" Bromide Formation of Oklahoma. But, as reported by Bauer (1994), conodonts indicate that the Mountain Lake Member is not Mid Ordovician but late Whiterockian to early Mohawkian in age, which corresponds to the early Caradoc.

The Upper Ordovician has received the greatest attention, and most reported occurrences come from locations with well-documented stratigraphic and paleontological control. Upper Ordovician localities from North America include Indiana (Loeblich and Tappan 1978; Colbath 1979), Kansas (Wright and Meyers 1981), Kentucky (Jacobson 1978; Loeblich and Tappan 1978), Missouri (Miller 1991; Wicander et al. 1999), Ohio (Loeblich and Tappan 1978), Oklahoma (Loeblich and Tappan 1978), Anticosti Island, Quebec, Canada (Staplin et al. 1965; Jacobson and Achab 1985; Jacobson 1987), St. Lawrence Lowland in the Ottawa, Montreal, and Quebec City areas, Ontario and Quebec, Canada (Martin 1983), and Gaspé, Quebec, Canada (Martin 1980). These assemblages are very diverse with representation of the following genera: *Baltisphaeridium, Dorsennidium, Eupoikilofusa, Leiofusa, Lophosphaeridium, Multiplicisphaeridium, Orthosphaeridium, Peteinosphaeridium, Polygonium,* and *Veryhachium.* Many of the species that occur in several North American localities are also found outside North America and are thus useful for correlating Upper Ordovician strata. These include *Dorsennidium hamii, Excultibrachium concinnum, Multiplicisphaeridium irregulare, Orthosphaeridium insculptum, O. rectangulare,* and *Villosacapsula setosapellicula.*

An understanding of biodiversification trends in North American (Laurentian) Ordovician acritarch assemblages remains still in its infancy. Only a few areas have been studied in the Lower Ordovician of Laurentia, making conclusions for this time interval speculative. Additionally, no North American Middle Ordovician acritarch assemblages have been reported in the literature. Even the best-known Upper Ordovician North American acritarch assemblages require further studies before any meaningful trends can be ascertained.

South China (LJ)

During the Ordovician, China was probably composed of a series of paleocontinents. Three of these major blocks are the North China (Sino-Korean), Tarim, and South China plates. More than 50 publications have dealt with Ordovician acritarchs of China, and some of these include detailed taxonomic analyses.

Only a few publications concern North China. This area has so far been investigated only for the biostratigraphy of acritarchs across the Cambro-Ordovician boundary, especially in the Dayangcha section (Yin 1985). Although the diversity trend in this section is not precisely established, a gradual increase in the number of species can be seen from the latest Cambrian to the early Tremadocian. The only studies from the Tarim Plate concern the Qilang Formation (e.g., Li 1995). The acritarchs are from the mid–Caradoc graptolite-based *Dicranograptus clingani* Zone. Diversity trends are not yet determinable because acritarch studies of the underlying and overlying strata are still in progress.

Most investigations have focused on the Lower and Middle Ordovician of South China, that is, on the Yangtze Platform and the Jiangshan-Changshan-Yushan (JCY) area, from levels between the late Tremadocian and early Darriwilian. The acritarchs of the Yangtze Platform have been detailed by several groups of workers but are principally based on the Ph.D. theses of Li (1991), Xu (1995), and Brocke (1998). Thirty-nine publications covering this region have been published to date and are listed in Li et al. (2002b).

The paleogeography and the paleoecology of the Yangtze Platform are fairly well understood, as this area has been better studied than any other region of China (Chen et al. 2001). The dominance of carbonates and marls indicates a relatively stable carbonate platform persisting from the late Tremadocian throughout the remainder of the Ordovician. Southeastward, these carbonate rocks gradually change into the graptolitic shale facies of the Jiangnan Belt, which includes the JCY area and locally comprises some intercalated, lenticular beds of limestone. Local lithofacies changes can be observed within the Yangtze Platform, and these are reflected by biofacies changes from shelly to graptolite-dominated faunas. Sea level on the platform generally rose through earliest Bendigonian (early Arenig) to Darriwilian time.

Acritarchs have been recovered from many sections of the Yangtze Platform. The assemblages clearly reflect a gradual lithofacies change from the northwest to the southeast as indicated by changing abundance and diversity patterns that can be observed in the assemblages recovered from samples in the graptolite-based *Azygograptus suecicus* Zone (earliest Mid Ordovician) (Li et al. 2002a). In the shallow-water part of the western Yangtze Platform in eastern Yunnan, the acritarch assemblages are not very rich, with low abundance and diversity. Acritarch assemblages from deeper-water conditions to the east show much higher diversity, but with variable composition, depending on their location on the platform. Within the deeper parts of the basin, that is, toward the JCY area, the diversity again decreases (albeit based on poorly preserved acritarch assemblages). These compositional differences probably reflect, in part, a nearshore to offshore trend (Li et al. 2002a).

In some continuous sections, acritarchs have been investigated from a succession of graptolite zones. Together with shorter stratigraphic sections representing shorter time intervals, the data set of acritarch samples is today quite large, providing a fairly complete spatial and temporal picture of acritarch distribution for this area.

The highest number of taxa recorded are from samples within the graptolite-based *A. suecicus* Zone. A review of the acritarchs from this zone indicates a total of 111 acritarch species, 26 of which were newly described with 35 species remaining in open nomenclature. This number is probably too high and reflects "splitting" of taxa by some authors. Tongiorgi et al. (1995), for example, named more than 60 taxa from a single sample of this interval in the Daping section, and Yin (1995) provided a different list of 60 species from a sample of the same interval from the nearby Huanghuachang section. Taxonomic reconsiderations including the analysis of synonymies are necessary in order to understand the real acritarch diversity in southern China. In the present study, we use an internally consistent acritarch taxonomy based on Brocke and his co-workers (Brocke et al. 2000; Li et al. 2002a) in order to establish the diversity trend in the Yangtze Platform, as shown in figure 32.3.

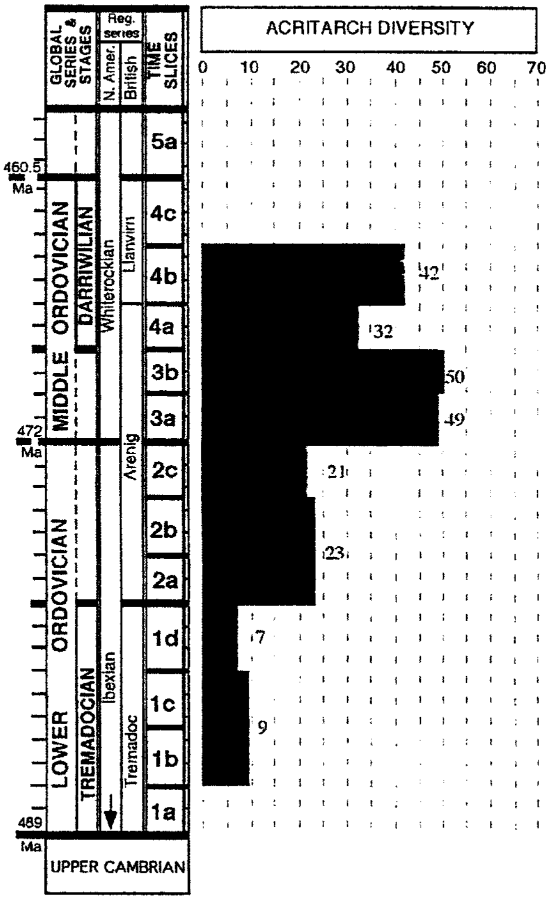

FIGURE 32.3. Diversity trends in the Yangtze Platform, South China (numbers refer to the species described from intervals between the middle Tremadocian and the lower Darriwilian). Time slices (*TS*) are after Webby et al., chapter 2.

Eight acritarch assemblages have been distinguished (Li 1987; Brocke 1997; Brocke et al. 2000; Li et al. 2002a). The first three acritarch assemblages have been documented by Brocke (1997). The oldest association appears in the early Tremadocian (conodont-based *Cordylodus angulatus* Zone) and continues into the mid Tremadocian, showing a low diversity of 9 species. This assemblage is here referred to *TS.*1b–c (figure 32.3; see time slices in chapter 2). The second assemblage of late Tremadocian (conodont-based *Paltodus deltifer* Zone, *TS.*1d) age also displays low diversity, with only 7 species recorded by Brocke (1997). The next assemblage, identified in the Yangtze Platform, is of latest Tremadocian and early Arenig age and is here attributed to *TS.*2a–b. It is moderately well preserved, with upwardly increasing diversity, and comprises 23 species (Brocke 1997). The assem-

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blage recorded in the graptolite-based *Didymograptus (Corymbograptus) deflexus* Zone (Li 1987, unpubl. data) and here assigned to *TS*.2c shows a similar diversity (21 species recorded).

The other four assemblages are documented in Brocke et al. (2000). A single acritarch assemblage is recorded from graptolite zones—the *A. suecicus* Zone and in the lower part of the *Exigraptus clavus* (formerly *sinodentatus/nexus*) Zone (*TS*.3a)—with a maximum of 49 species recorded (Brocke et al. 2000; Li et al. 2002a). In the lower part of this assemblage, that is, in the *A. suecicus* Zone, the diversity is higher than in the upper part, that is, in the lower *E. clavus* Zone; the middle part contains almost no acritarchs. This interval with no acritarchs corresponds to the reddish carbonates and nodular limestones of the middle parts of the Dawan and Meitan formations and is considered to represent a regressive marine phase. In the middle and upper parts of the *E. clavus* Zone (*TS*.3b), the diversity is highly variable and reflective of various sedimentologic facies (Brocke et al. 2000). The diversity in the samples from this interval is generally lower than in the previous assemblage, but the total number of species, recovered from different facies types, is closely consonant with the *A. suecicus* Zone (50 species). The next acritarch assemblage, from the base of the Darriwilian (graptolite-based *Undulograptus austrodentatus* Zone), is assigned to *TS*.4a and is only moderately diversified, with 32 species recorded by Brocke et al. (2000). The youngest assemblage so far recorded in the Yangtze Platform is placed approximately in *TS*.4b. Its diversity is still lower than that in the *A. suecicus* Zone, with some 42 species identified.

The Yangtze Platform studies demonstrate the difficulty of establishing diversity trends without knowledge of the biostratigraphy and lithofacies conditions of the wider area. Although the influences of lithofacies (nearshore-offshore trends) are not yet completely understood, and despite some remaining biostratigraphic problems, the following conclusions can be drawn:

1. There is evidence for a continuous increase in acritarch diversity from the lower Tremadocian up to the lowermost Middle Ordovician (*TS*.3a). This increase most probably corresponds to the general transgression observed in southern China.
2. The highest diversity is observed in the lower part of the Middle Ordovician (*A. suecicus* Zone). Following a brief regression, coinciding with the local occurrence of reddish carbonates and barren samples, the acritarch diversity remains high in the *E. clavus* Zone (*TS*.3b) and can possibly be attributed to renewed transgression.
3. At the base of the Darriwilian, a further decline in diversity is possibly related to the regional regression during this interval.

Further data from continuous acritarch successions in southern China, together with a more consistent taxonomic approach by all involved workers and greater biostratigraphic resolution, are needed to achieve a more comprehensive analysis.

North Africa (MV)

The analysis of Ordovician acritarch diversity of North Africa is based principally on borehole sections in Algeria, Libya, and Tunisia investigated by the present author (Vecoli 1996, 1999) and colleagues (Vecoli et al. in press). Other sources are published and unpublished data from palynologists working for the French oil industry during the 1960s and 1970s (e.g., Deunff 1961; Combaz 1967; Jardiné et al. 1974). More recently published work (e.g., Molyneux 1988; Oulebsir and Paris 1995; Paris et al. 2000a) was used mainly for calibrating the biostratigraphic correlations. Palynological data from other sources (e.g., the Ordovician of Morocco; Cramer and Díez 1977; Elaouad-Debbaj 1988a, 1988b, and references therein) were taken into account but not used directly to derive the current diversity curve, which is based only on the author's database.

Compared with other areas, and despite some problems of stratigraphic continuity as discussed later, the North African Ordovician acritarch record presents some advantages. These include accurate taxonomic studies of the acritarch floras (Vecoli 1996, 1999), typically excellent preservation, and very high palynomorph abundance, as well as independent biostratigraphic control provided by co-occurring macrofauna (graptolites; not very abundant but important at particular levels) and microfauna (chitinozoans; of great importance in all post-Tremadocian sedimentary strata).

Therefore, for the dating and correlation of Ordovician strata in the Sahara Platform subsurface,

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acritarchs can now be considered indispensable tools, complementary to the chitinozoans (Vecoli et al. in press). Recent acritarch studies in North Africa have permitted placement of the Cambrian-Ordovician boundary (Vecoli 1996), as well as paleobiogeographic (Colbath 1990) and paleoenvironmental reconstructions (Paris et al. 2000a; Vecoli 2000). Based on analyses of approximately 500 samples from several subsurface sections in Algeria (boreholes Ucl01 and Nl2), southern Tunisia (boreholes Ttl, Stl, Snl), and Libya (boreholes A1-70, A1-23, B1-23, B2-34, C1-34, A1-70, A2-70, and A3-70), a first attempt is made here to assess semiquantitatively the diversity dynamics and the main evolutionary trends of North African Ordovician acritarchs. Acritarch diversity has been calculated as simply the number of species per time slice (*TS*), thus representing the "standing diversity" for each time interval (figure 32.4). Mostly direct or indirect correlation of acritarch biostratigraphy with chitinozoan or macrofossil (i.e., graptolites) formal zonations permits a stratigraphic resolution comparable to the duration of a time slice (or a chitinozoan zone). In some specific chronostratigraphic intervals (i.e., the lower Tremadocian), it is even possible to propose a finer resolution, as discussed later.

The present study is only preliminary and, in part, incomplete because of the presence of two major stratigraphic hiatuses in the studied area (spanning the middle Tremadocian through the lower Arenig and the middle Caradoc through middle Ashgill; see figure 32.4). The author is currently completing a more comprehensive study of the area. Moreover, although the data used herein were derived from a relatively restricted area (i.e., approximately equivalent to the extension of the Ghadamis Basin sensu lato) and therefore might not be totally representative for the entire North Saharan Platform, they at least represent a workable base for future studies. Some important features of acritarch diversification dynamics can thus be outlined as follows.

1. Cambro-Ordovician radiation. Uppermost Cambrian acritarch associations of North Africa are fairly diversified. Together with some typical Cambrian genera that became extinct at or about the systemic transition (e.g., *Timofeevia, Trunculumarium, Ooidium, Cristallinium, Phenacoon, Ladogella*), Late Cambrian acritarchs already include taxa that became well established during the Early Ordovician (e.g., *Cymatiogalea, Stelliferidium, Acanthodiacrodium, Vulcanisphaera*). Overall, the Cambro-Ordovician transition is characterized by increased diversity.

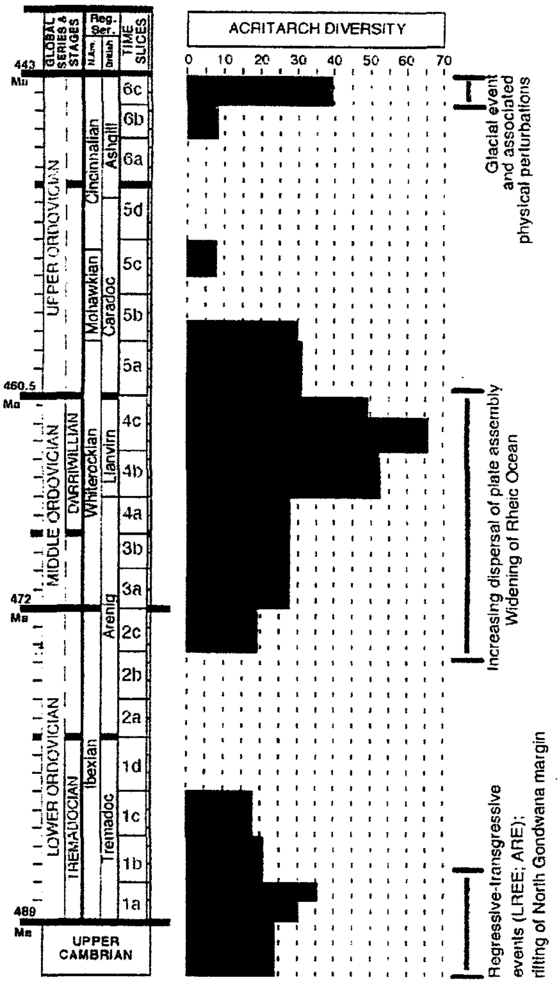

FIGURE 32.4. Diversity trends in North Africa (data from Algeria, Tunisia, and Libya). LREE = Lange Ranch Eustatic Event; ARE = Acerocare Regressive Event—see also chapter 10; and time slices (*TS*) after Webby et al., chapter 2.

2. Early Tremadocian differentiation. The early Tremadocian is characterized by a conspicuous increase in morphological variety among the diacromorph and galeate (herkomorph) acritarchs. The increase in diversity occurs entirely within *TS*.1a; according to Vecoli (1996), a lowermost assemblage is recognizable (HM/B of Vecoli 1996) that is here tentatively correlated with the lowermost part of *TS*.1a (figure 32.4). In general, *Stelliferidium, Cymatiogalea,* and *Acanthodiacrodium* tend to dominate the early Tremadocian assemblages, and innovative morphologies such those of *Arbusculidium* (probably related to

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the Upper Cambrian genus *Ladogella*) evolved. Numerous species of *Vulcanisphaera* also first appear during the early Tremadocian, as Rasul (1976) observed in the Tremadocian Shineton Shales of Shropshire, England. The FAD of the morphologically distinctive *Acanthodiacrodium angustum* can be considered as defining a horizon approximating the Cambrian-Ordovician boundary.

3. Middle to upper Arenig record. Arenig strata, only partly represented in the investigated North African sections, include relatively well-diversified acritarch assemblages, with first appearances of such genera showing innovative morphologies as *Coryphidium, Vavrdovella, Dicrodiacrodium,* and *Frankea.* The Tremadocian-Arenig transition corresponds to a stratigraphic hiatus in the study area, and therefore the acritarch dynamics of the transition from Tremadocian to typical Arenig are not observable.

4. Llanvirn radiation and differentiation. The basal Llanvirn exhibits a marked increase in acritarch diversity. The assemblages commonly contain up to 60–70 species, many with complex morphologies such as strongly sculptured, polyhedral vesicles bearing simple or, more commonly, complexly branched processes (e.g., species of *Arkonia, Frankea, Dicrodiacrodium, Coryphidium, Aureotesta, Striatoteca, Multiplicisphaeridium,* and *Vogtlandia*). Some genera that originated during Tremadocian-Arenig times show characteristic patterns of diversification, such as *Acanthodiacrodium* (*A. costatum, A. uniforme*), *Stelliferidium* (*S. striatulum, S. stelligerum*), *Cymatiogalea* (*C. granulata*), *Peteinosphaeridium* (*P. velatum*), and *Liliosphaeridium* (*L. pennatum*). The following genera were introduced in the North African region during Llanvirn times: *Ericanthea, Orthosphaeridium, Ordovicidium, Stellechinatum,* and *Villosacapsula.*

5. Lower Caradoc diversity decrease. Only data on acritarchs from the basal part of the Caradoc, which have a sufficient degree of taxonomic accuracy, are available. Correlation with the chitinozoan biozonation of Oulebsir and Paris (1995) and results from unpublished investigations by the present author shows that probably only *TS.*5a and 5b of the Caradoc are represented in northern Algeria, as well as the Ghadamis Basin of Libya. Upper Caradoc acritarchs have been recovered from the Illizi Basin in southern Algeria, but taxonomic information is not available. In general, Caradoc acritarch assemblages are of relatively low diversity and include species ranging from Llanvirn strata; they are dominated by both triangular and quadrangular forms of *Veryhachium,* netromorphic acritarchs, *Multiplicisphaeridium,* and less commonly species of *Ordovicidium.* Although incomplete, these data indicate that the Caradoc was most probably characterized by very low inception rates among microphytoplankton biotas.

6. Upper Ashgill record. In the upper Ashgill, the acritarch floras appear almost completely renewed and show relatively low generic yet high specific diversity. The most represented morphotypes are veryhachiid (both triangular and rectangular and including the genus *Villosacapsula*) and netromorphic acritarchs (e.g., *Dactylofusa, Poikilofusa*). Uncommon or rare occurrences of characteristic forms such as *Baltisphaeridium, Ordovicidium,* and *Multiplicisphaeridium* are noted. Just as important, the Ashgill record includes the first occurrence of distinct genera having a "Silurian" affinity, such as *Diexallophasis* (= *Evittia*) and *Oppilatala.*

The observed pattern of fossil microphytoplankton diversification in the Ordovician of North Africa is tentatively correlated with the main geologic and paleoenvironmental changes affecting the region during this time (figure 32.4). Given the complexity of factors influencing microphytoplankton dynamics, no direct causative relationships are implied in figure 32.4. The observed evidence suggests that the most abundant and diverse acritarch assemblages correspond to periods of intense tectonic activity that took place in the more peripheral parts of North Gondwana and also to periods of sea level highstand in the Gondwanan platforms. Latest Cambrian–early Tremadocian and Arenig-Llanvirn times were, in fact, periods of plume-induced rifting of the North Gondwanan margin (Winchester et al. 2002) that caused the separations of various terranes (including Avalonia) and perhaps were primarily responsible for sea level fluctuations. During late Arenig through Llanvirn times, the dispersal of the plate assembly in the region of the Gondwana-Baltica interface was at its maximum, and this paleogeographic and paleoceanographic situation was probably reflected in acritarchs by strong provincial differentiation.

The late Ashgill acritarch assemblages of the North Sahara Platform certainly reflect the response

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of microphytoplankton communities to the paleoenvironmental perturbations linked to the end Ordovician glaciation. It has been recently demonstrated (Paris et al. 2000a) that the upper Ashgill sediments of the Algerian basins actually correspond to the final stages of glaciation and the beginning of the postglacial climatic amelioration. Although of relatively low generic diversity, the late Ashgill North African acritarch floras are characterized by extreme polymorphism within the veryhachiid and netromorphic groups and by the first occurrences of numerous new morphotypes such as *Dicommopalla, Diexallophasis, Leprotolypa, Cheleutochroa,* and *Oppilatala.* It is interesting to note that most members of the latter group of acritarch genera have a definite "Silurian affinity" and survive the end Ordovician biotic crisis. The acritarch signal of the "end Ordovician mass extinction" is difficult to detect; actually, our data suggest that during the end Ordovician and the Ordovician-Silurian transitions, origination rates were unusually high, and hence it would be more suitable to use the term "end Ordovician turnover" rather than "mass extinction" for the acritarch flora.

■ Summary

It is impossible at this time to compile a global diversity curve, as the taxonomy of many species remains obscure and the exact stratigraphic ranges of most species are still unknown. However, regional diversity trends can be observed. The plotting of the information of the data set of British acritarchs by Downie (1984) indicates an ongoing diversification in the Early and Mid Ordovician with a peak of diversity in the mid to late Darriwilian (Llanvirn) before a decrease of the diversity in the Late Ordovician (figure 32.1).

Following detailed investigations in regional areas such as China (figure 32.3) and North Africa (figure 32.4), it appears that acritarch diversity basically mirrors transgressive-regressive trends. During marine transgressions, acritarch diversity increases, and during regressive phases the reverse applies. Similar trends can be seen among the Mesozoic-Cenozoic dinoflagellate floras in which diversity changes are closely linked to relative sea level fluctuations (Stover et al. 1996: figure 5). The present data set is not precise enough, however, to provide information about the nature of specific/generic diversifications/extinctions or turnover rates of the phytoplanktonic organisms that produced the resting cysts that were preserved in the fossil record. It is thus today still difficult to establish relations between the evolution of the marine phytoplankton and the invertebrate diversity in the Ordovician.

ACKNOWLEDGMENTS

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(*Addendum: the original references are separated from the article and grouped with all other references at the end of the book. For convenience, we provide the references of our article*)

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Article IV

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POPULATION DYNAMICS OF GALEATE ACRITARCHS AT THE CAMBRIAN–ORDOVICIAN TRANSITION IN THE ALGERIAN SAHARA

by THOMAS SERVAIS, LUDOVIC STRICANNE, MICHAEL MONTENARI *and* JÖRG PROSS

ABSTRACT. Galeate acritarchs are a major component of Late Cambrian and Early Ordovician palynological assemblages. The populations of galeate acritarchs from the Cambrian–Ordovician transition section in borehole Nl-2 of the Algerian Sahara show a gradual increase in process length and in complexity of the process structures through the succession. While the number of striate elements at the process base, the number of distal ramifications, and the number of membranes between the processes increases progressively, the central body diameter shows only minor variation within the succession. The galeate acritarchs are here interpreted as probably being resting cysts of a microorganism similar to modern dinoflagellates. Published laboratory culture experiments on living dinoflagellates document a considerable morphological variation with respect to the process morphology of the resting cysts that can be produced by a single biologically defined species. Based on these experiments, it is possible to interpret the morphological changes in the galeate acritarchs as being possibly related to changing ecological conditions. By analogy to the cyst distribution of modern dinoflagellates, changing salinity may have played an important role. Depending on environmental parameters, and perhaps on the maturity attained before rupture of the outer membrane during cyst formation, the galeate acritarchs may show a wide variety of process morphologies that have to date been used to describe four genera (morphogenera) and 84 species (morphospecies).

KEYWORDS: acritarchs, dinoflagellates, ecophenotypism, Cambrian–Ordovician, Algeria.

PALAEOZOIC acritarchs prove to be extremely useful for dating lithological units, even from tectonised and metamorphically affected areas where they are often the only fossils that have been preserved (e.g. Molyneux 1999; Montenari *et al.* 2000). Research on the biological affinities of Palaeozoic acritarchs, however, has been limited so far.

Because most acritarch studies have been biostratigraphically orientated, the acritarch classifications used were established such that they provided maximum biostratigraphical value. Cramer (1970), for example, noted that his system of acritarch classification was clearly defined by the stratigraphical purpose of his studies. Most other authors probably used a similar concept. This led to the morphological differences between specimens within a geological sequence being generally attributed to evolutionary changes in the acritarch-forming organism. Specifically, parameters such as variations in the number and length of the processes, the process arrangement or the structure of their distal terminations, or the presence of microsculptural elements have been considered to be of biostratigraphical importance (e.g. Sarjeant and Stancliffe 1994). Surprisingly, these parameters were rarely considered with respect to ecological conditions. This may be owing to the fact that sedimentological and palaeoecological data on the lithological succession containing the acritarchs were often not available. Some authors even proposed phylogenetic trends for acritarch taxa (e.g. Tappan and Loeblich 1971; Di Milia *et al.* 1989). These interpretations appear problematical because the specimens on which these models are based have to be considered to represent cysts of organisms that probably have a complex life cycle that is completely unknown.

Many acritarch species have been described based on a limited number of specimens, especially in the descriptions before the 1980s. During the last decade, however, new insights have been provided by

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variability studies that included biometrical investigations comprising bivariate and multivariate analyses on larger populations of selected acritarch taxa. The revisions of some Cambrian and Ordovician morphotypes, such as *Arbusculidium* (Fatka and Brocke 1999), *Aureotesta* (Brocke *et al.* 1998), *Cristallinium* (Vanguestaine 2002), *Dicrodiacrodium* (Servais *et al.* 1996), and *Frankea* (Servais 1993; Vecoli *et al.* 1999), have shown that morphological transitions can often be observed between taxa that had previously been considered to be separate species. Brocke *et al.* (1998), for example, demonstrated that *Aureotesta clathrata* and *Marrocanium simplex* belong to a single taxonomic unit, of which the two extreme morphologies were previously described as two different genera.

Although the studies cited above document that many acritarch morphotypes are highly variable, none of them interpreted these morphological changes in terms of genetics, palaeoecology, or functional biology. If a wide variability within one morphotype is observed in a single sample, it is impossible to attribute this variation to an evolutionary trend that can be used biostratigraphically. On the other hand, if the morphological changes are observed in different samples from a continuous section, it is difficult to interpret this variation. First, it is not always clear how genetic differences are expressed morphologically. Second, it is not possible to recognise which palaeoecological parameters influenced the morphology. Third, the biological function and the construction mechanism of morphological elements, such as acritarch processes, have never been discussed in acritarch literature so far.

The major resulting questions are, therefore, as follows: how much morphological variation was governed by the genotype? How much variation was the result of the palaeoecology, i.e. the result of physical and chemical parameters during development? And finally, what was the biological function of some morphologies?

Despite the scarcity of palaeoecological investigations on Palaeozoic acritarchs, it is widely accepted that some differences in the composition of acritarch assemblages reflect inshore–offhore trends. Less diverse associations are found in shallow-water and open marine environments, whereas the most diversified and richest assemblages generally occur on the shelf (e.g. Dorning 1981; Molyneux *et al.* 1996). However, the question of which environmental parameters (such as temperature, water chemistry, light, salinity or nutrient availability) influenced the morphology of an individual acritarch taxon within a continental-slope transect has never been discussed in detail and the possibility of ecophenotypism in acritarchs has not been mentioned so far.

In the present paper, we document and evaluate the variability of one particular group of acritarchs, the galeates, in order to understand if the morphological changes observed are related to evolutionary trends or to palaeoenvironmental changes. The galeates are very common in deposits of Late Cambrian and Early Ordovician age (e.g. Servais and Eiserhardt 1995). Our study focuses on excellently preserved material from the Algerian Sahara, the area from which Deunff (1961, 1964) originally described the first galeate morphotypes. The section investigated in borehole Nl-2 is particularly interesting because the Cambrian/Ordovician boundary has recently been defined in this borehole on the basis of acritarchs (Vecoli *et al.* 1995). The material investigated here was first studied by Stricanne and Servais (2002), who used a statistical approach for a reclassification of galeate acritarchs. Our paper aims to assess if the galeate acritarchs show clear evolutionary changes that enable the establishment of biozones, or if the different morphologies are the result of palaeoenvironmental changes and hence may represent ecophenotypes only.

ACRITARCHS VERSUS DINOFLAGELLATES

Following the original definition of the informal *incertae sedis* group Acritarcha by Evitt (1963) as a catch-all category to include all palynomorphs of unknown or uncertain biological affinities, acritarch morphotypes can by definition not be related to any living or fossil biological unit. Today, however, it is widely agreed upon that most Palaeozoic acritarch species are probably cyst stages of diverse algal groups such as dinophyceans, prasinophyceans, chlorophyceans or zygnemaphyceans (e.g. Colbath and Grenfell 1995). Only a minority of the described acritarch taxa are probably of non-algal affinity; these morphotypes may represent crustacean eggs or exoskeletal remains of higher organisms, plant spores, fungal palynomorphs, remains of cyanobacteria, or other groups (e.g. Servais *et al.* 1997). Hence, acritarchs very probably constituted the major component of the marine microplanktonic algae during the

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Palaeozoic. Many of them may be considered 'pre-dinoflagellates' (e.g. Le Hérissé 1989) that played a similar role in the Palaeozoic phytoplankton as dinoflagellates in Triassic–Recent phytoplankton.

Organic-walled microfossils that can without doubt be related to dinoflagellate cysts only appeared in the Middle Triassic, before the first major radiation of the group in the Jurassic (Fensome *et al.* 1996). However, Leppig and Montenari (2000) described 'protodinoflagellates' from the Lower Permian. In addition, comparative ultrastructural examinations (Taylor 1999), molecular phylogenic studies (Fensome *et al.* 1999) and biomarker investigations (e.g. Moldowan and Talyzina 1998) suggest that dinoflagellates originated in the late Precambrian and were already common in the early Palaeozoic, although some of the morphological criteria that characterise modern dinoflagellate cysts, such as a paratabulation and an archeopyle, have not yet been observed in organic-walled microfossils from pre-Mesozoic sediments.

In order to understand the environmental factors that may have influenced the morphology and distribution of Palaeozoic acritarchs, it may thus be useful to consider the environmental signals in present-day marine phytoplankton. Studies on modern dinoflagellates show that the morphology and size of dinoflagellate cysts may vary considerably within a single biological species (e.g. Kokinos and Anderson 1995; Lewis and Hallett 1997). The results of laboratory culture experiments indicate that the resting cysts may show a wide range of morphologies, particularly with respect to the number, distribution, length and structure of the processes. Kokinos and Anderson (1995), for example, observed that differences in the morphology of *Lingulodinium polyedrum*, the cyst of the modern dinoflagellate species *Gonyaulax polyedra*, are related to the degree of maturity that the cyst reached during its formation. An early rupture of the outer membrane surrounding the dinoflagellate theca and cyst during cyst formation resulted in a reduction of process length and modifications in process shape.

Since salinity is a prime factor controlling osmotic exchanges in microorganisms, it also plays a role in the distribution of dinoflagellates (e.g. de Vernal *et al.* 1993). The influence of salinity changes on dinocysts has been reconstructed by using morphological changes within specific dinocyst taxa and changes in assemblage composition.

Morphological changes in dinocysts resulting from low salinity or other environmental stress were first described by Wall *et al.* (1973) and Wall and Dale (1974) based on material from the Black Sea. Wall *et al.* (1973) interpreted the bulbous process terminations observed in the dinoflagellate cyst *Lingulodinium machaerophorum* from the Quaternary of the Black Sea to be the result of a low salinity estuarine environment. Wall and Dale (1974) not only observed an increased number of cysts with reduced processes, but also variations in septal development and a cruciform rather than a rounded endocyst in low-salinity environments as compared to normal-salinity assemblages. Moreover, changes in archeopyle formation have also been attributed to salinity fluctuations (Wall *et al.* 1977). Turon (1984) correlated reduced process length in *L. machaerophorum* with lower salinity. The hypothesis that salinity was a factor in determining process length in various chorate dinocysts was later corroborated by studies on *L. machaerophorum/L. polyedrum* (e.g. Nehring 1994), *Operculodinium centrocarpum* (e.g. de Vernal *et al.* 1989; Matthiessen and Brenner 1996), and *Spiniferites* spp. (e.g. Dale 1996; Ellegaard 2000). The idea that a cruciform endocyst may indicate the influence of a low-salinity environment has been corroborated by the work of Dale (1996) and a recent study on cruciform *Spiniferites* cysts from a lacustrine setting in northern Greece (Kouli *et al.* 2001). Ellegaard (2000) provided evidence that under reduced salinity conditions several modern dinoflagellate cysts, including *L. polyedrum*, display shorter processes. Taking these hypotheses a step further, Brenner (2001) used process length variations in *O. centrocarpum* to reconstruct Holocene salinity changes in the Baltic Sea.

Publications on ecophenotypy in fossil, pre-Quaternary dinoflagellate cysts remain scarce. Monteil (1991) reviewed the Cretaceous *Muderongia/Phoberocysta* cyst complex. He proposed that *Phoberocysta* (specimens with processes and scallops) represented ecotypes of *Muderongia* (without processes), with the genus *Phoberocysta* being abundant in inner shelf sediments. Feist-Burkhardt and Pittet (1996) pointed out that detailed morphological studies on the Jurassic *Mendicodinium/Ctenidodinium* dinoflagellate cyst plexus suggest that the two taxa are the final stages of a morphological series, and that the increase and decrease of surface ornamentation are the result of environmental factors following an inshore–offshore trend in the Swiss Jura Mountains.

Laboratory findings indicate a more complex relationship between cyst morphology and salinity. After

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the study of Lewis and Hallett (1997), who provided evidence that the process lengths in *L. machaerophorum* are reduced at low salinities, Lewis *et al.* (1999) demonstrated that the development of different morphotypes in *Spiniferites membranaceus* and *S. ramosus* also occurs under stable salinity. Thus, it appears that salinity is not the only controlling factor for these morphological changes. Combining data from the literature and the results of cultural experiments, Hallett (2000) finally demonstrated that the process length in *L. polyedrum* is essentially a function of temperature and salinity. On the whole, he found process length to increase in higher salinities and to decrease in higher temperature.

It is evident that these studies on modern phytoplankton have important repercussions for palaeontologists working with dinoflagellates and/or acritarchs. Acritarch specialists working as stratigraphical palynologists should probably reconsider not only the taxonomy of some of their species, but possibly also the interpretation of the distribution of these taxa, which may be more ecologically controlled than previously thought.

GALEATE ACRITARCHS AND POSSIBLE DINOFLAGELLATE EQUIVALENTS

Definition of the galeates

Deunff (1961, 1964) originally described two new acritarch genera from the Tremadocian (Early Ordovician) of the Algerian Sahara. Both genera are characterised by a hemispherical vesicle outline and a large circular opening (pylome) closed by an operculum. Deunff (1961) split this plexus of forms into the two following units: (1) the genus *Cymatiogalea*, which included all specimens showing polygonal fields on the vesicle, defined by sculptural elements such as processes, granules or membranes, and (2) the genus *Priscogalea*, comprising specimens without paratabulation. The taxonomic status of the two genera was debated in subsequent publications, and two additional genera have been added to describe this group of acritarchs. Deunff *et al.* (1974) erected *Stelliferidium* for specimens with 'crests radiating from the process bases'. Molyneux (*in* Molyneux and Rushton 1988) created *Caldariola* for specimens without ornament, processes or membranes.

Servais and Eiserhardt (1995) proposed the term 'galeate' for this group of acritarchs, containing over 80 species described in literature. They reviewed the different classification concepts and noted that, according to different authors, a distinction into four, three or two genera was used.

Stricanne and Servais (2002) aimed to resolve the classification problem by using a statistical approach. They listed the 84 species of the galeate plexus described in the literature and reviewed all morphological criteria that have been used for their description. Eleven of these criteria were used for multivariate and cluster analyses. The statistical analysis demonstrated that it is impossible to maintain the subdivision into the four genera *Caldariola*, *Cymatiogalea*, *Priscogalea* and *Stelliferidium*, because all intermediates exist between the individual morphotypes formerly considered separate entities. According to available data, the most important variables appear to be process length and presence/absence of distal process ramifications.

These results lead to the following dilemma: how can palaeontologists delimit and name taxa in an assemblage if all intermediates exist within a population? This question is a major problem in galeate classification and in acritarch classification in general. Should each morphotype receive its own name, or should all specimens be lumped together under one name representing a single taxonomical unit that is highly variable? The study of large numbers of specimens of individual morphotypes clearly shows that it may be problematical to use single specimens in order to answer geological questions. Only large populations can be used to understand the high variability of organisms such as the acritarchs. In order to depict biostratigraphical, palaeobiogeographical or palaeoecological changes, it appears evident that the evolution of an entire population of a given morphotype in time and space must be analysed.

Based on the results of Stricanne and Servais (2002), the major aim of the present paper is towards understanding the population dynamics of the galeate acritarch plexus within one continuous sequence, the Cambrian/Ordovician boundary in the Algerian Sahara, and to interpret the changes in comparison with examples known from Mesozoic and Cenozoic dinoflagellates.

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Galeate acritarchs: 'pre-dinoflagellates'?

As genetic compatibility is no longer possible to determine and because biochemical analyses have not yet been applied in order to detect the presence of dinosteranes in galeate acritarchs, the comparison of the galeates with fossil and living dinoflagellates is so far limited to morphological similarities. In some aspects, the galeate acritarchs strongly resemble dinoflagellates. Besides similar size ranges and morphology, the large 'polar' opening (pylome) of the galeates may be compared to the archeopyle of the dinoflagellates. However, in contrast to the dinoflagellates (which show a polygonal shape of the archeopyle following the plate organisation of the cyst), the opening of the galeates is always circular or rounded. Galeates attributed to the genus *Cymatiogalea* show an arrangement of polygonal fields on the vesicle surface that is similar to the paratabulation displayed by most dinoflagellate cysts. However, other galeates do not show these polygons. On the other hand, many dinoflagellate cysts also lack a paratabulation pattern. Although there is no evidence for a cingulum and a sulcus in galeate acritarchs, the process structure and large variation of the distal terminations, including the presence of membranes, is very similar to that of many dinoflagellates, among them the primitive Triassic dinoflagellate cyst genus *Suessia*, which is characterised by a large polar archeopyle and a vesicle covered by polygonal fields. Other dinoflagellates with a galeate-like morphology are classified in the family Areoligeraceae, which shows a wide variation of morphotypes in Cretaceous and Tertiary assemblages, and which displays a hemispherical vesicle with varying ornament. Specifically, *Eatonicysta*, a dinoflagellate cyst from the Eocene with a hemispherical vesicle with varying process terminations, strongly resembles the outline of galeate acritarchs.

GEOLOGICAL SETTING

The material investigated comes from the Cambrian–Ordovician transition in borehole Nl-2 (Bordj-Nili No. 2) from the Hassi-Rmel gas field, some 400 km south of Algiers, in the Algerian Sahara (Text-fig. 1). The general geology of the area has been described by Legrand (1985, and references therein). The borehole Nl-2 and other drillings from this area have been extensively studied for acritarchs and chitinozoans, starting with investigations by palynologists working for French oil companies in the 1960s and 1970s. A review of the palynological literature for the area has been provided by Vecoli (1999) and Paris *et al.* (2000).

According to Legrand (1974), the sedimentary succession of the Cambrian/Ordovician boundary in the Nl-2 borehole (Text-fig. 2) is characterised from the bottom to the top by (1) the 'grés de Hassi Miribel' Formation (also named 'grés de Miribel'), consisting of quartzites with rare intercalations of siltstones in the lowermost part and followed by quartzite-siltstone alternations that contain lingulids in the upper part; (2) the 'grés de Bordj Nili' Member, a sandstone-siltstone alternation of quartzitic sandstones and black shales with overlying interbedded shales and fine-grained chloritic sandstones with debris of lingulids and brachiopods; (3) the 'argiles d'El Gassi' Member, composed of a homogeneous interbedding of black and grey-green shales and siltstones. Levels of this unit have been dated as being of Tremadocian age based on the occurrence of the graptolite *Rhabdinopora flabelliformis s.l.* (Legrand 1974).

Legrand (1974, 1985) considered the first unit to be of latest Cambrian age and the last as belonging to the Ordovician. He noted that the Cambro-Ordovician boundary should be within the second unit. This boundary was defined in the borehole Nl-2 at the depth of 3048 m (± 2 m) by Vecoli *et al.* (1995) in the upper part of the 'Grés de Bordj Nili' Member, on the basis of the first occurrence of the acritarchs *Acanthodiacrodium* aff. *angustum* and *Stelliferidium furcatum*, the latter species belonging to the galeate plexus.

Detailed sedimentological studies of the succession in borehole Nl-2 are not available. However, a transition from sediments dominated by coarse-grained sandstones ('grés'), probably deposited in shallower water, to siltstone layers ('argiles'), very probably deposited in a deeper environment, has been described (Legrand 1974, 1985). This sedimentary facies transition is possibly a consequence of a gradual deepening of the basin, as the siltstone intercalations become more and more abundant towards the siltstones of the 'Argiles d'El Gassi' Member (Legrand 1974, 1985). However, the available dataset is too limited for clear statements about the evolution of the palaeoenvironment to be made.

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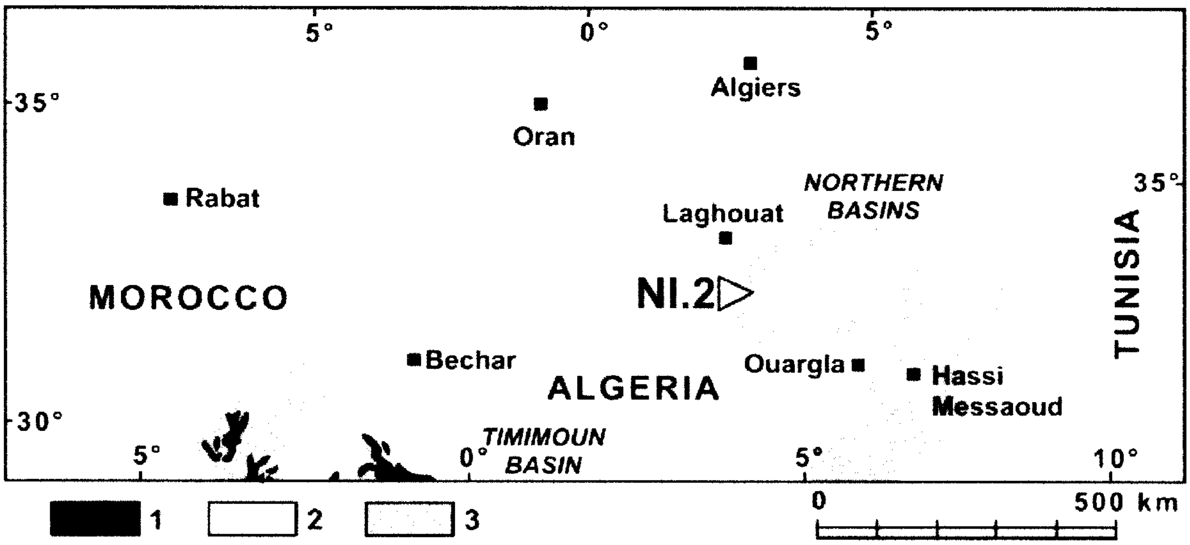
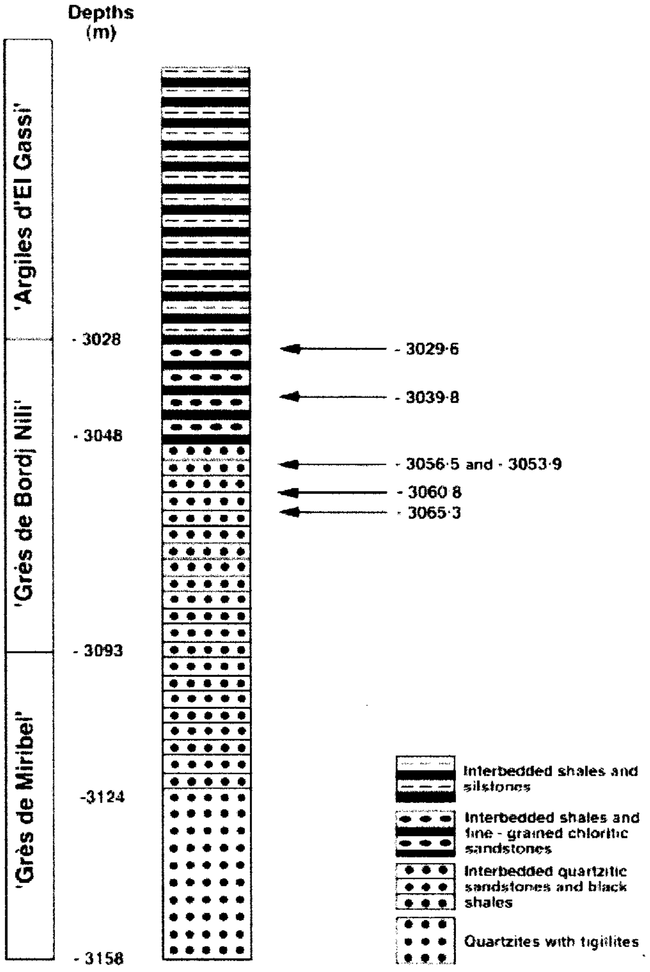
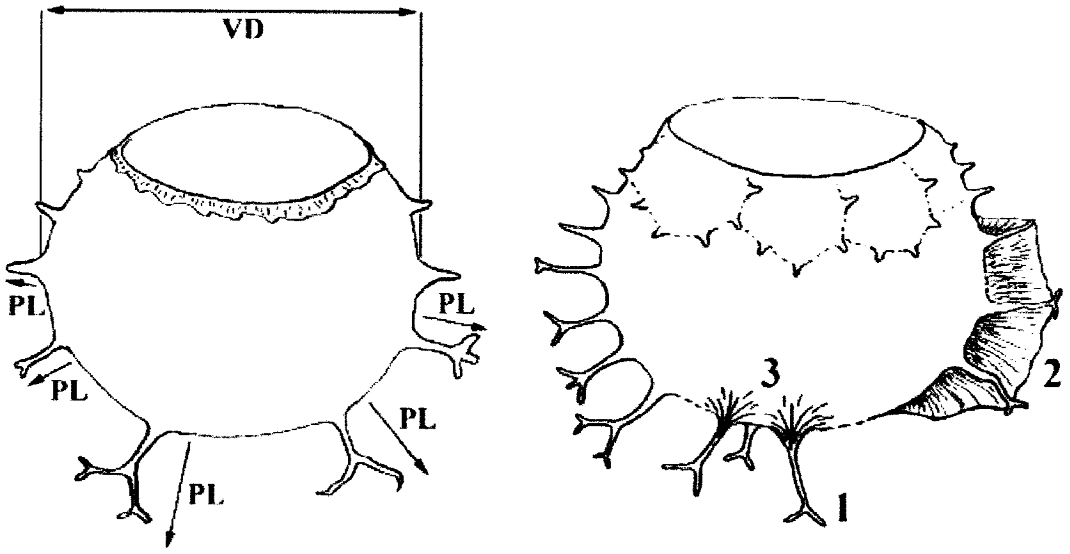


TEXT-FIG. 1. Geographical location of the NI-2 borehole near the gas field of Hassi-Rmel, Algerian Sahara (after Paris *et al.* 2000). 1, Ordovician outcrops; 2, Cambrian at the top of the basement; 3, Ordovician at the top of the basement.



TEXT-FIG. 2. Stratigraphical sequence of the Cambrian–Ordovician transition in borehole NI-2 and location of the samples investigated in the upper part of the 'Grès de Bordj Nili' Member (modified after Vecoli 1996).



TEXT-FIG. 3. Quantitative and qualitative parameters used in the galeate acritarch classification that proved to be useful for the statistical analyses. VD, vesicle diameter; PL, process length; 1, branching style of the distal termination of the process; 2, presence/absence of membranes between the processes; 3, presence/absence of striated ornament at the process bases (after Stricanne and Servais 2002).

MATERIAL AND METHODS

Six siltstone samples from the 'Grés de Bordj Nili' Member were taken at 3065·3, 3060·8, 3056·5, 3053·9, 3039·8 and 3029·6 m (Text-fig. 2). For palynomorph extraction, standard palynological techniques were used, including sieving with a 12 μm mesh. The palynological material was observed in transmitted and reflected light using Carl Zeiss Axioskop II and Axioplan II microscopes. Image aquisition and measurements were all made using optical microscopy and a Carl Zeiss Axiovision 2·0 image analysis program, using a standard CCD video camera. All material is housed in the collections of the Department of Palaeobotany and Palynology of Liège University, Belgium, except the SEM stubs, which are housed in the collections of the Institute of Geosciences of the University of Tübingen, Germany.

Only perfectly preserved galeate specimens (with an unfolded central body and complete, unbroken processes) were measured. Altogether 564 specimens were investigated. They are distributed in the six samples as follows: 3065·3 m (45 specimens measured), 3060·8 m (123), 3056·5 m (56), 3053·9 m (73), 3039·8 m (170) and 3029·6 m (97).

The morphological criteria selected by Stricanne and Servais (2002) for the statistical analyses to classify the galeates included six quantitative parameters (vesicle diameter, VD; pylome diameter, PD; process length, PL; total diameter, TD; the ratio PD/VD; and the ratio PL/VD), four qualitative parameters (presence/absence of polygonal fields, of membranes, of striae, and of distal ramifications), and one semi-quantitative parameter (ornamental structuration).

The changes of five morphological parameters measured in the galeate population through the six samples are discussed in this paper. These are the process length (PL), the vesicle diameter (VD), as well as the presence/absence of (1) distal ramifications of the processes, (2) membranes between the processes, and (3) striae radiating from the process bases (Text-fig. 3).

MORPHOLOGICAL CHANGES IN THE GALEATE POPULATION

The acritarch assemblages of the 'Grés de Bordj Nili' Member are rich, highly diverse and well preserved. Galeate acritarchs are abundant in all samples, forming a plexus with numerous morphotypes that are difficult to distinguish. Text-figure 4 illustrates the morphotypes recorded in the sequence. Smooth

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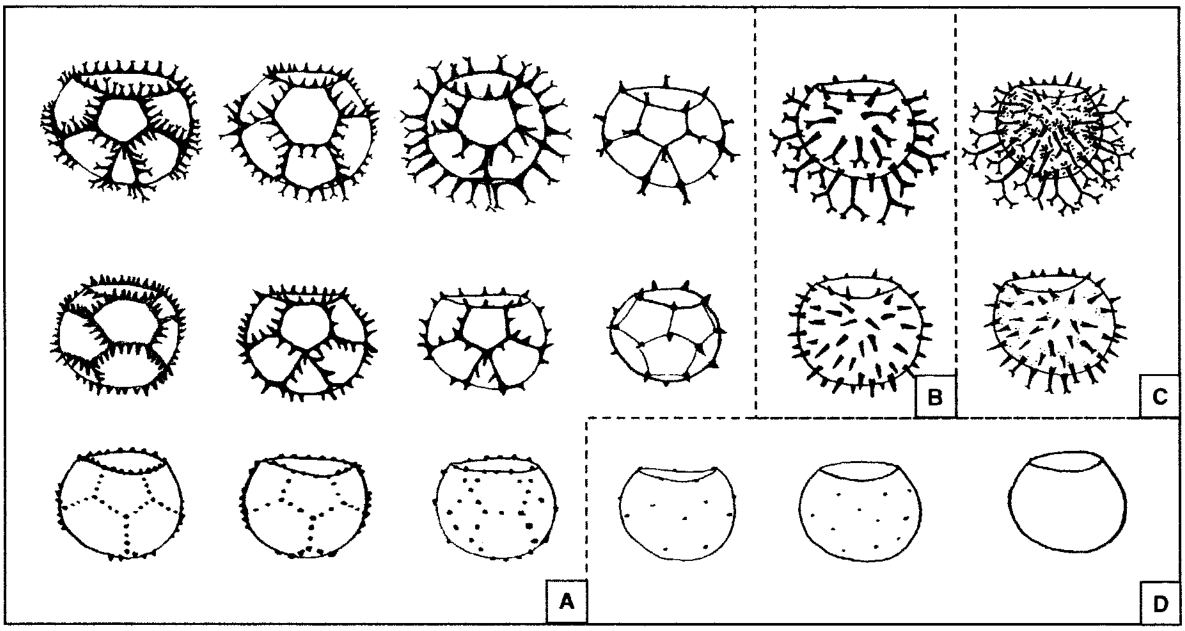
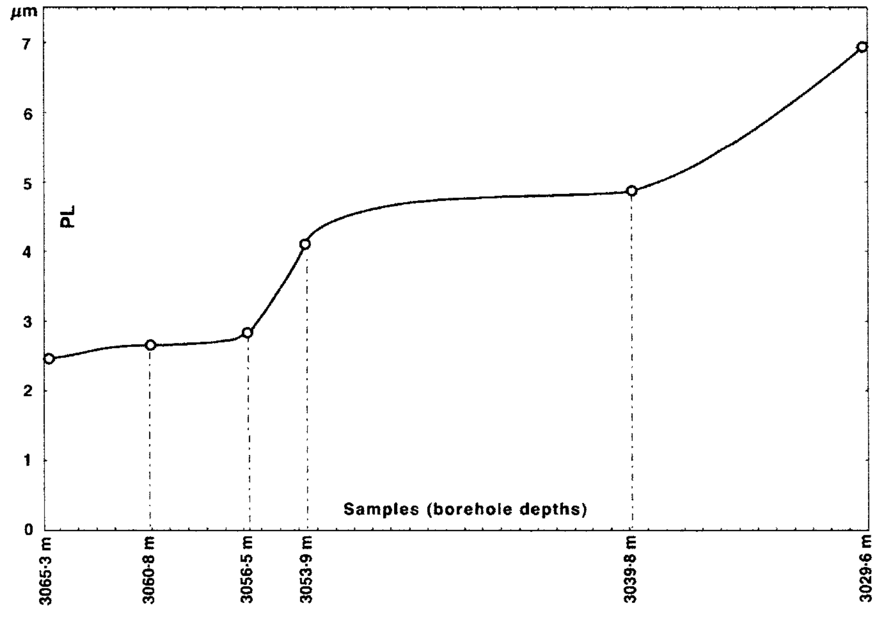


TEXT-FIG. 4. Idealised line drawings of some of the morphotypes of the galeate acritarch plexus present in the Algerian samples analysed in this study; for explanation, see text. Specimens can be attributed to the 'classical' genera as follows: A, *Cymatiogalea*; B, *Priscogalea*; C, *Stelliferidium*; D, *Caldariola*.



TEXT-FIG. 5. Fluctuation of the average process length (PL) within the galeate population in the sequence of the Cambrian–Ordovician transition in borehole NI-2.

specimens without ornamentation correspond to *Caldariola*; those with polygonal fields fit with the diagnosis of *Cymatiogalea*; specimens without polygonal fields have been attributed to *Priscogalea* if they show no ornament, or to *Stelliferidium* if they have striae radiating from the process bases. Specimens are frequently found that are intermediate between these four 'classical' genera. A selection of morphotypes is

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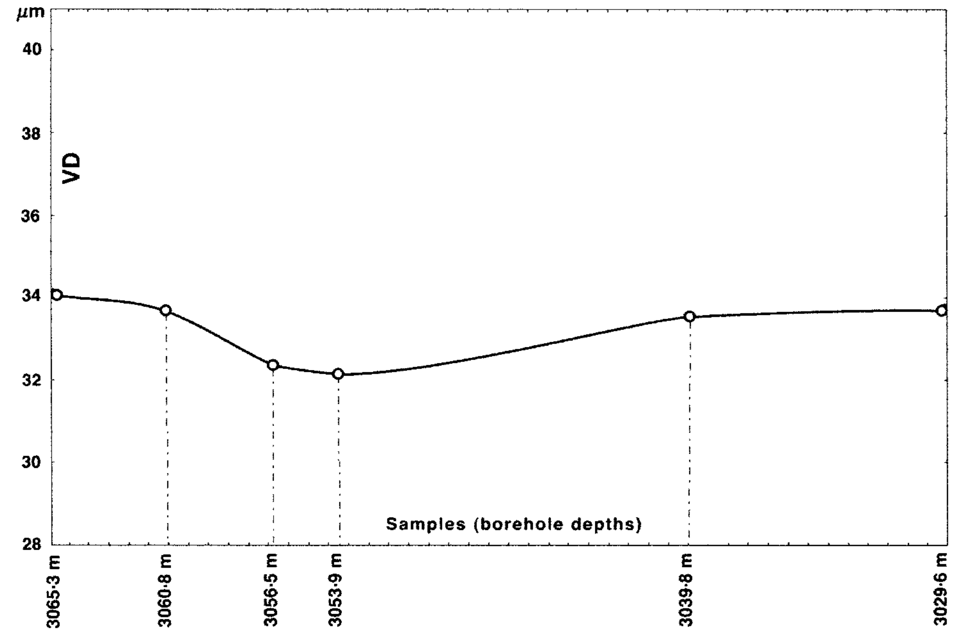

TEXT-FIG. 6. Fluctuation of the average vesicle diameter (VD) in the galeate population in the sequence of the Cambrian/Ordovician boundary in borehole NI-2.

illustrated in Plate 1, demonstrating the transition of specimens with short, commonly simple processes to those with longer, commonly furcated specimens. Plate 2 illustrates a selection of process types, including simple, bifurcated and multifurcated, but also truncated processes.

The measured values of the different morphological parameters in the galeate population through the six samples are indicated in Table 1. For each sample the mean values of both the average process length (PL) and the vesicle diameter (VD), the ratio PL/VD, and the percentages of specimens with (1) distal ramifications of the processes (BRA), (2) membranes between the processes (MEMB), (3) striae radiating from the process bases (STR), (4) no ornament (NO ORN) and (5) polygonal fields on the vesicle surface (POLYG) are indicated. In addition, the mean values of these parameters for all 564 specimens in the six samples have been calculated.

The change in process length (PL) through the succession is illustrated in Text-figure 5. For each of the 564 specimens in the succession, all processes were measured and the average for each specimen was used in the dataset. Subsequently the mean value of all specimens was calculated for each sample. These mean values are plotted in Text-figure 5. In the three lowermost samples (3065·3, 3060·8, and 3056·5 m) the mean value of the PL slowly increases from 2·4 to 2·8 μm, before reaching the value of 4·1 μm in sample 3053·9 m. The PL reaches the value of 4·9 μm in sample 3039·8 m and 6·9 μm in the uppermost sample in the borehole (3029·6 m). These values indicate that the PL increases in the six samples from the bottom to the top of the succession, and that in the uppermost sample the average length of the processes in the galeate population is almost three times longer than in the lowermost sample.

Text-figure 6 indicates the mean vesicle diameter (VD) of all of the specimens through the section. This parameter remains almost constant in all samples. The mean vesicle diameter of 34·0 μm in the lowermost sample (3065·3) m is almost identical to the value of 33·9 μm in the uppermost sample (3029·6), the lowest value of 32·2 μm being measured in sample 3053·9 m.

The proportion of specimens with polygonal fields among all galeate specimens varies through the six samples between 17·5 and 34·5 per cent, without showing a significant trend. These values are not, therefore, illustrated here.

The change of some of the qualitative parameters is particularly interesting (Text-fig. 7). The measurements illustrated in Text-figure 7 clearly indicate that there is an increase in the proportion of

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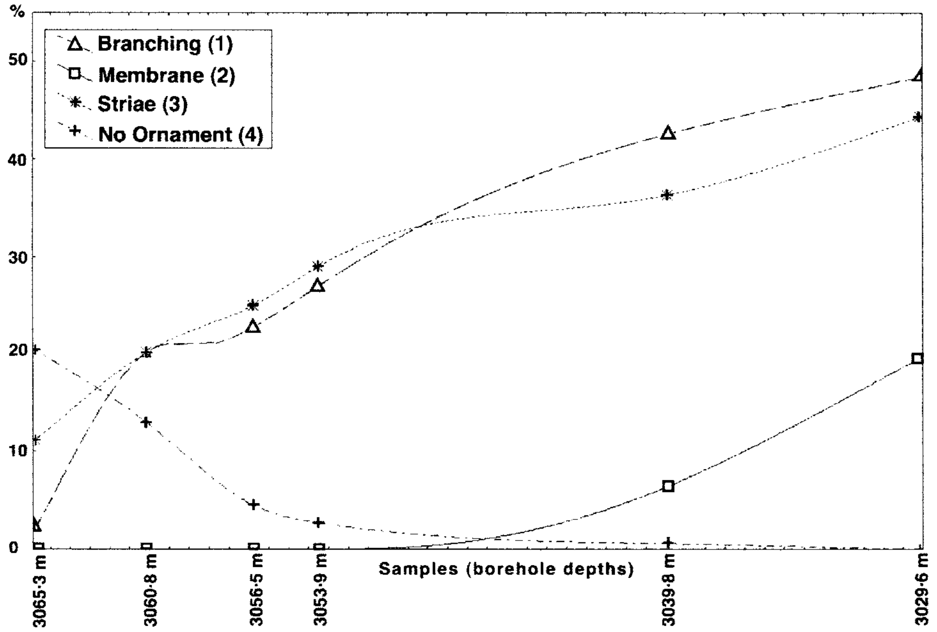

TEXT-FIG. 7. Fluctuation of the qualitative parameters in the galeate population in the sequence of the Cambrian/Ordovician boundary in borehole Nl-2.

specimens with processes (branching) ramified. In the lowermost sample (3065·3 m), only about 2 per cent of the specimens show ramified processes. This number increases to about 20 per cent in sample 3060·8 m, 22 per cent in sample 3056·5 m and 27 per cent in sample 3053·9 m, before finally reaching values of about 42 per cent and about 48 per cent, respectively, in the two uppermost samples, 3039·8 m and 3029·6 m. Hence, as for the evolution of the PL, a continuous increase in the proportion of specimens with ramified processes is observed between the bottom and the top of the succession.

A similar observation is made on the presence/absence of membranes between the processes (Text-fig. 7). None of the galeate acritarchs in the four lowermost samples has membranes. Membranes only appear in the samples at 3039·8 m (*c.* 6 per cent of all specimens) and 3029·6 m (*c.* 18 per cent).

The presence/absence of striae follows a similar trend to that of the previous two criteria (Text-fig. 7).

EXPLANATION OF PLATE 1

Scanning electron micrographs of galeate acritarch specimens from the Cambrian–Ordovician transition of borehole Nl-2, Algerian Sahara. All micrographs are from the sample at depth 3053·9 m.

Fig. 1. *Stelliferidium* sp., lateral view; × 1066.
Fig. 2. *Cymatiogalea* sp, lateral view; × 1366.
Fig. 3. *Cymatiogalea* sp., apical view; × 1250.
Fig. 4. *Priscogalea* sp., lateral view; × 1033.
Fig. 5. *Stelliferidium* sp., apical view; × 1100.
Fig. 6. *Stelliferidium* sp., lateral view; × 1400.
Fig. 7. *Stelliferidium* sp., lateral view; × 1200.
Fig. 8. *Stelliferidium* sp., lateral view; × 1350.
Fig. 9. *Stelliferidium* sp., lateral view; × 1050.
Fig. 10. *Stelliferidium* sp., lateral view; × 1265.
Fig. 11. *Stelliferidium* sp., lateral view; × 1150.
Fig. 12. *Stelliferidium* sp., lateral view; × 1100.

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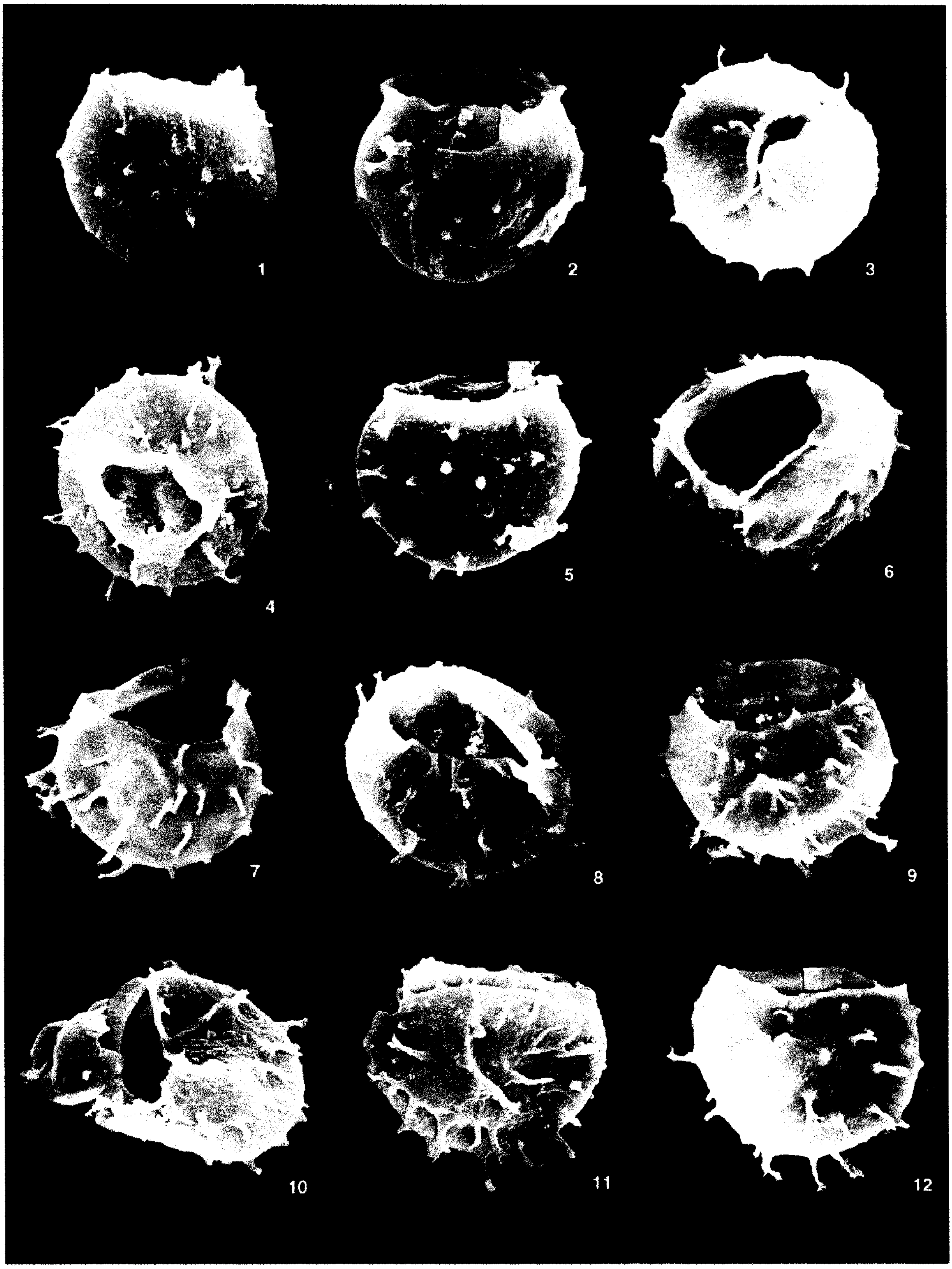
PLATE 1



SERVAIS *et al.*, galeate acritarchs

TABLE 1. Mean values in each of the six samples of both the average process length (PL), and the average vesicle diameter (VD); ratio PL/VD; and percentages of specimens with (1) distal ramifications of the processes (BRA), (2) membranes between the processes (MEMB), (3) striae radiating from the process bases (STR), (4) no ornament (NO ORN) and (5) polygonal fields on the vesicle surface (POLYG). Total: mean values for all 564 specimens in the six samples.

	3065·3 m	3060·8 m	3056·5 m	3053·9 m	3039·8 m	3029·6 m	Total
PL	2·4	2·7	2·8	4·1	4·9	6·9	4·3
VD	34·0	33·7	32·5	32·2	33·6	33·9	33·4
PL/VD	0·07	0·08	0·09	0·13	0·14	0·21	0·13
% BRA	2·2	20·7	22·4	27·8	42·7	48·5	31·7
% MEMB	0·0	0·0	0·0	0·0	6·4	18·7	5·9
% STR	11·1	20·3	25·5	28·7	36·3	44·3	33·0
% NO ORN	20·0	13·2	3·6	2·7	1·1	0·0	5·7
% POLYG	17·8	22·8	34·5	34·2	24·6	17·5	24·7

Only about 11 per cent of the specimens show striae radiating from the process bases in the lowermost sample (3065·3 m). This value continuously increases in the overlying samples: 3060·8 m (*c.* 20 per cent), 3056·5 m (*c.* 25 per cent), 3053·9 m (*c.* 29 per cent), 3039·8 m (*c.* 36 per cent) and 3029·6 m (*c.* 44 per cent).

In addition to these parameters, the number of specimens without ornamentation (*Caldariola*-type) has also been plotted on Text-figure 7. The high proportion of 20 per cent of smooth specimens in the lowermost sample (3065·3 m) decreases towards the top of the succession: 3060·8 m (*c.* 13 per cent), 3056·5 m (*c.* 4 per cent), 3053·9 m (*c.* 3 per cent), 3039·8 m (*c* .1 per cent) and 3029·6 m (no smooth specimens recorded).

The results, illustrated in Table 1 and in Text-figures 5–7, thus indicate that some parameters do not evolve significantly through the succession: the vesicle diameter remains almost constant, whereas the proportion of specimens with polygonal fields shows no significant trend. However, other criteria evolve progressively from the lowermost (3065·3 m) to the uppermost (3029·6 m) sample. The mean value of the process length increases together with (1) the number of specimens with distal ramifications, (2) the number of specimens that show striae at the bases of the processes, and (3) the number of specimens with membranes.

INTERPRETATION OF THE POPULATION DYNAMICS OF THE GALEATES AT THE CAMBRIAN–ORDOVICIAN TRANSITION IN BOREHOLE NL-2

Process structure and functional morphology

The measurements of 564 galeate specimens from six samples covering the Cambrian–Ordovician transition in borehole Nl-2 clearly indicate that the most important morphological changes through the sequence concern the process development, but not the vesicle size nor the percentage of specimens showing polygonal fields. Hence, three criteria concerning the processes evolve with a similar tendency. The process length (PL) increases, together with the frequency of star-shaped striae at the process bases, ramifications at their distal end, and membranes between the process stems.

A first conclusion is that a population with numerous specimens with longer processes commonly contains more specimens with a striate ornament at their bases. The process structure of a galeate acritarch can be schematically explained as shown in Text-figure 8. The processes that seem to grow out from the membrane of the central vesicle, probably from an external layer ('ectophragm', compare the scanning electron micrographs of galeates in Servais and Eiserhardt 1995, pl. 4, fig. 4), start to build longitudinally arranged structural elements at the process base, presumably in order to provide greater stability (Plate 2). The crests or striae radiating out from the process bases would thus very probably be an element of functional morphology and not a simple decoration or ornament. Thus, in terms of classification of the

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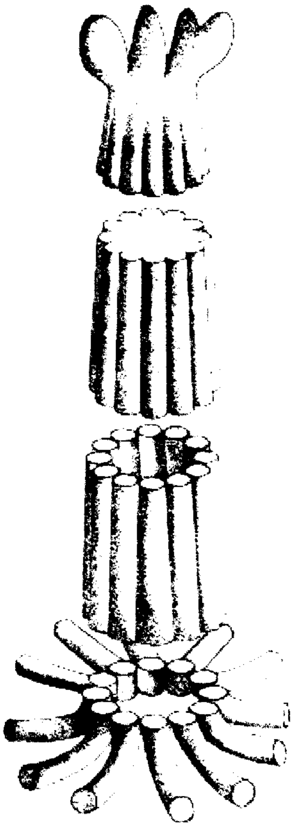
TEXT-FIG. 8. Idealised reconstruction of the process of a galeate acritarch; for explanation, see text.



galeate acritarchs, they should not be considered as parameters to distinguish different taxa, and certainly not at the generic level. This interpretation is in agreement with the classification model of Rasul (1974), who considered the striae of low taxonomic importance and who retained only two genera for the classification of the galeates (*Cymatiogalea* and *Priscogalea*). The interpretation is, however, in direct opposition to the taxonomic scheme of Deunff *et al.* (1974) who added a third genus (*Stelliferidium*) for specimens with star-shaped striae at the bases of the processes.

A similar conclusion concerns the tips of the processes. According to the galeates analysed in our study, a population containing numerous specimens with short processes includes only a few morphotypes with distally ramified processes, and most of the processes are simple and not ramified. The ramifications, including different styles (bifurcate, trifurcate or multifurcate; with first, second or third etc. order branching), generally occur only on longer processes in the galeates of the Algerian sequence. In addition, with increasing process length, the number of membranes between the process stems are also found in greater numbers.

Comparison with laboratory culture experiments on dinoflagellates

Laboratory culture experiments on modern dinoflagellates have provided evidence that the processes of resting cysts grow within a relatively short time interval. The transition from the motile planozygote to the resting cyst of *Lingulodinium polyedrum* takes approximately 10–20 minutes (Kokinos and Anderson 1995). According to this latter study, the development of the resting cyst ends with process formation, just before the rupture of the outer membrane surrounding theca and cyst. *L. polyedrum* cyst process formation comprises two steps. First, the shafts develop centrifugally and secondly the tips are formed. These tips show a very large morphological variability (Kokinos and Anderson 1995; Hallett 2000). As noted by Kokinos and Anderson (1995), the distal endings of the processes only appear if maturity is reached in the

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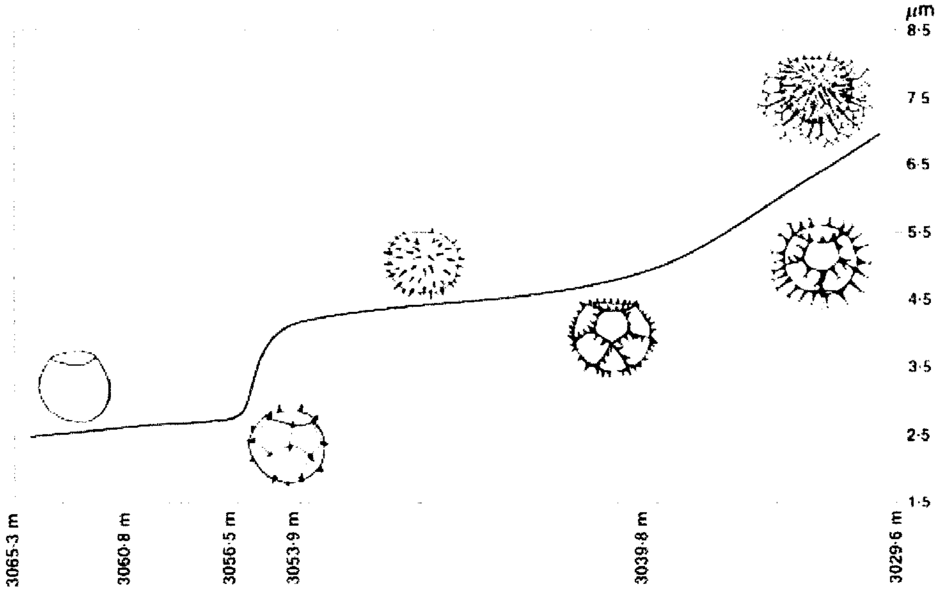

TEXT-FIG. 9. Morphological changes in the morphotypes of the galeate acritarch plexus in the sequence of the Cambrian/Ordovician boundary in borehole Nl-2. The line represents the change in process length. For explanation, see text.

cyst construction. In most cases, the outer membrane ruptured prematurely before the processes were morphologically mature, resulting in fewer processes with an irregular distribution or truncated processes (Kokinos and Anderson, 1995).

In light of these studies on their presumed modern equivalents, it is possible to imagine that the galeate acritarchs may represent resting cysts of possibly a single biological species. Depending on the prevailing ecological parameters (e.g. salinity, temperature) and on the maturity attained before rupture of the outer membrane, these cysts may show a wide variety of process morphologies, which so far have been described under four generic (morphogenera) and 84 specific (morphospecies) names.

Interpretation: a change of salinity?

Text-figure 9 summarises schematically the results obtained concerning the morphological changes of the galeate specimens in the Cambrian/Ordovician boundary interval in the upper part of the 'Grés de Bordj

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EXPLANATION OF PLATE 2

Figs 1–12. Scanning electron micrographs of processes of *Stelliferidium* specimens from the Cambrian–Ordovician transition of borehole Nl-2, Algerian Sahara. All micrographs are from the sample at depth 3053·9 m. 1, Trifurcate process with first order branching and striae at the process base; ×5500. 2, distally ramified, multifurcate process with striae at the process base; ×5500. 3, ramified and truncated processes with basal striae; ×2600. 4, multifurcate process with basal striae joining those radiating from neighbouring processes; ×7500. 5, complexely ramified (third order branching) process, with characteristic basal striae on the vesicle; ×9000. 6, heterogeneous (distally simple and branching) processes with basal striae; ×5000. 7, process with striae reaching the process step; ×6600. 8, truncated process with characteristic striae; ×12,000. 9, vesicle with joining basal striae between the processes; ×4000. 10, truncated and ramified processes (second order branching) with basal striae; ×2100. 11, truncated, multifurcate and simple process with basal striae; ×3300. 12, long, multifurcate processes with striae on the vesicle; ×2300.

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PLATE 2

SERVAIS *et al.*, *Stelliferidium*

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Nili' Member. The only sedimentological data available are the lithological change that possibly indicates that the lowermost levels (at 3065·30 m) were deposited in a shallower water environment than the uppermost level analysed here (at 3029·60 m). More precise sedimentological data are needed, however, to confirm such an interpretation. Nevertheless, it is clear that most morphological parameters observed in the galeate populations seem to have changed gradually, possibly reflecting a continuous change in the conditions affecting the variability.

Based on observations of modern marine dinoflagellates (e.g. Wall *et al.* 1973; Turon 1984; de Vernal *et al.* 1989; Nehring 1994; Matthiessen and Brenner 1996; Ellegaard 2000; Brenner 2001) and cultural experiments (see discussion above), it appears that at least some groups of living microplankton produce longer processes under higher salinity. Temperature may also influence process formation in the dinoflagellate cysts (e.g. Hallett, 2000), but no information is available concerning temperature changes in the sequence of the borehole Nl-2.

Hence, a tentative interpretation could suggest that the process length of the galeates increases with greater salinity, i.e. in offshore environments. This interpretation is plausible, as it is probable that in the deeper facies (in the uppermost samples) the salinity was higher (open marine environment) than in the shallower facies (in the lowermost samples). A similar observation has been made for the galeates in the Lower–Middle Ordovician of the Yangtze Platform, southern China (Brocke 1998; Li Jun, pers. comm. 2002), where specimens with longer processes were observed more commonly in deeper water environments.

The fact that the vesicle diameter in the galeate populations examined is rather constant is compatible with observations on living marine dinoflagellates in cultural experiments.

Future studies are needed to confirm the tentative interpretation provided in this paper. Many parameters interact in acritarch distribution. Salinity is probably an important factor, but future research is needed, including investigations on the taphonomy and on the hydrodynamic properties of the different morphotypes, in order to propose complete, representative models.

POSSIBLE FUTURE AIMS OF ACRITARCH RESEARCH

The interpretations presented above can possibly be extended to other acritarch morphotypes. Future studies on large numbers of specimens are necessary for a better understanding of the population dynamics of other morphologically highly variable acritarchs such as *Baltisphaeridium*, *Goniosphaeridium*, *Micrhystridium* or *Multiplicisphaeridium*. These taxa are of limited biostratigraphical significance and currently serve as dustbin genera for morphotypes of spherical, polygonal, small and complexely branched forms, respectively. They may possibly become more useful for palaeoecological considerations if the fluctuation of some of their morphological criteria in different depositional environments can be detected.

One of the form-groups for which such a study may yield positive results is the Ordovician plexus of peteinosphaerid acritarchs that includes the genera *Cycloposphaeridium*, *Liliosphaeridium* and *Peteinosphaeridium*. These genera and their species are highly variable and are essentially distinguished on differences in process size and morphology. The recent description of new species of *Liliosphaeridium* from the Middle Ordovician of Öland, Sweden, by Bagnoli and Ribecai (2001) indicate a trend in two sections towards a progressive reduction in the vesicle wall ornamentation and an increase in the height of the 'calyx' of the processes. These progressive changes may be of palaeoecological significance and it would be very interesting to re-interpret the documented distribution of the genus *Liliosphaeridium* by considering sedimentological and palaeoecological information from the sections analysed.

Another field for such analyses would be the Silurian genus *Visbysphaera*, which is known to be extremely variable in process morphologies (Le Hérissé 1989; Mullins 2001). A re-investigation of this genus, including sedimentological and palaeoecological investigations in the type sections of the Welsh Borderland, United Kingdom, and the well-studied sequences of the island of Gotland, Sweden, would very probably lead to new interpretations.

Studies on the population dynamics could also be undertaken on acritarchs with triangular and rectangular vesicles in order to understand better the relationships between veryhachid acritarchs (e.g. *Veryhachium*, *Dorsennidium*). The different populations of *Frankea sartbernardensis* observed by Servais

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(1993) may possibly be interpreted as environmentally influenced. The assemblages of the type levels at Sart-Bernard, Belgium, considered to be deeper water facies owing to the presence of cyclopygid trilobites (Owens *et al.*, 2001), show only a little intraspecific variability. However, the assemblages from samples of the Czech locality of Krusna Hora, deposited in a shallower water facies, display not only a much higher diversity (Vavrdová 1990), but also a larger variation of process morphologies of the species *F. sartbernardensis* (see Servais 1993). The biostratigraphical significance of *Frankea* species may thus be less than suggested by Vecoli *et al.* (1999). Different process lengths in *Frankea* may not necessarily indicate a different age, but possibly different palaeoenvironmental conditions.

CONCLUSIONS

An important result from cultural experiments on modern dinoflagellates is the observation that considerable morphological variation with respect to the size and shape of the processes can be produced by a single biologically defined species. This result is particularly significant from a palaeontological point of view. The galeate acritarchs in the Cambrian–Ordovician transition in borehole NI-2 show a gradual increase in the average process length and complexity of their structure through the six samples that were investigated. The number of striae at the process bases, which are considered here to stabilize the processes, increases together with the process length and the ramifications on the distal termination of the processes. The gradual increase in average process length, number of basal striae and distal ramifications is possibly related, by analogy with modern dinoflagellates, to increasing salinity, i.e. possibly with more open marine conditions. Striae at the bases of processes, the distal terminations and the presence of membranes can be used as parameters to distinguish groups of morphotypes. However, this classification may not necessarily reflect biological species and therefore must be regarded very critically before drawing biostratigraphical conclusions.

As the galeates occur continuously and with wide variability in the Cambrian–Ordovician transition of the borehole studied, it is difficult to determine the Cambrian/Ordovician boundary on the basis of the galeate acritarch biostratigraphy. The selection of a galeate acritarch (*Stelliferidium furcatum*) as a biostratigraphical marker (Vecoli *et al.* 1995) may, therefore, be questionable.

These results do not diminish the stratigraphical importance of acritarchs. However, in order to detect significant biostratigraphical markers, the First Appearance Datum (FAD) of clearly distinguishable taxa must be selected, and not arbitrarily chosen morphotypes that show only a few differences from comparable taxa.

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Acritarch distribution along an inshore–offshore transect in the Gorstian (lower Ludlow) of Gotland, Sweden

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Abstract

To better understand palaeoecological signatures in Palaeozoic acritarch assemblages, the distribution of palynomorphs has been quantitatively studied in eight localities from the Gorstian, lower Ludlow (Late Silurian) of Gotland, Sweden. The localities are situated along an inshore–offshore transect comprising shallow marine lagoonal environments to distal shelf facies. Process-bearing acritarchs and sphaeromorphs constitute the main components within the palynomorph assemblages. The lateral distribution of palynomorphs exhibits characteristic features at three different levels as follows. (1) With regard to the overall composition of the palynomorph assemblages, the abundance of process-bearing acritarchs increases towards the distal shelf, while the abundance of sphaeromorphs decreases. (2) At the generic level, the acritarchs *Micrhystridium* and *Dilatisphaera* are more abundant in the proximal facies, while *Evittia*, *Percultisphaera* and *Oppilatala* are more common in distal environments. (3) At an infrageneric level, *Micrhystridium* morphotypes with shorter processes are mainly present in proximal environments, while those with longer and ramified processes occur in more distal shelf environments. The palynomorph distribution along the inshore–offshore transect highlights the potential of acritarchs and prasinophytes as palaeoenvironmental indicators.

Keywords: acritarchs; palynomorphs; palaeoecology; Gotland; Silurian; Ludlow

1. Introduction

It is well known that the Silurian sediments of Gotland contain abundant and very well preserved palynomorphs, with three-dimensional preservation being recognized in micritic limestones (Munnecke and Servais, 1996). The Late Silurian palynological assemblages of Gotland are mainly composed of process-bearing acritarchs, sphaeromorphs and prasinophytes. They have been previously investigated in detail by Le Hérissé (1989). Other less abundant palynomorphs are chitinozoans (Laufeld, 1974b), scolecodonts (Bergman, 1989), trilete spores and cryptospores (Hagström, 1997) and some tubular- or

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filamentous debris attributed to the nematophytes (Le Hérissé, 1989).

Classical studies in Silurian palynology (e.g., Cramer, 1970) demonstrated that acritarchs are of great biostratigraphical value. Accordingly, the first investigations on acritarchs from Gotland also helped to establish their biostratigraphical distribution in the Silurian (Eisenack, 1954, 1959, 1965; Cramer et al., 1979). To date, however, attempts to decipher the palaeoecological potential of Palaeozoic palynomorphs have been rare. This is in contrast with the situation in the Mesozoic where many studies over the last 30 years have concentrated on dinoflagellate cyst-based palaeoenvironmental reconstructions or dinoflagellate (cyst) palaeobiology. Such studies have highlighted the potential of dinoflagellate cysts as palaeoceanographical or palaeoclimatic indicators in the Quaternary (e.g., Wall et al., 1977; de Vernal et al., 2001), Neogene (e.g., Versteegh, 1994), Palaeogene (e.g., Brinkhuis, 1994, Pross and Schmiedl, 2002), Cretaceous (e.g., Brinkhuis et al., 1998), and Jurassic (e.g., Riding and Hubbard, 1999) (see Pross and Zonneveld, in press, for a detailed review). However, the palaeobiological and palaeoecological characteristics of Palaeozoic, marine, organic-walled microphytoplankton assemblages remain poorly known.

Some palynological studies on Upper Palaeozoic sediments have attempted to locate the palaeoshoreline or to recognize transgressive/regressive cycles within vertical or lateral transects by using the fluctuations of microphytoplankton/spore ratios (e.g., de Jekhowsky, 1963; Richardson and Rasul, 1990; Wicander and Wood, 1997). However, in lateral transects without land plant-derived spores or in Lower Palaeozoic sections where land plant-derived spores are absent, the palaeoshoreline cannot be directly indicated based on this approach. A few quantitative studies have described acritarch assemblages that were interpreted to be characteristic of specific palaeoenvironments (e.g., Staplin, 1961; Jacobson, 1979; Dorning, 1981b, 1987; Al-Ameri, 1983; Dorning and Bell, 1987; Richardson and Rasul, 1990). Hence, the use of differences in the composition of acritarch assemblages may provide an interesting approach of palaeoenvironmental reconstructions in the Palaeozoic.

This paper describes the lateral distribution of Late Silurian (Ludlow) palynomorphs from the island of Gotland, Sweden, based on the quantitative investigation of large populations from localities situated along an inshore–offshore transect in the Gorstian (lower Ludlow). We have deciphered a relationship between facies distribution and palynomorph assemblages at three different levels: (1) changes in the overall palynomorph distribution; (2) fluctuations at the generic level; and (3) variations at the infrageneric level. The results of these observations are compared with the data available from previous studies, especially with those from the transects in the Wenlock and Ludlow of the Welsh Borderland, Great Britain (Dorning, 1981b, 1987; Dorning and Bell, 1987).

2. Previous research on the palynomorphs of Gotland and on Palaeozoic acritarch palaeoecology

2.1. Palynomorphs of Gotland

Based on several hundred samples, Le Hérissé (1989) investigated the organic-walled microphytoplankton of Gotland in great detail. According to his study, the acritarch and prasinophyte assemblages of Gotland were less diverse in the Ludlow than in the Llandovery or the Wenlock. Some genera [e.g., *Domasia* Downie 1960, *Deunffia* (Downie 1960) Thusu 1973] disappeared, while other genera became more common and diverse in the Ludlow. The list of acritarchs in the Ludlow of Gotland is generally limited to the following genera: *Micrhystridium* Deflandre 1937, *Evittia* Brito 1967 (sensu Lister 1970), *Dilatisphaera* Lister 1970, *Oppilatala* Loeblich and Wicander 1976, and *Percultisphaera* Lister 1970 (acanthomorphs); *Eupoikilofusa* Cramer 1970, *Leiofusa* Eisenack 1938 (netromorphs); *Veryhachium* Deunff 1954, *Neoveryhachium* Cramer 1970, and *Dorsennidium* Wicander 1974 (*sensu* Stancliffe and Sarjeant, 1996) (polygonomorphs). The assemblages also include the prasinophyte genera *Cymatiosphaera* Wetzel 1933, *Dictyotidium* Eisenack 1955, and *Duvernaysphaera* Staplin 1961. In the Ludlow of Gotland, Laufeld (1974b) observed a reduced diversity in the chitinozoan assemblages, which are dominated by the genera *Conochitina* Eisenack 1931,

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Ancyrochitina Eisenack 1955, *Angochitina* Eisenack 1931, *Linochitina* Eisenack 1968, *Gotlandochitina* Laufeld 1974b and *Sphaerochitina* Eisenack 1955. Scolecodonts are represented by the genera *Kettnerites* Zebera 1935 and *Lanceolatites* Bergman 1987 (Bergman 1989).

Although previous studies mainly focused on taxonomy or biostratigraphy, Le Hérissé (1989) also discussed the influence of palaeoenvironmental parameters on the composition of the assemblages and the morphology of the taxa he observed. In addition, Le Hérissé (1989) also recorded acritarchs with abnormal process morphologies (e.g., in some species of the genera *Evittia*, *Salopidium* and *Veryhachium*) which he related to palaeoecological disturbances.

2.2. Previous investigations on Palaeozoic acritarch/prasinophyte palaeoecology

The earliest paper on acritarch palaeoecology (Staplin, 1961) interpreted the distribution and abundance of Devonian microplankton from Alberta, Canada. Staplin (1961) observed the common occurrence of thin-spined acritarch specimens close to reef areas and a higher abundance of morphotypes with longer and thicker ornamentation at a greater distance from the reefs.

A palaeoecological approach was also tentatively introduced by Riegel (1974) in his investigation of Lower and Middle Devonian rocks of western Germany. According to his study, acritarch diversities may be used to differentiate between a low-diversity neritic facies and a higher diversity pelagic facies. Riegel (1974) concluded that the composition of the microphytoplankton assemblages was probably controlled more by facies differences than by climatic or phylogenetic variations.

Jacobson (1979) reported the abundance of several Middle and Upper Ordovician acritarch groups in vertical sections of North American strata and suggested that some of them follow the distribution patterns of conodonts and chitinozoans. He retained three acritarch categories and concluded that the "leiosphaerid class" reflected near-shore shallow water environments, while the "peteinosphaerid-*Dicommopalla*" and "baltisphaerid-veryhachid-*Polygonium* class" reflected shoal and open-sea environments, respectively.

Colbath (1980) studied the abundance variations of Late Ordovician acritarchs from the Eden Shale of Indiana, USA. He defined a model where changes in microplankton abundance were explained by water mass fluctuations.

Models for the lateral distribution patterns of Silurian palynomorphs include a study from Libya by Al-Ameri (1983), and four papers on the distribution of acritarchs in the Welsh Borderland and Wales (Dorning, 1981b, 1987; Dorning and Bell, 1987; Richardson and Rasul, 1990). Dorning (1981b) reported the occurrence of acritarch "bloom assemblages" in the late Ludlow at some localities. Following a semiquantitative approach, he divided the assemblages into three classes which were named "near-shore", "offshore" and "deep water". Dorning (1987) and Dorning and Bell (1987) subsequently observed similar patterns on the Wenlock shelf of the same area. Dorning and Bell (1987) reported four typical assemblages: the "*Leiosphaerridia wenlockia* Assemblage" was recorded from the reef limestone; the "*Leiofusa tumida* Assemblage" from shallow shelf carbonates; the "*Micrhystridium intonsurans* Assemblage" from open shelf carbonates, and the "*Salopidium granuliferum* Assemblage" from deeper shelf environments. In the same area, Richardson and Rasul (1990) described the vertical distribution of the palynological components in the regressive sequence of the Ludlow and Pridoli Series. They proposed a palynofacies interpretation in which specific associations of microphytoplankton ("phases") correspond to the depositional environments observed. They showed that sphaeromorphs (together with micrhystrids) were well represented in the marine environment while sporomorphs occurred in large quantities during an episode of shoaling in the upper part of the studied section. The lower part of the section was characterized by high percentages of various polygonomorphs and acanthomorphs. Thus, the acritarch, chitinozoan, and scolecodont associations were used to define a marine influence, while sporomorphs, micrhystrids and tasmanitids were used to assess the proximity of the shoreline.

Vanguestaine et al. (1997) observed variations in diversity and generic content in acritarch assemb-

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lages from two Late Frasnian sections from Belgium. Finely ornamentated specimens attributable to the acritarch genera *Elektoriskos*, *Gorgonisphaeridium*, *Lophosphaeridium*, and prasinophyte genera such as *Cymatiosphaera*, *Duvernaysphaera*, *Maranhites* and *Pterospermella* are present in the lower part of the sections, interpreted as a semireefal shallower environment. The upper part of the sections (attributed to

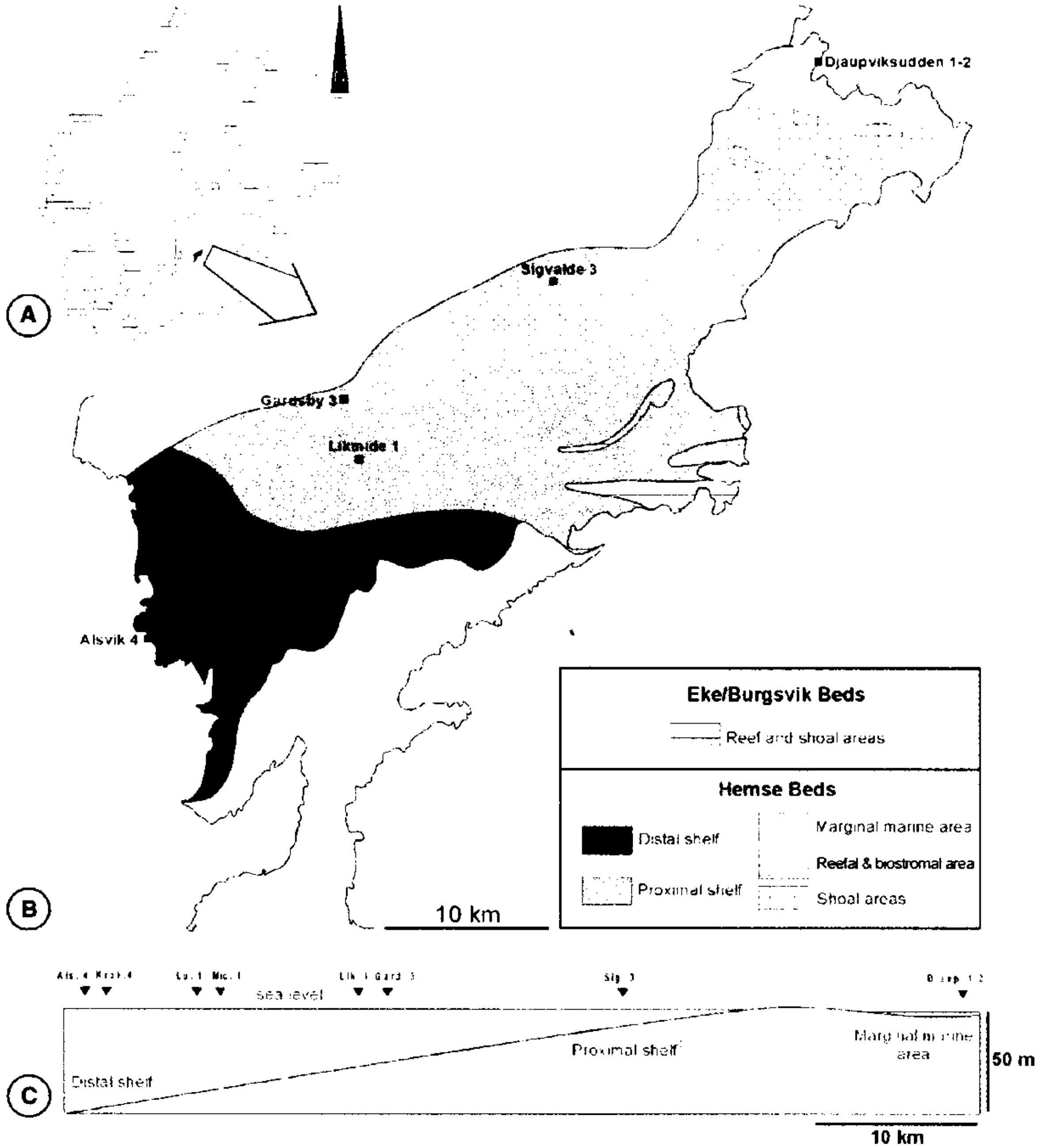

Fig. 1. (A) Position of the island of Gotland in the Baltic Sea. (B) Facies distribution mapped for the Hemse Beds and sample localities (after Samtleben et al., 2000). (C) Position of the eight localities on the supposed Ludlow carbonate shelf.

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deep-sea off-reef conditions) was characterized by the association of acritarch genera such as *Micrhystridium*, *Solisphaeridium* and *Unellium*. Vanguestaine et al. (1997) concluded that these observations are consistent with the model of Staplin (1961) in which hystrichosphere becomes more abundant with increasing distance from the reef.

More recently, Li et al. (2004-this volume) evaluated the distribution of acritarchs along an inshore–offshore transect based on seven localities exposing the Early/Middle Ordovician boundary in the Yangtze Platform, southern China. Their main conclusion is that the offshore assemblages are more diverse and complex than the assemblages from neritic environments.

3. Geological and palaeoenvironmental setting

The Silurian sediments of Gotland (Sweden) were deposited in a warm epicontinental sea situated near the Silurian equator. The island of Gotland is situated on the Baltic shield (Fig. 1A) which protected the sediments from deep burial or tectonic stress. Therefore, the rocks are undeformed. The unfolded strata dip less than 1° towards the SE. Lithification took place in the shallow marine burial realm, and late diagenetic alteration is negligible (Munnecke and Samtleben, 1996). These conditions have resulted in exceptionally well-preserved calcareous and organic-walled fossils and thus are responsible for the reputation of Gotland as one of the world's most famous Silurian *Fossillagerstätte*.

The oldest sediments on Gotland are situated on the NW coast of the island and are of late Llandovery age. The youngest rocks are of late Ludlow age and crop out along the SE coast. The Silurian sequence is mainly built up of limestone–marl alternations interrupted four times by massive stromatopore and coral reef structures and extended carbonate platforms (Samtleben et al., 1996).

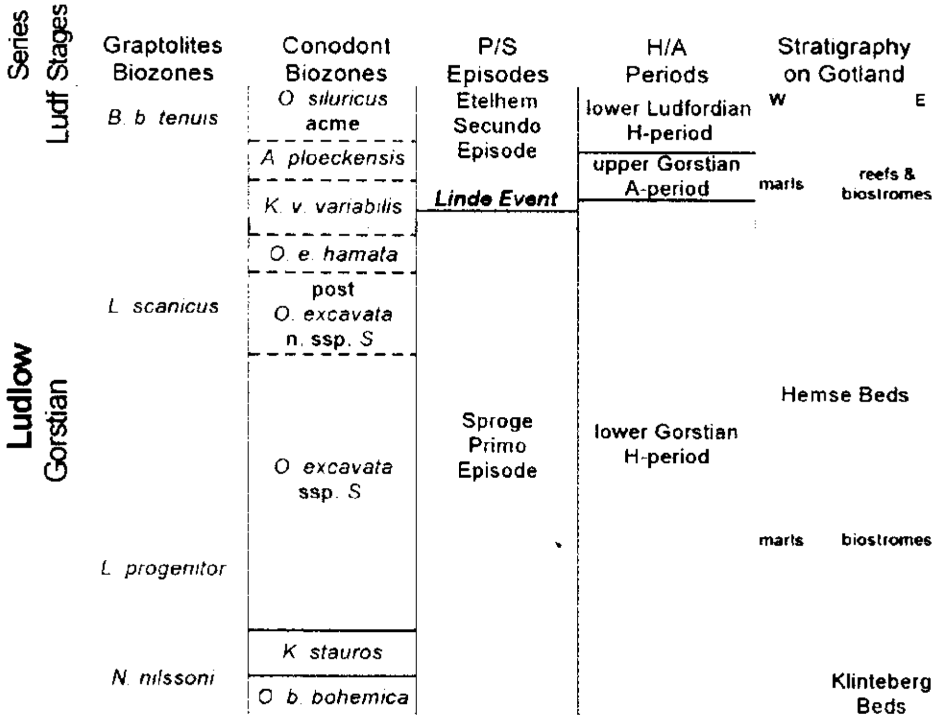

Fig. 2. Synoptic presentation of the biostratigraphic zonations (graptolites and conodonts). P/S episodes after Jeppsson and Aldridge (2000) and H/A periods after Bickert et al. (1997) and Samtleben et al. (2000). The sampled time slice is marked in grey.

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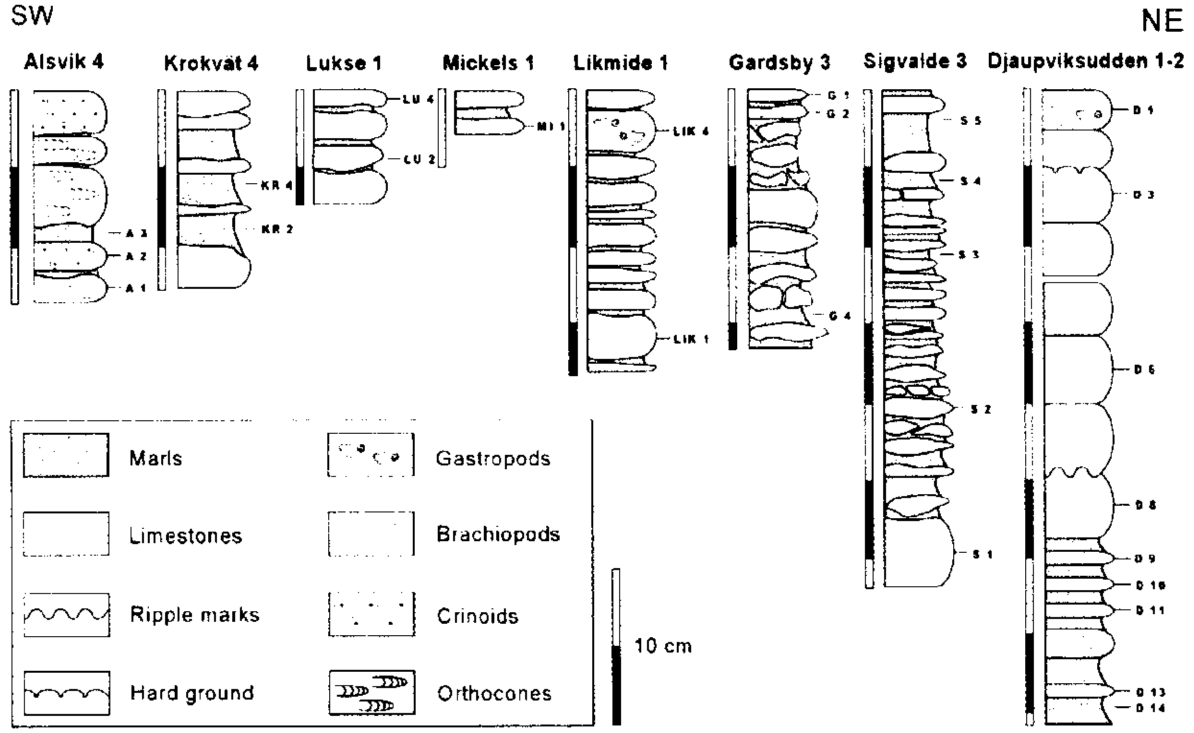

Fig. 3. Lithological succession and sample sites in the short sections of the eight localities.

These temporal facies changes coincide with partly very large changes in the stable carbon and oxygen isotope values (up to 9 ‰ in δ^{13}C, Samtleben et al., 1996, 2000), and with changes in the composition of conodont communities (Jeppsson, 1990). Although the oceanic circulation is interpreted differently, Jeppsson (1990) and Bickert et al. (1997) agree that times of increased reef and carbonate platform growth represent intervals of arid conditions in low palaeolatitudes, whereas times of increased deposition of marly sediments are interpreted as resulting from higher terrigeneous input during more humid conditions. According to Jeppsson (1990), humid and arid times are termed P and S episodes, respectively, (with the transitions being termed "Events"), whereas they are referred to as H and A periods in Bickert et al. (1997) (Fig. 2).

Plate I. For all photographs, scale bars: 20 μm.

1. *Micrhystridium* morphotype with short processes, attributable to *Micrhystridium parinconspicuum* Deflandre 1945. Slide G 4 a.
2. *Micrhystridium stellatum* Deflandre 1945. Slide MI 1 a.
3. *Micrhystridium* morphotype with ramified processes, attributable to *Micrhystridium imitatum* Deflandre 1945. Slide G 4 a.
4. *Oppilatala septispinosa* Lister 1970. Slide G 1 a.
5. *Percultisphaera stiphrospinata* Lister 1970. Slide MI 1 a.
6. *Evittia denticulata* Cramer 1970. Slide MI 1 a.
7. *Leiofusa parvitatis* Loeblich 1970. Slide MI 1 a.
8. Four-processed veryhachid attributable to *Dorsennidium europaeum* (Stockmans and Willière, 1960) Sarjeant and Stancliffe 1994. Slide MI 1 a.
9. *Neoveryhachium carminae* Cramer 1970. Slide S 5 a.
10. Leiosphere. Slide KR 4 a.
11. *Pterospermopsis martinii* Cramer 1967. Slide G 2 a.

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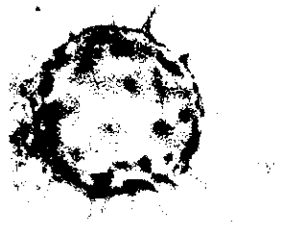

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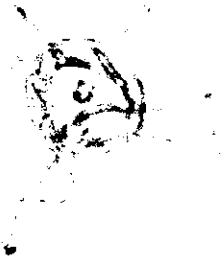

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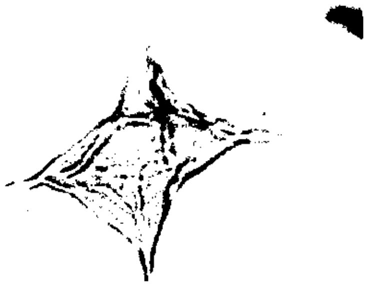

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In the present study, eight localities have been investigated. These localities lie along an inshore–offshore transect from extremely shallow marine environments in the NE coast to distal shelf facies in the SW coast of the island of Gotland (Fig. 1B and C). According to the isotope stratigraphy of Samtleben et al. (2000), the deposits in the sampled localities are nearly contemporaneous. The samples belong to the upper part of the lower Gorstian H period of Samtleben et al. (2000), roughly corresponding to the late Sproge Primo Episode of Jeppsson and Aldridge (2000) (Fig. 2). During this humid interval (H period), reef formation was strongly reduced (Samtleben et al., 2000). Along this transect, the localities investigated are Djaupviksudden 1 and 2, Sigvalde 3, Gardsby 3, Likmide 1, Mickels 1, Lukse 1, Krokvät 4 and Alsvik 4 (Fig. 1B and C). Further information about the location and description of these localities is provided by Laufeld (1974a), Ramsköld (1986) and Samtleben et al. (2000).

The marginal marine facies in the northeastern part of the transect (locality Djaupviksudden 1–2) is characterized by rapid alternations of mudstones and grainstones (Samtleben et al., 2000). Some beds are devoid of macrofossils, while others are extremely rich in low-diversity assemblages of, e.g., brachiopods, gastropods or bryozoans. These abundant, but low-diversity benthic communities are typical for extreme environmental conditions. Additionally, oscillation ripple marks and dessication cracks indicate shallow environments and intervals of subaerial exposure.

The sediments in Sigvalde, Gardsby and Likmide (Fig. 1B and C) have been deposited in open marine proximal shelf environments in moderate water depth between fair weather wave base and storm wave base (Samtleben et al., 2000). The sediments consist mostly of alternating grey, bioturbated, wavy to nodular bedded, micritic limestones and marls. The lithology is dominated by wackestones, but mudstones, packstones and grainstones are also observed. The micritic rocks point to a depositional environment below fair weather wave base. However, the intercalated grainstones indicate short intervals when the wave base reached the sea floor. The rocks contain an abundant and fully marine benthic fauna with brachiopods, molluscs, trilobites, ostracods, crinoids, bryozoans, stromatopores and corals.

Four localities have been sampled in the distal facies area (Mickels 1, Lukse 1, Krokvät 4, Alsvik 4; Fig. 1B and C). The sediments consist of alternations of bioturbated micritic limestones and marls (mostly mudstones to wackestones) deposited below storm wave base. Fossils are relatively rare, but the general composition of the communities is similar to those of the shallower proximal shelf environment. The palaeowaterdepth has been estimated at 50 m maximum (Samtleben et al., 2000).

4. Material and methods

The localities used in this study have been precisely located from the coordinates indicated in Samtleben et al. (2000). A description of the

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Plate II. Scale Bar: 10 μm (specimens 1 to 4; 7 to 12), 2 μm (5 and 6).

1. *Micrhystridium* morphotype with short processes, attributable to *Micrhystridium nannacanthum* Deflandre 1945. Mount G4-Gardsby.
2. *Micrhystridium* morphotype with short processes, attributable to *Micrhystridium parinconspicuum* Deflandre 1945. Mount G4-Gardsby.
3. *Micrhystridium stellatum* Deflandre 1945. Mount D1-Djaupviksudden.
4. *Micrhystridium* morphotype with ramified processes, attributable to *Micrhystridium imitatum* Deflandre 1945. Mount G4-Gardsby.
5. Vesicle ornamentation of *Micrhystridium stellatum*. Detail picture of the specimen figured in 3.
6. Detail of the vesicle ornamentation of *Micrhystridium stellatum*. Mount D1-Djaupviksudden.
7. *Dilatisphaera tubula* Le Hérissé 1989. Mount D8-Djaupviksudden.
8. *Evittia denticulata* Cramer 1970. Mount G4-Gardsby.
9. *Pterospermopsis martinii* Cramer 1967. Mount G4-Gardsby.
10. Dilatisphaera tubula Le Hérissé 1989. Mount D1-Djaupviksudden.
11. Percultisphaera stiphrospinata Lister 1970. Mount G4-Gardsby.
12. *Hapsidopalla jeandeunffii* Le Hérissé 1989. Mount G4-Gardsby.

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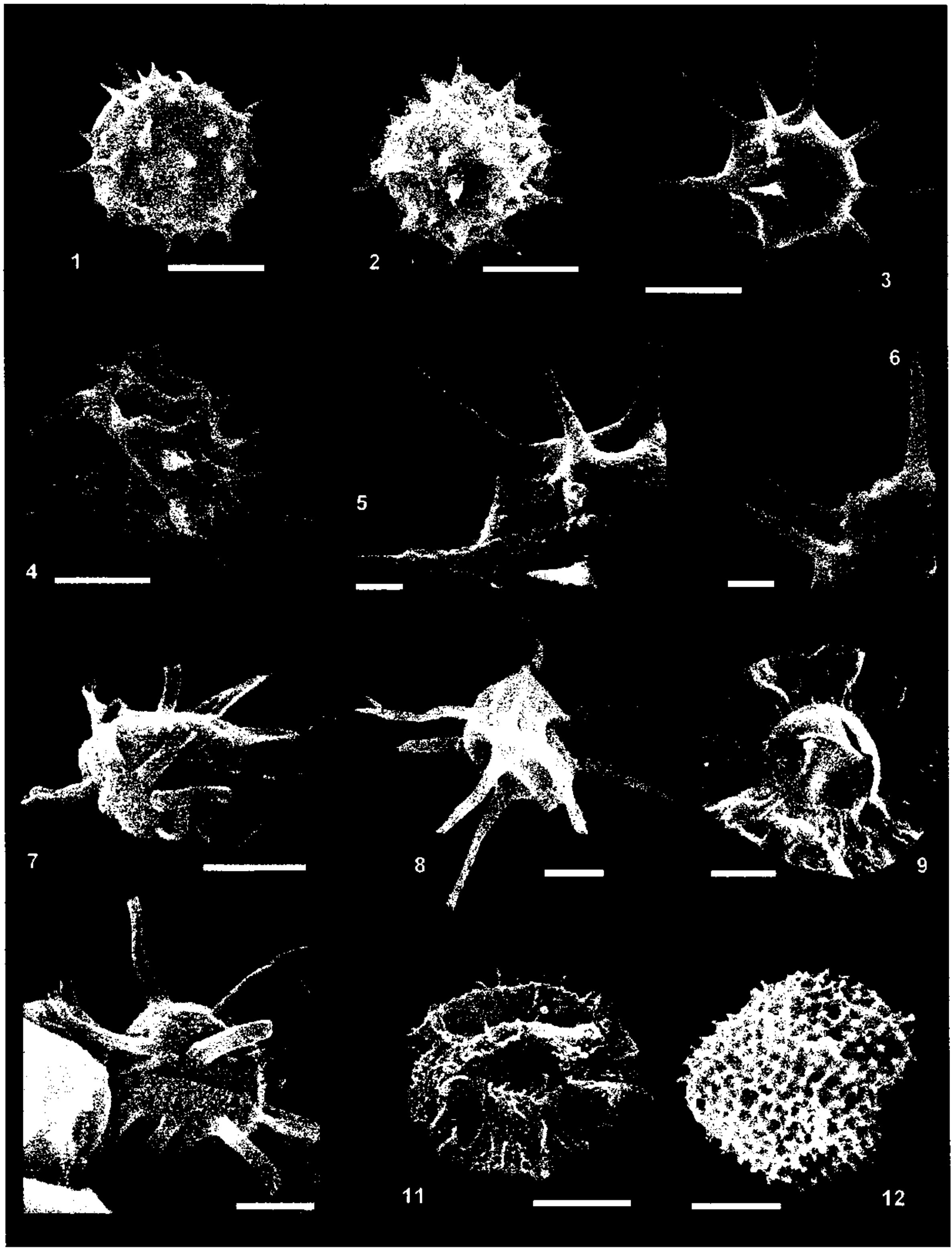

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sample area was given by Laufeld (1974a). The number of samples varies for each locality (Fig. 3). At some localities, several samples (up to nine) have been collected in order to analyze the palynological content from different lithologies in the same outcrop. A total of 27 samples from the eight localities has been investigated, including nine from Djaupviksudden, five from Sigvalde, three from Gardsby, two from Likmide, one from Mickels, two from Lukse, two from Krokvät and three from Alsvik.

Sample preparation was conducted using standard palynological processing techniques. One hundred grams for limestones and 50 g for marls were used for each preparation. The material was boiled in 33% HCl and treated with 40% HF. Subsequent to chemical preparation, the material was sieved using a 11-μm nylon mesh. Five *Lycopodium* tablets were used for limestone samples and eight tablets for marl samples in order to facilitate the calculation of absolute palynomorph abundances (per g of sample). Relative (%) abundances have been calculated based on the total number of specimens of all palynomorph categories. The slides were prepared using glycerine jelly as an embedding medium.

The palynological slides were studied by transmitted light microscopy, using an Olympus BX 51 microscope with UplanFl 40 × and Achromat 60 × objectives. Photomicrographs were made using an Olympus CAMEDIA digital camera. Scanning Electron Microscope (SEM) photomicrographs were digitally acquired from a LEO 1450 VP GEMINI. The figured material is housed in the Institute for Geosciences, University of Tübingen, Germany.

5. Results

For each sample, a minimum of 250 acritarch specimens was counted. All acritarchs and prasinophytes were identified at the species level where possible (Appendix A). Together with the other components (chitinozoans, spores, scolecodonts), the relative and absolute abundance of the microphytoplankton are listed in Appendix B.

5.1. General microphytoplankton distribution along the transect

The organic-walled microphytoplankton has been divided into the following three categories: sphaeromorphs, process-bearing acritarchs, and prasinophytes. The sphaeromorphs include all spherical palynomorphs with neither processes nor ornamentation. They constitute most probably a polyphyletic unit that, despite their simple morphologies (e.g., Plate I, 10), may include unornamented acritarchs, but also alete spores or cryptospores (land plant-derived) and/or prasinophytes (e.g., *Tasmanites* Wall 1962). The process-bearing acritarchs include all acritarchs with processes that cannot be attributed to the prasinophytes. The latter unit constitutes a group of the unicellular green algae that includes both some sphaeromorphs (see above) and morphotypes resembling recent prasinophyte phycomata (e.g., Tappan, 1980). As the identification of leiospherid prasinophytes is difficult with the optical microscope, only the ornamented morphotypes belonging to the genera *Cymatiosphaera* Wetzel 1933, *Dictyotidium* Eisenack 1955, *Duvernaysphaera* Staplin 1961, *Glyptosphaera* Kirjanov 1978, *Melikeriopalla* Tappan and Loeblich 1971, and *Pterospermopsis* Wetzel 1952 (e.g., Plates I, 11 and II, 9) are here attributed to the prasinophyte group.

Fig. 4A and B illustrate the relative and absolute abundance of process-bearing acritarchs, sphaeromorphs and prasinophytes as well as the genus- and species-level diversities of the process-bearing acritarchs (Fig. 4C). The process-bearing acritarchs are generally the most common component of the organic-walled microplankton in the transect. Their mean relative abundance increases from 37% in the proximal facies of Djaupviksudden to 72% in the offshore environments in the distal shelf facies at Alsvik. This increase is almost continuous, with the only break in the regular pattern observed between the two most offshore localities (Krokvät and Alsvik). The proportion of sphaeromorphs shows an opposite trend. It decreases regularly from a mean of 58% in the proximal facies to 19% in the most distal facies.

Absolute abundance counts (in specimens/g of sediment) indicate increasing values for both the process-bearing acritarchs and the sphaeromorphs from proximal to distal settings (Fig. 4B). The former

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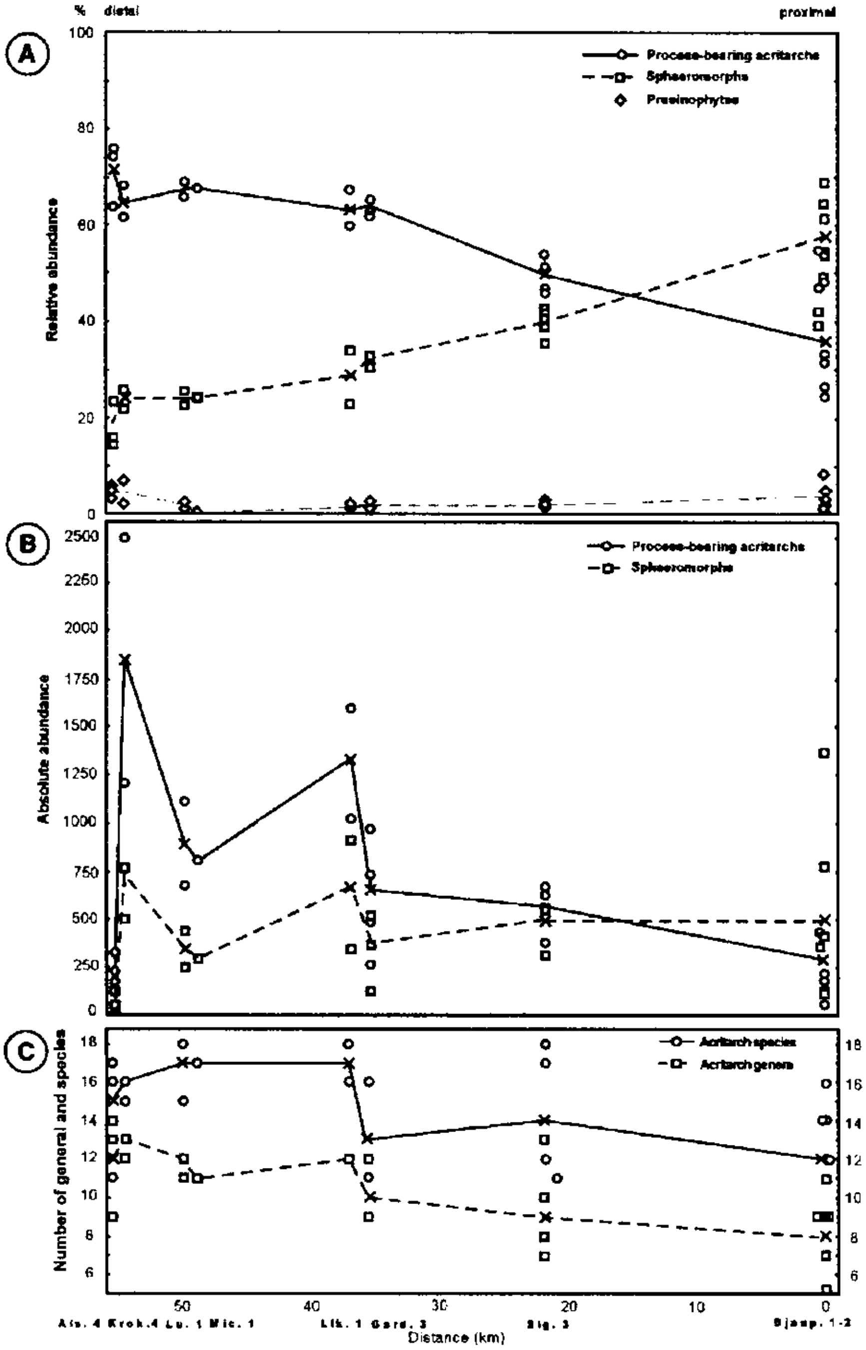

Fig. 4. (A) Relative abundance (*Y*-axis) and mean values of the main palynomorph groups along the transect (lateral distance in km taken from Djaupviksudden). (B) Absolute abundance of the main palynomorph groups along the transect. (C) Process-bearing acritarch generic and specific diversity across the transect. The mean value for localities with several samples is indicated with an oblique cross.

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varies from a mean of 300 in Djaupviksudden up to more than 1800 specimens per g of sediment in Krokvät, and the latter varies from a mean of 460 (in Djaupviksudden) up to 650 specimens per g of sediment (in Krokvät). The most distal locality, Alsvik, contains fewer specimens with about 250 specimens of process-bearing acritarchs and about 70 specimens of sphaeromorphs per g of rock.

The generic and specific diversity of process-bearing acritarchs through the transect is illustrated in Fig. 4C. The number of process-bearing acritarchs increases from a mean of 12 species for the most proximal locality up to 17 species at the localities Likmide and Mickels. Within the same transect, the variations of the generic diversity values increase from a mean of 4 genera at Djaupviksudden to 12 genera at Alsvik.

5.2. Distribution of process-bearing acritarch genera through the transect

The most common acanthomorph acritarch (spherical morphotypes with processes) genera in the transect are *Micrhystridium* (Plates I, 1–3 and II, 1–6), *Dilatisphaera* (Plate II, 7 and 10), *Evittia* (Plates I, 6 and II, 8), *Percultisphaera* (Plates I, 5 and II, 11) and *Oppilatala* (Plate I(4). Other genera that occur with lower frequencies are: *Salopidium* Dorning (1981a), *Histopalla* Playford (1977) (Plate II, 12), *Multiplicisphaeridium* Staplin (1961), *Gorgonisphaeridium* Staplin et al. (1965) and, even less common, *Visbysphaera* Lister (1970) and *Baltisphaeridium* Eisenack (1958). Within the polygonomorph acritarchs (morphotypes with polygonal central body and processes), *Dorsennidium* (Plate I, 8), *Neoveryhachium* (Plate I, 9) and *Veryhachium* constitute the most common genera. The netromorph acritarchs (with a fusiform central body) are represented by the two genera *Leiofusa* (Plate I, 7) and *Eupoikilofusa*.

Fig. 5 illustrates the distribution of the five most common acritarch genera along the inshore–offshore transect. *Micrhystridium* and *Dilatisphaera* show generally decreasing proportions from proximal to more distal settings. However, while *Micrhystridium* is present in all localities, *Dilatisphaera* is limited to the three most proximal

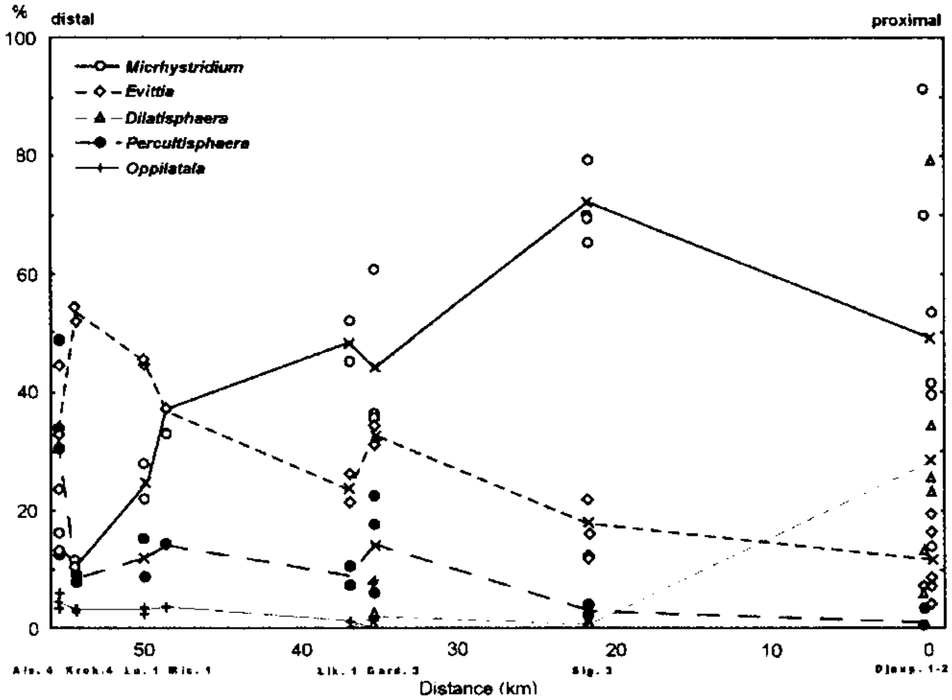

Fig. 5. Distribution of the acritarch genera within the profile. The mean value for localities with a large numerical variation is indicated with an oblique cross.

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localities (from Djaupviksudden to Gardsby). *Micrhystridium* is the most common genus, with about a mean of 47% in the proximal locality of Djaupviksudden. The highest proportion is reached at Sigvalde, where *Micrhystridium* represents about 73% of all process-bearing acritarchs. This proportion decreases progressively to the lowest values at Alsvik (13%). On the other hand, *Evittia*, *Oppilatala* and *Percultisphaera* generally show increasing proportions from proximal to distal localities, although *Evittia* percentages decline in Alsvik.

5.3. Micrhystridium morphotypes through the transect

As indicated above, *Micrhystridium* is the most abundant genus in the samples analyzed in this study. This genus, to which several hundreds of species have been attributed (Fensome et al., 1990), is extremely variable, and intermediate morphotypes between previously described species can easily be observed.

Micrhystridium is here divided into three categories, following a taxonomical proposal of Deflandre 1945. The first category includes all morphotypes with short processes that correspond to the species *Micrhystridium nannacanthum* Deflandre 1945 and *Micrhystridium parinconspicuum* Deflandre 1945. The former species has a globular vesicle (less than 20 μm in diameter) with very short, densely distributed, processes, that are not longer than 1 μm. *Micrhystridium parinconspicuum* also has a globular vesicle with longer processes, of about 1/3 of the body diameter. The second category is represented by the species *Micrhystridium stellatum* Deflandre 1945, which has simple processes that are longer than the half of the body diameter. Deflandre 1945 attributed specimens with long and ramified processes (only bifurcate) to the species *Micrhystridium imitatum* Deflandre 1945, which corresponds to our third category. Sarjeant and Stancliffe (1994) indicated in their revised diagnosis of the genus *Micrhystridium* the existence of small distal bifurcations of the processes in some specimens. The variability of the process ramification on the specimens of *Micrhystridium* from the Ludlow of Gotland is generally

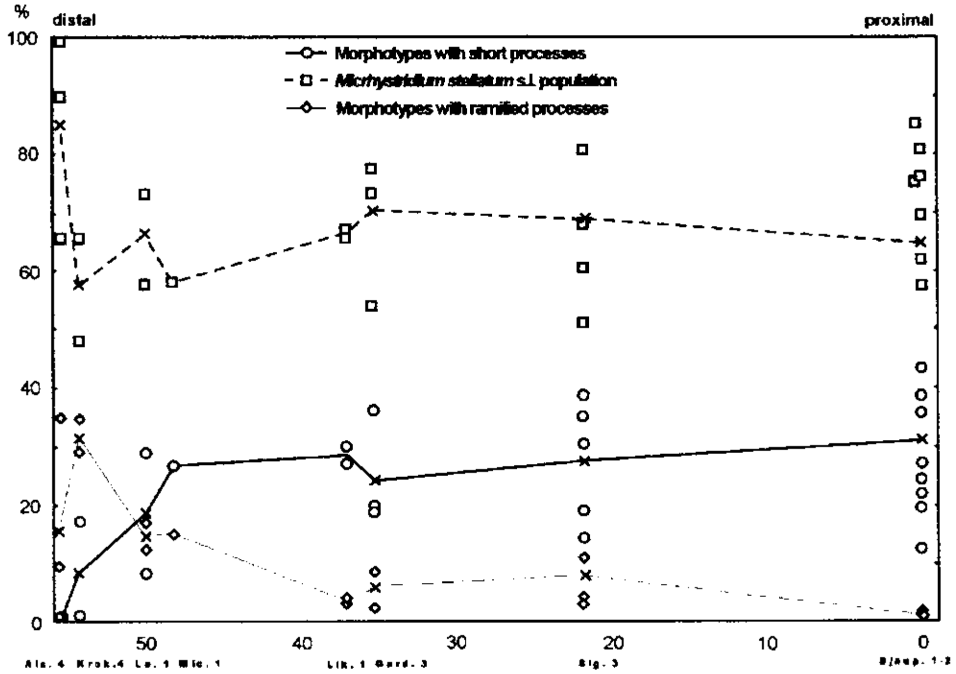

Fig. 6. Diagram showing the distribution of the *Micrhystridium* morphotypes within the profile. The mean value for localities with a large numerical variation is indicated with an oblique cross.

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limited to a single short bifurcation at the tip of the processes and is here considered as an infrageneric variation. Thus, we decided to retain the morphotypes with these bifurcate processes in the genus *Micrhystridium*, although they could be attributed to *Multiplicisphaeridium* by other authors.

In this study, all *Micrhystridium* morphotypes with processes that are not longer than one-half of the vesicle diameter are included in the first category "morphotypes with short processes" (Plates I, 1 and II, 1 2). All specimens with processes that are longer than one-half of the vesicle diameter, but without ramifications, are included in the second category that is here named "*Micrhystridium stellatum* s.l." (Plates I, 2 and II, 3). All morphotypes with long and ramified processes represent the third category (Plates I, 3 and II, 4).

Fig. 6 illustrates the relative abundance of the three categories listed above. The *Micrhystridium* morphotypes with short processes show a rapid decline in the most distal parts of the section. In contrast, those with long and ramified processes become more abundant towards the distal part of the shelf. The *Micrhystridium stellatum* population is the most abundant category. It represents about 60% of all micrystrids counted. They occur in more or less stable proportions, except for the most distal locality (Alsvik) where they increase.

6. Discussion and conclusions

Based on 27 samples collected from different lithologies at eight localities, the qualitative and quantitative evaluation of the organic-walled microplankton indicates distribution patterns along an inshore–offshore transect that can be observed at three different levels.

The distribution of all of the components of the organic-walled microplankton indicates that proximal, shallow water environments yielded low quantities, while samples collected from the shelf area contained the highest numbers of organic-walled microphytoplankton specimens. The process-bearing acritarchs become more frequent (% abundance) and more abundant (per g of sample) towards the distal part of the shelf. Sphaeromorphs represent the most frequent marine organic-walled microphytoplankton in shallow water, proximal environments. The number of morphotypes that can be attributed to ornamented prasinophytes (i.e., with membranes) is not sufficiently high to draw any conclusions.

The five most abundant process-bearing acritarch genera in the Ludlow transect of Gotland are *Micrhystridium*, *Dilatisphaera*, *Evittia*, *Percultisphaera* and *Oppilatala*. While *Micrhystridium* and *Dilatisphaera* are more frequent in more proximal assemblages, *Evittia*, *Percultisphaera* and *Oppilatala* become increasingly more frequent towards the shelf. *Micrhystridium* is generally the most abundant genus. It has been recorded in all localities, but with a relative abundance decreasing towards offshore environments. A tentative distinction into three morphotypes [(1) morphotypes with processes shorter than a half of the central body diameter; (2) with processes longer than a half of the central body diameter; (3) morphotypes with long and ramified processes] indicates a tendency towards higher relative abundance of forms with long and ramified processes towards the distal shelf, while specimens with short processes are relatively more frequent in proximal environments. Forms with simple processes are generally equally abundant in all localities except the most distal locality (Alsvik) where they increase.

In summary, it appears that in the Ludlow shelf section investigated in this study the organic-walled microphytoplankton (including acritarchs, sphaeromorphs and prasinophytes) are more abundant towards the distal shelf area. The microplankton with processes and complex process structures are also more abundant towards the distal shelf area. More simple morphologies (acritarchs with short processes or without processes, i.e., sphaeromorphs) are more frequent in the proximal environments of the transect.

Since the early 1960s (e.g., de Jekhowsky, 1963) it has been well known that marine microplankton is most abundant on the shelf areas, with numbers decreasing towards both proximal and open marine environments. This general trend can also be observed on our transect of Gotland.

Previously published studies on the lateral distribution of Palaeozoic organic-walled microphytoplankton along inshore–offshore transects generally provided only estimated frequencies and abundances of individual morphotypes. Estimations of the distribution of selected Silurian taxa through the Wenlock

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and Ludlow shelves of the Welsh Borderland were given by Dorning (1981b, 1987). In addition, the publication of Dorning and Bell (1987) included a semiquantitative analyses, with the relative abundances of selected taxa through a Wenlock carbonate shelf transect. It is particularly interesting to compare the results from the Wenlock transect in the Welsh Borderland and the Ludlow transect of Gotland. Dorning and Bell (1987) distinguished four different "assemblages" from shallow to deep-water environments that cannot be recognized on Gotland. Indeed, the Ludlow acritarch assemblages of the Welsh Borderland are of different taxonomical composition compared to our study material. Some genera such as *Cymbosphaeridium* Lister 1970 or some species such as *Micrhystridium intonsurans* (Lister 1970) Dorning 1981a are not recorded in our study. However, the relative abundances indicated by Dorning and Bell (1987, fig. 15.8) indicate some analogies with the results of our study. Dorning and Bell (1987) recorded the genus *Leiosphaeridia* all over the platform with decreasing proportions towards offshore environments. This distribution corresponds to the observation on the carbonate shelf platform of Gotland. The distribution of *Micrhystridium* in Dorning and Bell (1987) also corresponds to our observations, with a presence all along the transect, but higher abundances on the middle part of the shelf. Both *Evittia* [classified as *Diexallophasis* by Dorning and Bell (1987) following Loeblich (1970)] and *Oppilatala* were indicated to be very rare in the proximal environments of the Wenlock platform of the Welsh Borderland, but were shown to be more abundant in the distal parts of the shelf. This distribution is also confirmed in our study.

Other comparisons are possible with Ordovician distribution schemes along lateral transects. Jacobson (1979) interpreted the acritarch assemblages from the Middle and Upper Ordovician of the American mid-Continent in terms of palaeoenvironment, attributing a "leiospherid class" to near-shore shallow water environments. The "peteinosphaerid-*Dicommopalla* class", i.e., assemblages including morphotypes with complex process structures, was considered to correspond to shelf environments, while the "baltisphaerid-veryhachid-*Polygonium* class", i.e., assemblages with morphotypes with simple processes, was attributed to open-sea environments. Li et al. (2004-this volume) described the distribution of acritarch assemblages on the Lower–Middle Ordovician Yangtze Platform in southern China and concluded that the composition of the assemblages changes from more simple morphologies in near-shore environments to specimens with longer and more complexly branched processes on the shelf.

Despite the differences in the composition of the assemblages, partly due to different compositions between Ordovician and Silurian assemblages, it appears that genera with a more complex ornamentation are more frequent in offshore environments, not only in the Ordovician (Yangtze Platform and American mid-Continent), but also in the Silurian (Welsh Borderland and Gotland) and in the Devonian (Belgium and Alberta).

The increasing process length towards offshore environments, occurring in the morphotypes of the genus *Micrhystridium*, possibly represents a response to palaeoenvironmental changes. However, it would be premature to attribute these morphological changes to any specific parameter, such as salinity (compare Servais et al., in press). Future research is needed to better understand the variability of the micrhystrid plexus before any ecophenotypism can clearly be identified.

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Appendix A

Counts of prasinophyte, sphaeromorph, and acritarch species in the marginal marine locality (Djaupviksudden), proximal shelf localities (Sigvalde, Gardsby and Likmide), and distal shelf environments localities (Mickels, Lukse, Krokvät and Alsvik).

Marginal marine area										
Genus	Species	D14	D13	D11	D10	D9	D8	D6	D3	D1
Prasinophytes										
Cymatiosphaera	*salopensis*	16	9	20	26	6	2	6	0	10
Cymatiosphaera	*mirabilis*	0	0	0	0	0	0	0	36	0
Dictyotidium	*stenodictyum*	0	0	0	0	0	0	3	0	0
Dictyotidium	*alveolatum*	3	2	0	0	4	0	3	9	0
Dictyotidium	*faviforme*	0	0	9	0	0	1	0	0	1
Duvernaysphaera	*aranaides*	0	0	0	0	0	1	0	0	0
Pterospermopsis	*martinii*	0	1	4	0	6	0	0	0	0
Glyptosphaera	*speciosa*	0	0	0	0	0	0	0	0	0
Melikeriopalla	*amydra*	0	2	0	0	0	0	2	0	0
Sphaeromorphs										
Leiosphaeridia	sp.	538	477	371	663	447	252	496	209	324
Tasmanites	sp.	15	0	5	0	7	5	4	0	0
Acritarchs										
Ammonidium	*microcladum*	0	0	0	0	0	0	0	0	0
Baltisphaeridium	*muricatum*	0	0	2	0	0	0	2	0	1
Comasphaeridium	*brevispinosum*	0	3	0	8	0	2	2	0	0
Dilatisphaera	*laevigata*	0	14	14	25	41	60	32	0	4
Dilatisphaera	*tubula*	25	53	33	33	129	123	39	10	18
Evittia	*denticulata*	29	17	26	17	24	10	30	3	3
Evittia	*sanpetrensis*	20	0	6	0	0	0	13	0	0
Dorsennidium	*europaeum*	34	37	31	8	14	11	11	18	81
Dorsennidium	*inflatum*	5	12	2	0	0	2	4	0	5
Eisenackidium	*wenlockensis*	5	18	20	25	0	0	0	0	0
Eupoikilofusa	*tenuistriata*	25	19	15	0	0	4	2	1	1
Florisphaeridium	*castellum*	0	0	0	8	0	1	2	0	0
Gorgonisphaeridium	*succinum*	0	0	0	0	0	0	6	0	0
Hapsidopalla	*jeandeunffii*	0	0	0	0	0	0	0	0	0
Helosphaeridium	*pseudodictyum*	0	0	0	0	0	0	0	0	0
Histopalla	*margarita*	5	11	0	0	0	0	2	0	0
Leiofusa	*parvitatis*	0	0	0	8	0	0	9	0	0
Michrystridium	*imitatum*	0	1	0	0	0	0	0	3	0
Michrystridium	*nannacanthum*	5	9	12	33	4	0	41	1	12
Michrystridium	*parinconspicuum*	39	15	22	8	12	6	19	25	53
Michrystridium	*stellatum*	59	52	60	66	30	25	34	185	228
Multiplicisphaeridium	*arbusculum*	0	0	0	0	0	0	0	0	0
Multiplicisphaeridium	*forquillum*	0	0	0	0	0	0	0	0	0
Neoveryhachium	*carminae*	0	0	0	0	0	0	0	0	0
Onondagaella	*asymmetrica*	0	0	0	0	0	0	0	0	0
Oppilatala	*frondis*	0	0	0	0	0	0	0	0	0
Oppilatala	*septispinosa*	0	0	0	0	0	1	0	1	0
Percultisphaera	*stiphrospinata*	0	0	0	0	0	0	0	1	2
Quadraditum	*fantasticum*	0	0	0	0	0	0	0	0	0

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Appendix A (*continued*)

Marginal marine area

Genus	Species	D14	D13	D11	D10	D9	D8	D6	D3	D1
Salopidium	*wenlockensis*	0	0	0	0	0	0	0	0	0
Schismatosphaeridium	*rugulosum*	0	0	0	0	0	0	0	0	0
Tunisphaeridium	*parvum*	0	0	0	0	0	0	0	0	0
Tylotopalla	*deerlijkianum*	0	0	0	0	0	0	0	0	0
Veryhachium	*reductum*	0	12	6	8	0	4	0	0	0
Veryhachium	*trispinosum*	0	0	0	0	2	0	0	1	21
Visbysphaera	*microspinosa*	0	0	2	0	0	0	0	0	0

Proximal shelf

Genus	Species	S1	S2	S3	S4	S5	G4	G2	G1	LIK1	LIK4
Prasinophytes											
Cymatiosphaera	*salopensis*	6	8	11	13	8	0	0	1	0	0
Cymatiosphaera	*mirabilis*	0	0	0	0	0	3	4	0	3	10
Dictyotidium	*stenodictyum*	0	0	0	0	0	0	0	0	0	0
Dictyotidium	*alveolatum*	1	0	5	0	0	0	0	0	0	0
Dictyotidium	*faviforme*	0	0	0	0	4	0	0	0	0	0
Duvernaysphaera	*aranaides*	0	0	0	0	0	1	0	2	2	0
Pterospermopsis	*martinii*	0	0	0	1	0	0	8	3	0	1
Glyptosphaera	*speciosa*	0	0	0	0	0	0	0	0	0	0
Melikeriopalla	*amydra*	1	3	3	5	0	0	0	0	0	0
Sphaeromorphs											
Leiosphaeridia	sp.	192	237	266	231	161	133	119	137	89	148
Tasmanites	sp.	0	0	13	0	0	3	8	1	0	0
Acritarchs											
Ammonidium	*microcladum*	1	0	0	0	0	0	0	0	0	0
Baltisphaeridium	*muricatum*	1	0	0	0	0	0	0	6	0	0
Comasphaeridium	*brevispinosum*	5	3	3	3	0	0	0	0	3	7
Dilatisphaera	*laevigata*	1	3	3	0	0	0	7	4	0	0
Dilatisphaera	*tubula*	0	0	0	0	0	0	0	0	0	0
Evittia	*denticulata*	27	39	27	41	37	71	69	22	42	39
Evittia	*sanpetrensis*	0	0	0	0	0	0	0	0	4	0
Dorsennidium	*europaeum*	65	45	63	56	61	43	45	37	39	61
Dorsennidium	*inflatum*	5	9	36	8	9	7	4	49	4	9
Eisenackidium	*wenlockensis*	0	0	0	0	0	0	0	0	0	0
Eupoikilofusa	*tenuistriata*	1	0	0	0	0	0	1	7	0	0
Florisphaeridium	*castellum*	0	1	0	0	0	0	0	0	0	0
Gorgonisphaeridium	*succinum*	1	0	0	0	0	1	0	0	5	0
Hapsidopalla	*jeandeunffii*	0	0	0	0	0	0	0	0	4	0
Helosphaeridium	*pseudodictyum*	0	0	0	0	0	1	0	3	0	0
Histopalla	*margarita*	16	2	7	5	9	0	0	0	15	11
Leiofusa	*parvitatis*	0	0	0	0	0	0	0	1	40	2
Michrystridium	*imitatum*	11	5	16	11	6	1	5	8	3	4
Michrystridium	*nannacanthum*	2	20	33	14	2	0	3	8	5	0
Michrystridium	*parinconspicuum*	16	36	37	29	15	11	13	29	19	27
Michrystridium	*stellatum*	65	93	92	86	96	47	60	54	52	66
Multiplicisphaeridium	*arbusculum*	7	0	0	0	0	0	4	4	0	6
Multiplicisphaeridium	*forquillum*	0	0	0	0	0	0	0	0	0	0
Neoveryhachium	*carminae*	1	0	0	0	8	0	0	0	1	0

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Appendix A (*continued*)

Proximal shelf

Genus	Species	S1	S2	S3	S4	S5	G4	G2	G1	LIK1	LIK4
Onondagaella	*asymmetrica*	0	0	0	0	0	0	0	0	0	0
Oppilatala	*frondis*	0	0	0	0	0	0	0	0	0	0
Oppilatala	*septispinosa*	0	0	0	0	0	17	18	13	0	2
Percultisphaera	*stiphrospinata*	9	1	5	2	5	45	41	10	19	13
Quadraditum	*fantasticum*	0	0	0	0	0	0	0	0	0	0
Salopidium	*wenlockensis*	0	4	0	3	0	0	0	1	4	9
Schismatosphaeridium	*rugulosum*	0	0	0	0	0	0	0	0	0	0
Tunisphaeridium	*parvum*	0	0	0	0	0	0	0	0	0	0
Tylotopalla	*deerlijkianum*	0	0	0	0	0	1	0	0	0	0
Veryhachium	*reductum*	0	0	0	0	2	0	0	0	2	3
Veryhachium	*trispinosum*	0	1	0	3	2	0	0	0	7	6
Visbysphaera	*microspinosa*	0	0	0	0	0	3	3	0	0	1

Distal shelf

Genus	Species	MI1	LU2	LU4	KR2	KR4	A1	A2	A3
Prasinophytes									
Cymatiosphaera	*salopensis*	0	0	0	0	0	2	0	0
Cymatiosphaera	*mirabilis*	0	9	2	2	19	16	6	12
Dictyotidium	*stenodictyum*	0	0	0	0	0	0	0	0
Dictyotidium	*alveolatum*	0	0	0	0	0	0	0	0
Dictyotidium	*faviforme*	0	0	0	0	1	0	0	0
Duvernaysphaera	*aranaides*	0	2	0	2	11	3	4	2
Pterospermopsis	*martinii*	1	0	0	3	0	0	1	0
Glyptosphaera	*speciosa*	0	0	2	2	0	0	0	1
Melikeriopalla	*amydra*	0	0	0	0	0	0	8	0
Sphaeromorphs									
Leiosphaeridia	sp.	96	94	99	92	110	58	54	101
Tasmanites	sp.	0	0	0	0	0	0	0	0
Acritarchs									
Ammonidium	*microcladum*	0	0	0	0	0	1	0	0
Baltisphaeridium	*muricatum*	0	0	0	0	0	0	0	0
Comasphaeridium	*brevispinosum*	3	0	0	0	0	0	0	0
Dilatisphaera	*laevigata*	0	0	0	0	0	0	0	0
Dilatisphaera	*tubula*	0	0	0	0	0	0	0	0
Evittia	*denticulata*	27	65	76	114	113	85	42	34
Evittia	*sanpetrensis*	0	1	2	5	0	0	0	0
Dorsennidium	*europaeum*	54	59	32	37	16	23	26	47
Dorsennidium	*inflatum*	15	28	18	16	14	42	23	3
Eisenackidium	*wenlockensis*	1	0	0	0	0	0	0	0
Eupoikilofusa	*tenuistriata*	0	3	0	0	0	0	0	0
Florisphaeridium	*castellum*	0	0	0	0	0	0	0	0
Gorgonisphaeridium	*succinum*	0	0	0	0	0	0	0	0
Hapsidopalla	*jeandeunffii*	0	0	0	9	0	0	0	0
Helosphaeridium	*pseudodictyum*	0	0	0	0	0	0	0	0
Histopalla	*margarita*	6	4	6	20	4	0	2	0
Leiofusa	*parvitatis*	27	8	10	1	10	8	12	13
Michrystridium	*imitatum*	12	4	8	7	8	3	0	14
Michrystridium	*nannacanthum*	2	3	0	0	0	0	0	0

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Michrystridium	*parinconspicuum*	21	7	4	0	4	0	0	0

Appendix A (*continued*)

Distal shelf									
Genus	Species	MI1	LU2	LU4	KR2	KR4	A1	A2	A3
Michrystridium	*stellatum*	47	19	34	17	11	28	22	26
Multiplicisphaeridium	*arbusculum*	0	0	0	2	0	1	7	0
Multiplicisphaeridium	*forquillum*	0	0	0	0	0	1	0	2
Neoveryhachium	*carminae*	0	0	0	0	1	1	8	17
Onondagaella	*asymmetrica*	0	4	0	0	11	2	3	0
Oppilatala	*frondis*	0	0	0	0	0	5	5	11
Oppilatala	*septispinosa*	6	4	6	7	5	4	1	0
Percultisphaera	*stiphrospinata*	23	22	16	21	16	58	88	106
Quadraditum	*fantasticum*	0	0	0	0	1	0	0	0
Salopidium	*wenlockensis*	5	6	4	14	3	0	1	0
Schismatosphaeridium	*rugulosum*	0	1	0	0	26	0	0	0
Tunisphaeridium	*parvum*	0	0	2	0	0	0	3	0
Tylotopalla	*deerlijkianum*	0	0	0	0	0	0	0	0
Veryhachium	*reductum*	2	6	4	0	0	1	1	1
Veryhachium	*trispinosum*	6	6	28	17	13	2	3	0
Visbysphaera	*microspinosa*	0	0	0	8	0	0	1	0

Appendix B

Table showing the relative (%) and absolute (per g of sample) abundance of palynomorph components within the transect. For convenience, the samples of the first rows are indicated by the first letters of the locality denomination followed by a sample number: D x—Djaupviksudden; S x—Sigvalde; G x—Gardsby; LIK x—Likmide; MI x—Mickels; LU x—Lukse; KR x—Krokvät; A x—Alsvik.

	D14	D13	D11	D10	D9	D8	D6	D3	D1	S1	S2	S3	S4	S5
Components (%)														
Process-bearing acritarchs	24.4	36.0	36.9	26.1	34.6	48.6	32.4	47.0	55.6	51.1	47.0	46.5	44.2	53.9
Sphaeromorphs	54.5	58.4	55.4	69.4	61.6	49.6	64.7	39.4	42.0	41.6	42.5	40.3	39.1	35.1
Prasinophytes	1.9	1.9	4.8	2.7	2.2	0.8	1.8	8.4	1.4	1.7	2.0	2.7	3.2	2.6
Chitinozoans	9.9	0.9	0.5	0.0	0.8	0.0	0.0	0.0	0.1	0.2	0.7	0.1	2.9	1.3
Scolecodonts	9.4	2.8	2.5	1.8	0.8	1.0	1.1	4.4	0.9	5.4	7.7	10.3	10.5	7.1
Spores	0	0	0	0	0	0	0	0.8	0	0	0.2	0	0.2	0
Particles (/g sed)														
Process-bearing acritarchs	187	468	214	506	177	105	56	435	519	675	614	382	632	497
Sphaeromorphs	417	758	321	1344	315	107	111	364	392	549	556	331	559	324
Prasinophytes	14	23	26	50	11	2	3	64	13	22	25	21	42	22
Chitinozoans	76	12	3	0	4	0	0	0	1	3	9	1	41	12
Scolecodonts	72	36	15	35	4	2	2	41	12	72	101	84	150	66
Genera (%)														
Micrhystridium	55.3	39.9	48	44.8	19.0	13.5	39.3	93.1	91.1	57.9	74.4	79.8	72.2	70.3
Evittia	28.2	8.8	16.5	7.4	10	4.4	19.6	7.4	0.9	16.5	18.8	12.1	21.1	21.6
Dilatisphaera	13.2	34.7	23.6	24.1	71.0	80.4	29.5	4.6	6.9	0.8	1.4	1.3	0	0
Percultisphaera	0	0	0	0	0	0	0	0.6	0.7	5.3	0.5	2.2	1.0	2.7
Oppilatala	0	0	0	0	0	0.4	0	0.6	0	0	0	0	0	0

(continued on next page)

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Appendix B (*continued*)

	D14	D13	D11	D10	D9	D8	D6	D3	D1	S1	S2	S3	S4	S5
Micrhystrids (%)														
Short processes	42.9	31.2	36.1	38.5	34.2	19.4	63.6	12.3	22.1	19.5	36.4	39.3	30.7	14.1
stellatum s.l	57.1	67.5	63.9	61.5	65.8	80.6	36.4	86.5	77.9	68.8	60.4	51.7	61.4	80.8
Ramified processes	0	1.3	0	0	0	0	0	1.2	0	11.7	3.2	9.0	7.9	5.1

	G4	G2	G1	LIK1	LIK4	MI1	LU2	LU4	KR2	KR4	A1	A2	A3
Components (%)													
Process-bearing acritarchs	62.6	65.2	62.3	67.9	60.2	67.5	64.9	67.8	68.8	61.1	76.4	75.2	63.1
Sphaeromorphs	33.8	30.2	33.3	23	33.5	25.7	24.4	26.8	21.4	25.6	16.7	15.6	23.5
Prasinophytes	1.1	2.9	1.5	1.3	2.5	0.3	2.9	1.1	2.1	7.3	6	5.4	3.5
Chitinozoans	0	0	0	4.3	2.0	3.7	4.2	1.6	4.9	3.8	0.6	2.2	6.5
Scolecodonts	2.5	1.7	2.7	1.8	1.6	2.9	2.1	1.6	1.9	1.9	0.3	1.0	3.5
Spores	0	0	0.2	1.8	0.2	0	1.6	1.1	0.9	0.2	0	0.6	0
Particles (/g sed)													
Process-bearing acritarchs	734	269	978	1037	1651	806	681	1122	2504	1204	235	171	326
Sphaeromorphs	396	124	523	351	919	306	256	444	778	504	51	36	121
Prasinophytes	12	11	22	18	64	3	27	17	69	112	14	9	16
Chitinozoans	0	0	0	66	56	44	44	27	178	75	2	5	33
Scolecodonts	29	7	42	27	43	35	22	27	68	37	1	2	18
Genera (%)													
Micrhystridium	29.8	36.4	60.4	31.3	51.3	39.6	21.1	25.8	10.6	10.5	15.2	11.1	18
Evittia	35.5	30.9	13.4	18.0	20.6	13.0	42.1	43.8	52.7	50.5	41.7	21.2	15.8
Dilatisphaera	0	3.2	2.4	0	0	0	0	0	0	0	0	0	0
Percultisphaera	22.7	18.2	6.1	7.4	6.9	11.1	14.0	9	9.3	7.3	28.4	43.9	48.6
Oppilatala	8.5	8.2	7.9	0	1.1	2.9	2.6	3.4	3.1	2.3	4.4	3.2	5
Micrhystrids (%)													
Short processes	19	20	37.4	30	27.8	28	29.2	8.7	0	17.4	0	0	0
stellatum s.l.	78.6	73.8	54.5	66.3	68	57.3	58.3	73.9	70.8	47.8	90.3	100	65
Ramified processes	2.4	6.3	8.1	3.8	4.1	14.6	12.5	17.4	29.2	34.8	9.7	0	35

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Article VI

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Assessing mechanisms of global change in the Late Silurian: Palynological data from Gotland, Sweden.

Palaeogeography, Palaeoclimatology, Palaeoecology.

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Assessing mechanisms of global change in the Late Silurian: Palynological data from Gotland, Sweden

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Abstract

The Silurian is characterised by strong environmental changes, as indicated by several pronounced positive $\delta^{13}C$ and $\delta^{18}O$ excursions. The mechanisms responsible of these isotopic shifts are a matter of intense debate. The purpose of the present study is a quantitative high-resolution evaluation of the palynomorph distribution across the late Ludfordian isotope excursion on Gotland. Marine and terrestrial palynomorphs have been chosen as palaeoenvironmental indicators because they are widely distributed and exceptionally well preserved. Moreover the combined analysis of marine and terrestrial palynomorphs allows the reconstruction of contemporaneous palaeoenvironmental change in the marine and terrestrial realms. In order to correlate our results exactly with the carbon isotope stratigraphy, we have sampled only localities with published isotope data from diagenetically unaltered brachiopod shells. Our results show that the acritarchs are closely correlated with the stable isotope development. Low abundances of acritarchs occur in times of high stable isotope values, and vice

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versa indicating that an increase in marine productivity cannot have been the reason for the positive $\delta^{13}C$ excursion. The results are in good agreement with climatic models for the Silurian assuming alternating humid and arid climatic conditions in low latitudes. Times of high isotope values correspond to arid climatic conditions in low latitudes, with low input of terrestrial nutrients resulting in impoverished acritarch and conodont communities, whereas times of low isotope values correlate with humid climate, high nutrient input, and abundant and diverse acritarch communities. The major change in the acritarch communities took place during the increase of the isotope values after hemipelagic planktic or nektonic organisms (graptolites, conodonts) have been affected. This indicates that environmental changes connected with the isotope excursion at first affected deeper-water settings, and later on the photic zone. The abundance of terrestrial spores closely mirrors the marine $\delta^{13}C$ and $\delta^{18}O$ development showing that both the marine and the terrestrial realm are synchronously affected by the climatic changes. The high abundance of spores during the isotope excursion might be explained by an increased aeolian input caused by an intensified atmospheric circulation.

Keywords: palynomorphs; Gotland; Silurian; Ludlow; stable isotopes; bioevents

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1. Introduction

Over the last decade, the Silurian has been increasingly recognised as a time of pronounced environmental changes. Several distinct positive oxygen and carbon isotope excursions have been identified on various low-latitude palaeo-continents (e.g., Andrew et al. 1994; Samtleben et al. 1996, 2000; Wenzel and Joachimski 1996; Kaljo et al 1997, 1998, 2003; Wigforss-Lange 1999; Bourque et al. 2001; Saltzman 2001). These isotope excursions coincide with distinct lithological and biotic changes (see summary in Munnecke et al. 2003). Although each of these events has its own characteristics, their conspicuous similarities indicate similar controlling mechanisms (Munnecke et al. 2003). The amplitudes of the Silurian stable isotope excursions are extremely high compared to Mesozoic and Cenozoic excursions. "Classical" approaches such as productivity changes (for $\delta^{13}C$) and temperature changes and/or glacial effects (for $\delta^{18}O$) therefore fail to account for the extreme amplitudes observed (see discussion in Bickert et al. 1997). The identification of the strongest $\delta^{13}C$ excursion of the entire Phanerozoic

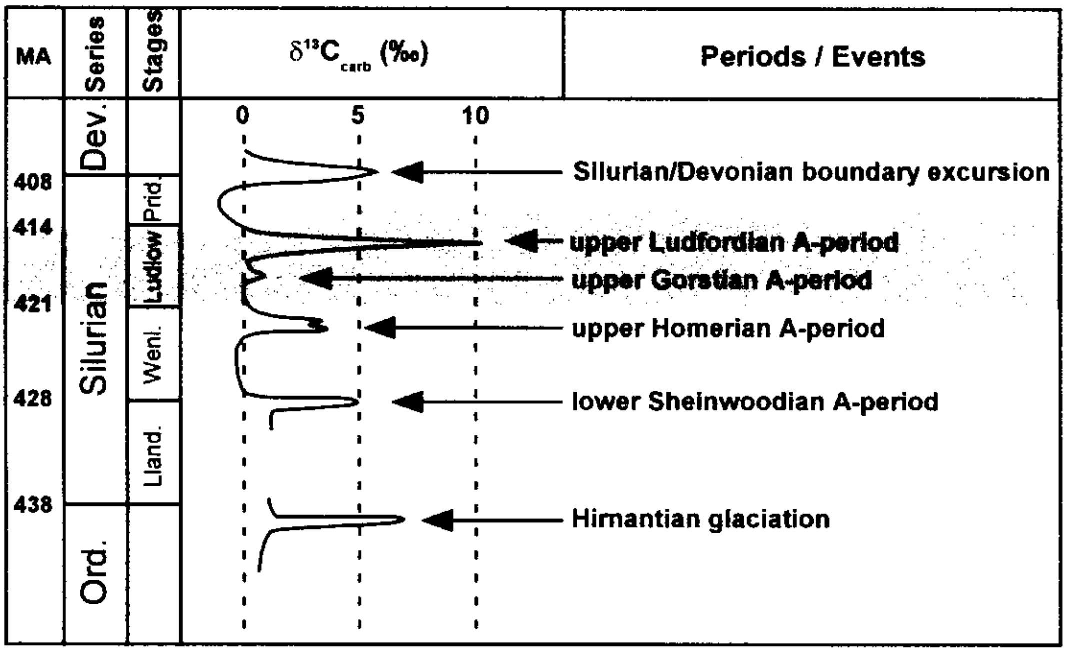

Fig. 1: Compilation of positive $\delta^{13}C$ excursions in the late Ordovician, Silurian, and early Devonian (adapted from Munnecke et al. 2003; excursion in the early Devonian after Saltzman 2002).

in this time interval (late Ludfordian; compare Munnecke et al. 2003; Fig. 1) with up to 4‰ for $\delta^{18}O$ and 12‰ for $\delta^{13}C$ values appears especially surprising given the fact that the Silurian previously had been considered a time of relatively stable environmental conditions (Bassett and Edwards 1991). To explain the Silurian C- and O-isotope excursions, different models have been proposed. Wenzel and Joachimski (1996) suggested periods of high $\delta^{13}C$ values on Gotland to have been characterised by high productivity resulting from high nutrient supply caused by continental runoff during times of low sea level. Kump et al. (1999) proposed a "weathering hypothesis" as explanation for the isotope excursion of the late Ordovician glaciation, and from the similarity between the late Ordovician and the Silurian events, Kump et al. (1999) and Kaljo et al. (2003) inferred the existence of glaciations also in the Silurian.

Bickert et al. (1997) and Munnecke et al. (2003) attributed the repeated shifts from low to high C- and O-isotope values in the late Ordovician and Silurian to changes from relatively humid ("H-periods") to relatively arid climate conditions ("A-periods") in the low latitudes.

As already noted above, the isotope excursions are all associated with biotic extinction events. At the very beginning or even prior to the increase of C- and O-isotope values, many groups of organisms are affected. Especially conodonts, graptolites and trilobites, but also acritarchs, chitinozoans, ostracods, brachiopods, and corals show extinctions, sometimes with a step-wise nature, and organisms living in hemipelagic environments were more strongly affected than organisms dwelling in shallow-water settings (e.g., Le Hérissé, 1989; Melchin, 1994; Jeppsson, 1997a, b, c, 1998; Jeppsson et al., 1994, 1995; Kaljo et al., 1995; Mikulic and Kluessendorf, 1999; Nestor et al. 2002). However, little information is yet available on the reactions of organisms from the photic zone (i.e., phytoplankton). Despite the fact that in the Late Silurian a pronounced adaptive radiation of spores took place (Richardson and Lister, 1969; Burgess and Richardson, 1995; Steemans, 1999), it is also yet completely unknown how the record of early land plants correlates with the marine stable isotope data.

The purpose of the present study is a quantitative high-resolution evaluation of the palynomorph distribution in the Ludlow of Gotland across the upper Ludfordian A-period, which is the strongest positive $\delta^{13}C$ excursion of the Phanerozoic (Fig. 1). Marine and terrestrial palynomorphs have been chosen as palaeoenvironmental proxies for several reasons. Firstly, they are useful palaeoenvironmental indicators in a wide variety of depositional settings. The combined analysis of marine (acritarchs, chitinozoans prasinophytes, scolecodonts) and terrigenous palynomorphs (miospores) in marine sediments allows to reconstruct coeval palaeoenvironmental change in the marine and terrestrial realms, yielding a one-to-one land/sea correlation. Within the spectrum of marine palynomorphs, acritarchs and prasinophytes reflect surface water conditions, whereas scolecodonts provide data on benthic environments. Moreover, palynomorphs are excellently preserved in the Silurian of Gotland. The relative timing of facies changes, stable isotope shifts, and the development of different marine and terrestrial palynomorph groups is presented and their palaeoclimatic implications are discussed.

2. Facies and stable isotope development in the Silurian of Gotland

The Silurian sediments on Gotland have been deposited in a shallow, warm, epicontinental sea slightly south of the Silurian equator. They represent a time span from the late Llandovery to the late Ludlow, and show an extremely low diagenetic overprint because they never underwent deep burial conditions and tectonic stress (Jeppsson 1983, Hagenfeldt 1996). They are built up by about 450m of carbonate rocks covering a wide variety of carbonate facies. While on the western side of Gotland nearly the entire succession is developed as alternations of limestones and marls deposited in an open-marine distal shelf environment, the central and

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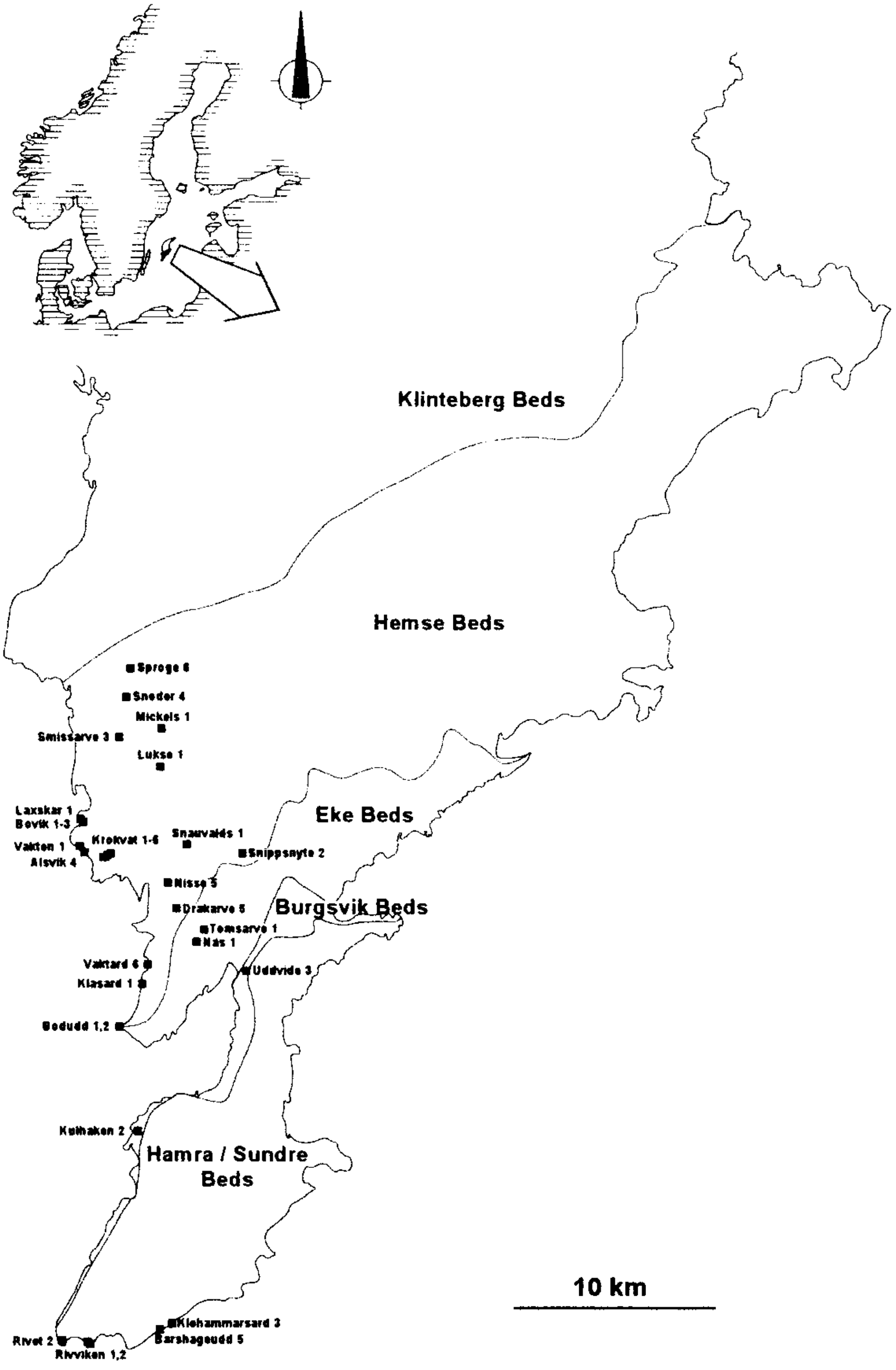


Fig. 2: Geological map and sampled localities on southern Gotland.

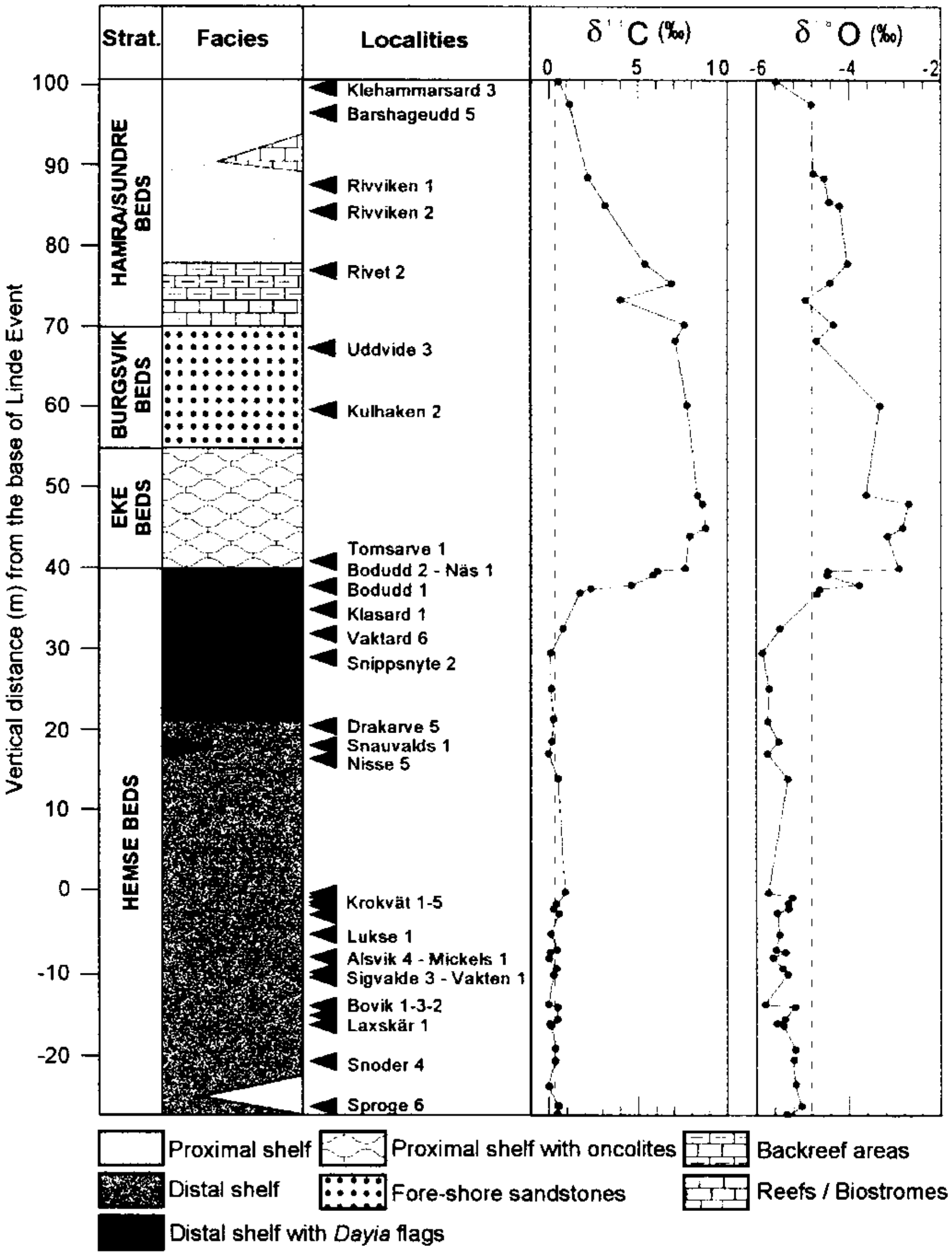


Fig. 3: Lithostratigraphy of the Ludlow succession of western Gotland, with localities sampled for the present study and stable isotope stratigraphy. Stable isotope data are from Samtleben et al. 2000.

eastern parts consist of reefs, back reef sediments, and other rocks of very shallow water environments (Samtleben et al. 1996, 2000).

The succession is characterised by repeated facies changes (Jeppsson 1990, Samtleben et al. 1996, 2000). In the early Sheinwoodian, late Homerian, late Gorstian, and late Ludfordian, carbonate platforms expanded and reefs were abundant. The times in between are dominated by uniform sequences of micritic limestones and marls, with reef development being considerably reduced. The carbon and oxygen isotope records measured from diagenetically unaltered brachiopod shells correspond closely to the facies development (Samtleben et al. 1996). Lower values are recorded in periods dominated by deposition of argillaceous sequences, while higher values are observed in periods dominated by reefs and extended carbonate platforms. As already noted in Chapter 1, the transitions from low to high isotope values are associated with marked extinction events in several groups of organisms (see overview in Munnecke et al. 2003). Generally, the oxygen isotope data show similar trends as the carbon isotope curve. However, $\delta^{18}O$ values exhibit a higher variability than the $\delta^{13}C$ curve, and, especially in extremely shallow environments, a trend to more negative values. This is interpreted as an effect of local warming in restricted shallow-water areas (Samtleben et al. 2000). The present investigation focuses on the Ludlow sediments from western and southern Gotland (Fig. 2; for a detailed description of the facies development see Samtleben et al., 2000).

These sediments are attributed to the Hemse Beds, Eke Beds, Burgsvik Beds, and Hamra/Sundre Beds (Fig. 3). On western Gotland, the lower and middle part of the Hemse Beds (maximum thickness: 90 m) is composed of alternations of grey, bioturbated, wavy-bedded to nodular micritic limestones and marls of an open-marine shelf facies deposited below the storm wave base (Samtleben et al. 2000).

This facies is characterised by sparse, but diverse benthic assemblages mainly composed of brachiopods, ostracods, and trilobites. Grainstones are very rare. In the upper part of the Hemse Beds, the facies changes into laminated, grey, silty, well-bedded micritic limestones and marls. Benthic fossils are very rare, and the laminated nature of the sediments points to oxygen-depleted, probably anoxic bottom water. In some beds, the small brachiopod *Dayia navicula* is very common ("*Dayia*-flags"). It is not clear if this species was able to tolerate low-oxygen conditions or if it lived in a pseudoplanktonic mode, attached to drifting organisms such as cephalopods (Samtleben et al. 2000).

In the uppermost part of the Hemse Beds, the lamination decreases, and the benthic fauna (mainly brachiopods) becomes increasingly diverse. These rocks grade into grey, thinly bedded, argillaceous, micritic limestones and marls of the Eke Beds. The boundary to the overlying Eke Beds (thickness: 15m) is defined by the first occurrence of oncolites. The latter differ from the underlying Hemse Beds by the great abundance of oncolites and oncolitic crusts, the abundant and fully marine diverse benthic fauna (especially brachiopods), and the bioturbated character of the sediments. Most fossils are more or less intensively encrusted by cyanobacteria (*Girvanella*, *Rothpletzella*) forming oncoids.

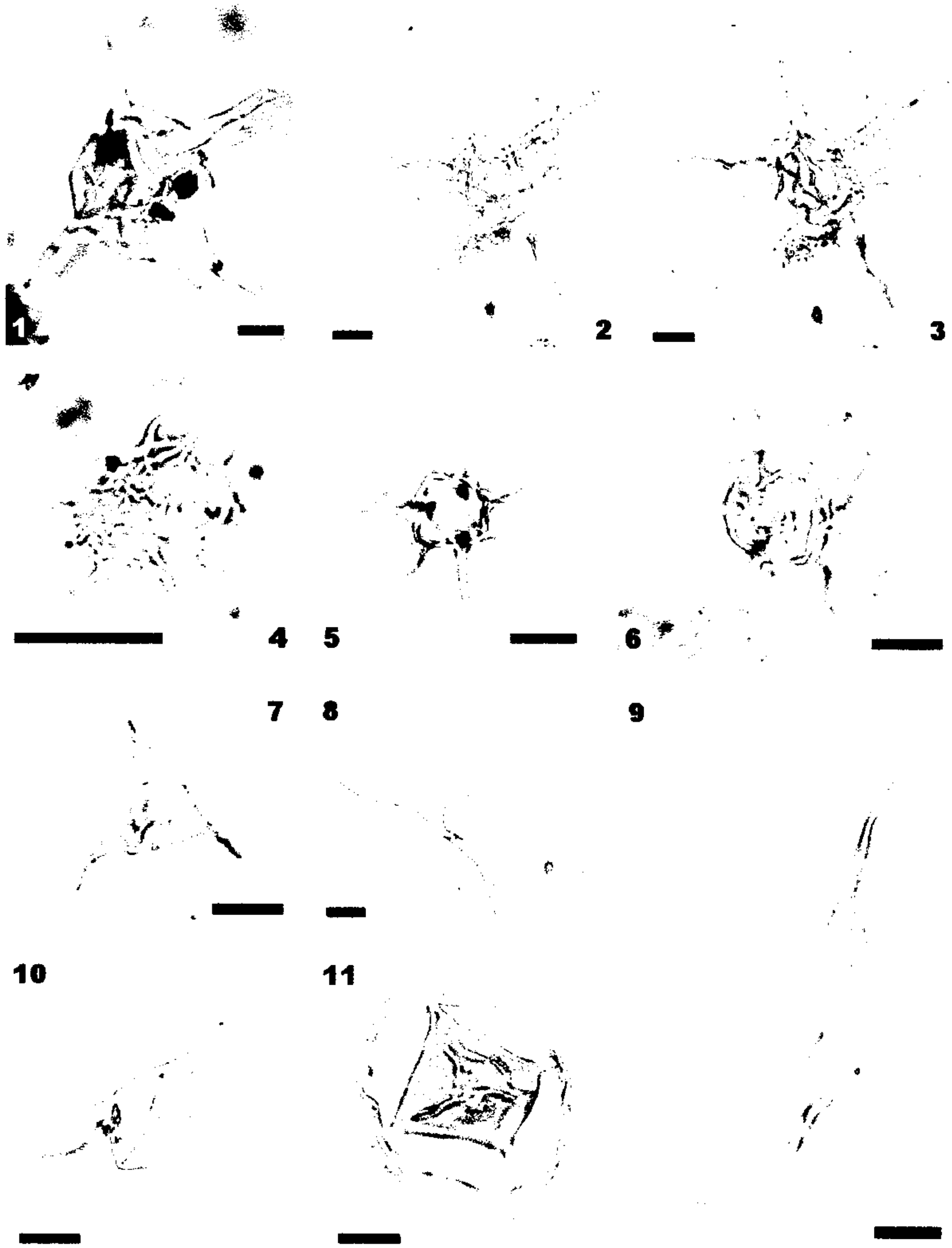
In the shallower facies areas on eastern Gotland, a discontinuity surface is developed at the boundary between the Hemse and Eke Beds (Cherns, 1982). The deposits overlying this surface are composed of detritic limestones, small reef mounds, and stromatolithic algal deposits. In the lower part of the Eke Beds several small hollows, separated by sharp-crested ridges occur. They are interpreted as erosional features in coastal or subaerial environments (Cherns, 1982).

The Hemse-Eke boundary interval is characterised by a strong increase of stable carbon and oxygen isotope values (Fig. 3; 0 to 8.5 ‰ for $\delta^{13}C$ and -6 to -2.5‰ for $\delta^{18}O$; Samtleben et al. 2000). This interval spans the top of the *P. siluricus* and the *C. dubius* conodont zones, and comprises a sequence of five conodont extinction events (Jeppsson and Aldridge, 2000). The first two extinctions occur within the *Dayia*-flags and coincide with the initial $\delta^{13}C$ increase. The second event, located in the upper part of the *Dayia*-flags, is associated with the disappearance of *P. siluricus* and is located within the hiatus in the eastern part of Gotland. The last three events occur within the Eke Beds (Jeppsson 1998). Furthermore, the Hemse-Eke boundary interval corresponds to minor extinctions of graptolites, chitinozoans, and fishes (summarised in Jeppsson and Aldridge 2000).

Plate I

For all microphotographs, scale bars: 20 µm, except Pl. IV-3, where scale bar: 1 µm.

1. *Evittia denticulata* (Cramer 1970) Le Hérissé 1989. Slide B1-55a. Bodudd 1.
2. *Evittia denticulata* (Cramer 1970) Le Hérissé 1989. Slide B1-14a. Bodudd 1.
3. *Evittia denticulata* (Cramer 1970) Le Hérissé 1989. Slide B1-14a. Bodudd 1. Same specimen as in 3.
4. *Micrhystridium* morphotype with short processes, attributable to *Micrhystridium nannacanthum* Deflandre 1945. Slide RI2-1a. Rivet 2.
5. *Micrhystridium stellatum* Deflandre 1945. Slide KR3-4b. Krokvät 3.
6. *Oppilatala septispinosa* Lister 1970. Slide KR3-4b. Krokvät 3.
7. *Veryhachium reductum* Deunff 1958. Slide B1-14a. Bodudd 1.
8. *Veryhachium trispinosum* Eisenack 1938. Slide B1-20a. Bodudd 1.
9. *Dorsennidium europaeum* (Stockmans & Willière 1960) Sarjeant and Stancliffe 1994. Slide KR3-4b. Krokvät 3.
10. *Quadraditum fantasticum* Cramer 1964. Slide KR3-4b. Krokvät 3.
11. *Leiofusa parvitatis* Loeblich 1970. Slide KR3-4b. Krokvät 3.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The Eke Beds are overlain by well-sorted foreshore sandstones of the Burgsvik Beds (maximum thickness: 47 m) with a sparse, but fully marine brachiopod fauna. Cross bedding, ripple marks, and load casts are common. The uppermost part of this series consists of thinly cross-bedded oolitic limestones. The stable isotope values of the Burgsvik Beds are slightly lower than those of the upper part of the Eke Beds, but are still very high (>7‰ $\delta^{13}C$). The oolitic limestones of the upper Burgsvik Beds pass gradually into oncolites of the Hamra/Sundre Beds (thickness: 50 m), containing bioclasts of normal marine fauna. Reefs and crinoidal limestones interlocking with back-reef deposits towards the NE and open marine shelf deposits towards the SW overlie these deposits. On southernmost Gotland, the carbonate platform of the Hamra/Sundre Beds passes into a limestone-marl sequence of proximal shelf facies.

3. Material and methods

104 samples from 33 localities have been investigated on their palynomorph contents (Fig. 2). To correlate our results exactly with the carbon isotope stratigraphy, we have sampled only localities with published isotope data from diagenetically unaltered brachiopod shells (Samtleben et al. 2000). The description of localities is given in Samtleben et al. (2000). In the Hemse Beds, a minor positive isotope excursion (1‰ $\delta^{13}C$) has been reported by Samtleben et al. (2000).

Plate II

1.*Multiplicisphaeridium saharicum* Lister 1970. Slide B1-55a. Bodudd 1.
2.*Visbysphaera microspinosa* (Eisenack 1954) Lister 1970. Slide KR4-2d. Krokvät 4.
3.*Eupoikilofusa tenuistriata* Pothé de Baldis 1975. Slide K1-1a. Klasard 1.
4.*Cymbosphaeridium pilaris* (Cramer 1964) Lister 1970. Slide RVK1-1a. Rivviken 1.
5.*Onondagella asymmetrica* (Deunff 1954) Cramer & Díez 1972. Slide B1-39a. Bodudd 1.
6.*Cymatiosphaera octaplana* Deunff 1958. Slide B1-39a. Bodudd 1.
7.*Cymatiosphaera octaplana* Deunff 1958. Slide B1-39a. Bodudd 1. Same specimen as in 6.
8.*Pterospermopsis martinii* Cramer 1967. Slide BOV3-7a. Boviken 3.
9.*Cymatiosphaera mariae* Cramer, Díez, Rodriguez & Fombella 1976. Slide B1-39a. Bodudd 1.
10.*Cymatiosphaera mariae* Cramer, Díez, Rodriguez & Fombella 1976. Slide B1-39a. Bodudd 1. Same specimen as in 9.
11. *Dictyotidium stenodictyum* Eisenack 1965. Slide B1-74a. Bodudd 1.

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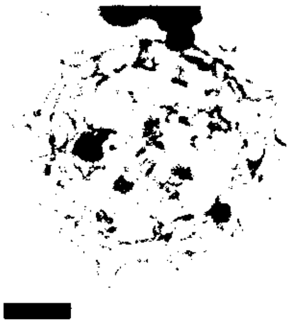
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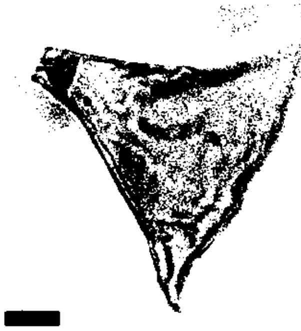
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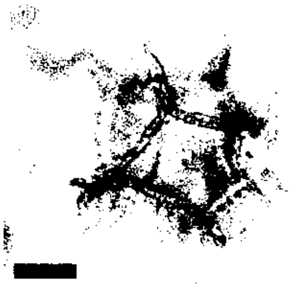
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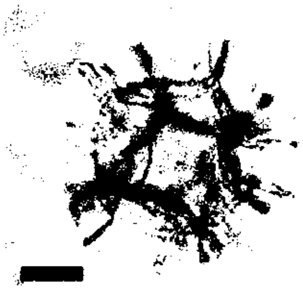
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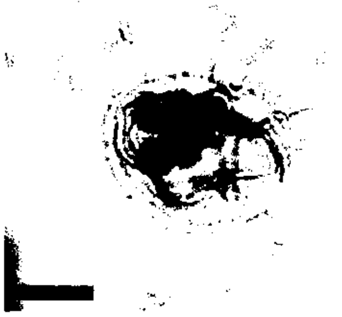
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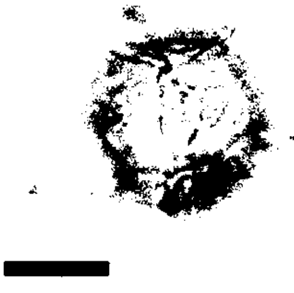
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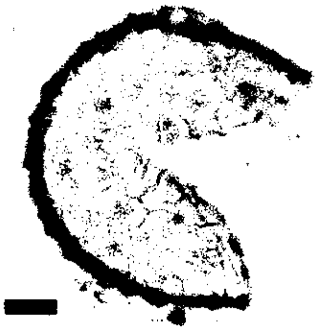
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The base of this isotope excursion has been chosen as reference level by Samtleben et al. (2000) ("base of Linde Event" = 0 m). For consistency, we use the same reference level in the present paper. Palynological sample preparation followed standard techniques (e.g., Wood et al., 1996). After spiking with *Lycopodium* marker spores to facilitate the calculation of absolute palynomorph abundances, 100 g (limestones and sandstones) or 50 g (marls) of sample material were treated with 33% HCl and 40% HF. Subsequent to each chemical preparation step, the residue was sieved through a 11 µm nylon mesh. Strew mounts were prepared using glycerine jelly as mounting medium.

For each sample, a minimum of 250 palynomorphs were counted using an Olympus BX 51 light microscope and identified to the species level. For a broad characterization of the palynological assemblages, the identified palynomorphs were attributed to the following groups: process-bearing acritarchs (for convenience here termed "acritarchs"), sphaeromorphs (acritarchs devoid of processes and ornamentation; Pl. IV 6), acanthomorph acritarchs (all acritarchs with more than 10 processes), polygonomorph acritarchs (all acritarchs than 3 to 6 processes), netromorph acritarchs (acritarchs with two processes at the ends), prasinophytes (Pl. II 6-11), scolecodonts, chitinozoans, and spores (land plant-derived palynomorphs; Pl. III 2-3).

Microphotographs were made with an Olympus CAMEDIA digital camera. Scanning Electron Microscope (SEM) photographs were digitally acquired using a Cambridge Stereoscan 240. All material is filed in the collection of the Institute of Geological Sciences, University of Tübingen, Germany.

4. Results

4.1 Distribution patterns in major palynomorph groups

4.1.1 Absolute abundances

Acritarchs and sphaeromorphs are by far the most abundant components of the palynomorph assemblages throughout the sections examined, with maximum abundances reaching up to 10.000 specimens per gram of sediment (Fig. 4a).

The absolute abundance curves of all marine palynomorph groups show a trend towards reduced values during the δ^{13}C excursion. In the late stage of the excursion, with δ^{13}C values approaching pre-excursion levels, absolute acritarch, sphaeromorph, prasinophyte, chitinozoan, and scolecodont abundances increase steadily until pre-excursion values are reached. In contrast,

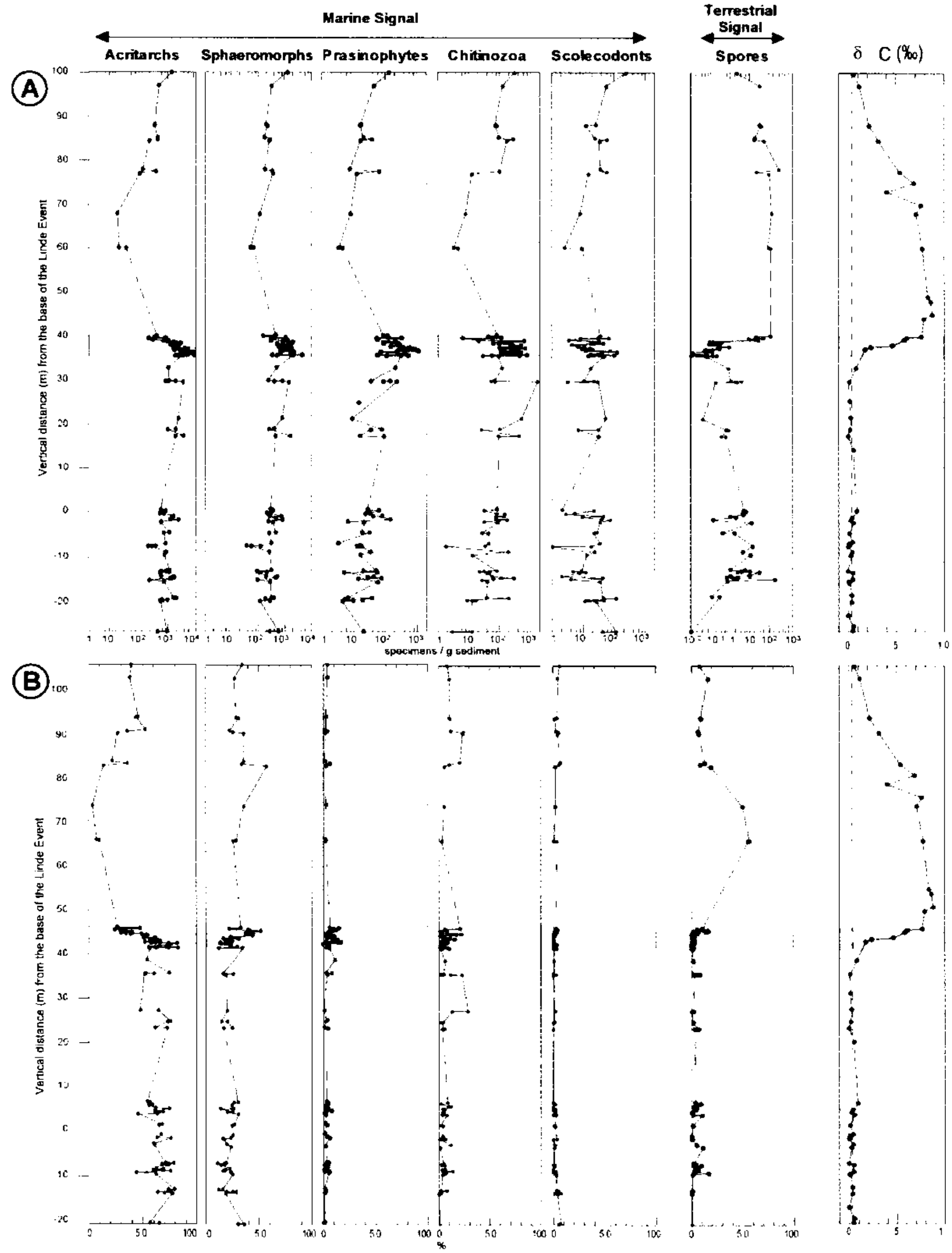


Fig. 4: Absolute (A) and relative abundances (B) of acritarchs, sphaeromorphs, prasinophytes, chitinozoans, scolecodonts , and spores throughout the sampled section. Note logarithmic scale of the X-axis in Fig. 4A. $\delta^{13}C$ data shown for comparison are from Samtleben et al. (2000).

absolute spore abundances, which represent a terrestrial signal, show an opposite distribution pattern. With the onset of the $\delta^{13}C$ excursion, they increase strongly, reaching values of 100 and more specimens per gram of sediment. Absolute spore abundances remain high throughout the excursion interval and decrease again when $\delta^{13}C$ values reach pre-excursion levels.

4.1.2 Relative abundances

Whereas the relative abundances of the marine palynomorph groups show only low fluctuations throughout the pre-excursion interval of the examined succession, strong changes can be observed with the onset of the $\delta^{13}C$ excursion. Towards the end of the excursion, relative percentages of all marine palynomorph groups approach pre-excursion levels (Fig. 4b).

More specifically, acritarchs make up for more than 50% of the total pre-excursion palynomorph assemblages. A strong drop in relative acritarch abundances accompanies the decline of $\delta^{13}C$ values. Throughout the excursion interval, acritarch percentages remain low, and only in the late stage of the excursion (with strongly declining $\delta^{13}C$ values) they rise to near pre-excursion levels. Sphaeromorph, prasinophyte, chitinozoan, and scolecodont percentages show only minor changes throughout the examined succession. The curve of spore percentages, in contrast, closely mirrors the $\delta^{13}C$ curve. Pre-excursion percentages do not exceed 3% of total palynomorphs, but a strong increase (to up to 10% of total palynomorphs) occurs during the major isotope shift. With the decline of $\delta^{13}C$ values later during the excursion, spore percentages also decrease until pre-excursion percentages are reached.

4.2 Distribution patterns in process-bearing acritarch groups

4.2.1 Absolute abundances

Before the onset of the $\delta^{13}C$ excursion, the absolute abundances of acanthomorphs and polygonomorphs are mostly between 100 and more than 1.000 specimens per gram of sediment (Fig. 5a). Netromorphs are somewhat rarer and their absolute abundances are predominantly between 10 and 100 specimens per gram of sediment.

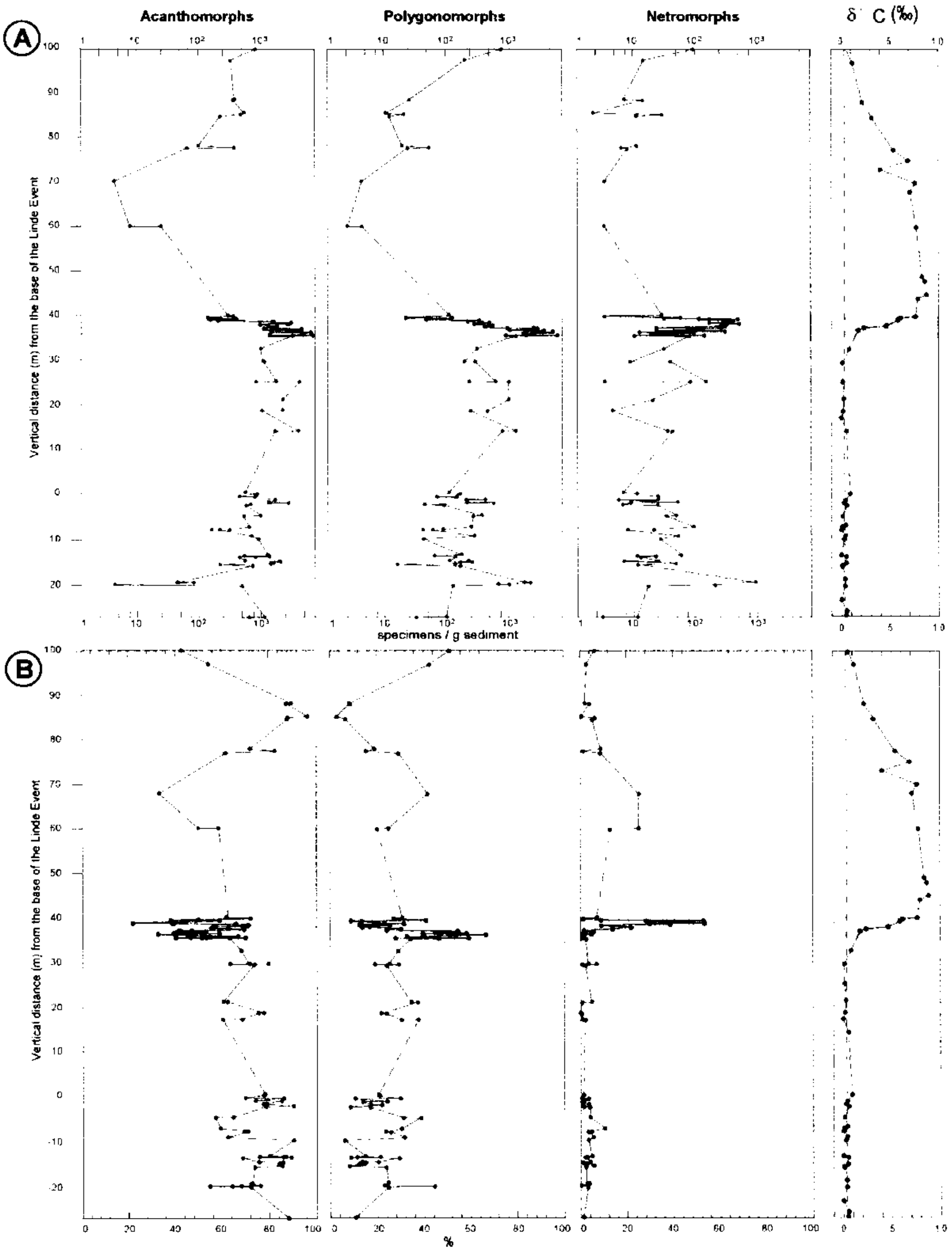


Fig. 5: Absolute (A) and relative abundances (B) of acanthomorph, polygonomorph, and netromorph acritarchs throughout the sampled section. Note logarithmic scale of the X-axis in Fig. 5A. $\delta^{13}C$ data shown for comparison are from Samtleben et al. (2000).

With the onset of the $\delta^{13}C$ excursion, absolute abundances of process-bearing acritarchs rise to the highest values throughout the examined succession (Fig. 5a). Subsequently, they show a pronounced drop, with absolute abundances of acanthomorphs and polygonomorphs decreasing from more than 1.000 to a minimum of less than 10 specimens per gram of sediment in the middle part of the excursion. The decrease in absolute netromorph abundances is slightly less pronounced, but still clearly visible. With the decline of $\delta^{13}C$ values later during the excursion, absolute abundances of acanthomorphs, polygonomorphs, and netromorphs increase again until pre-excursion percentages are reached.

4.2.2 Relative abundances

In the lower part of the profile, acanthomorphs and polygonomorphs together usually make up more than 90% of the acritarch assemblage and thus their percentages show an inverse correlation (Fig. 5b). The percentages of acanthomorphs and polygonomorphs are highly variable. Percentages of netromorphs remain low and never exceed 10% of total process-bearing acritarchs.

During the strong rise of $\delta^{13}C$ values at the onset of the excursion, polygonomorph percentages show a pronounced maximum. Subsequently, they decrease and a simultaneous rise in netromorph percentages can be observed. Acanthomorph percentages peak between the highs of the polygonomorph and netromorph percentages (Fig. 5b).

Later during the excursion, acanthomorph percentages fall and then rise again, whereas polygonomorph percentages show an inverse pattern. After reaching a maximum during the onset of the excursion, netromorph percentages show a second peak in the middle part of the excursion. With $\delta^{13}C$ values approaching pre-excursion levels, netromorph percentages also return to pre-excursion values. Acanthomorph percentages, however, do not recover to pre-excursion levels, whereas polygonomorph percentages steadily increase in the topmost part of the succession (Fig. 5b).

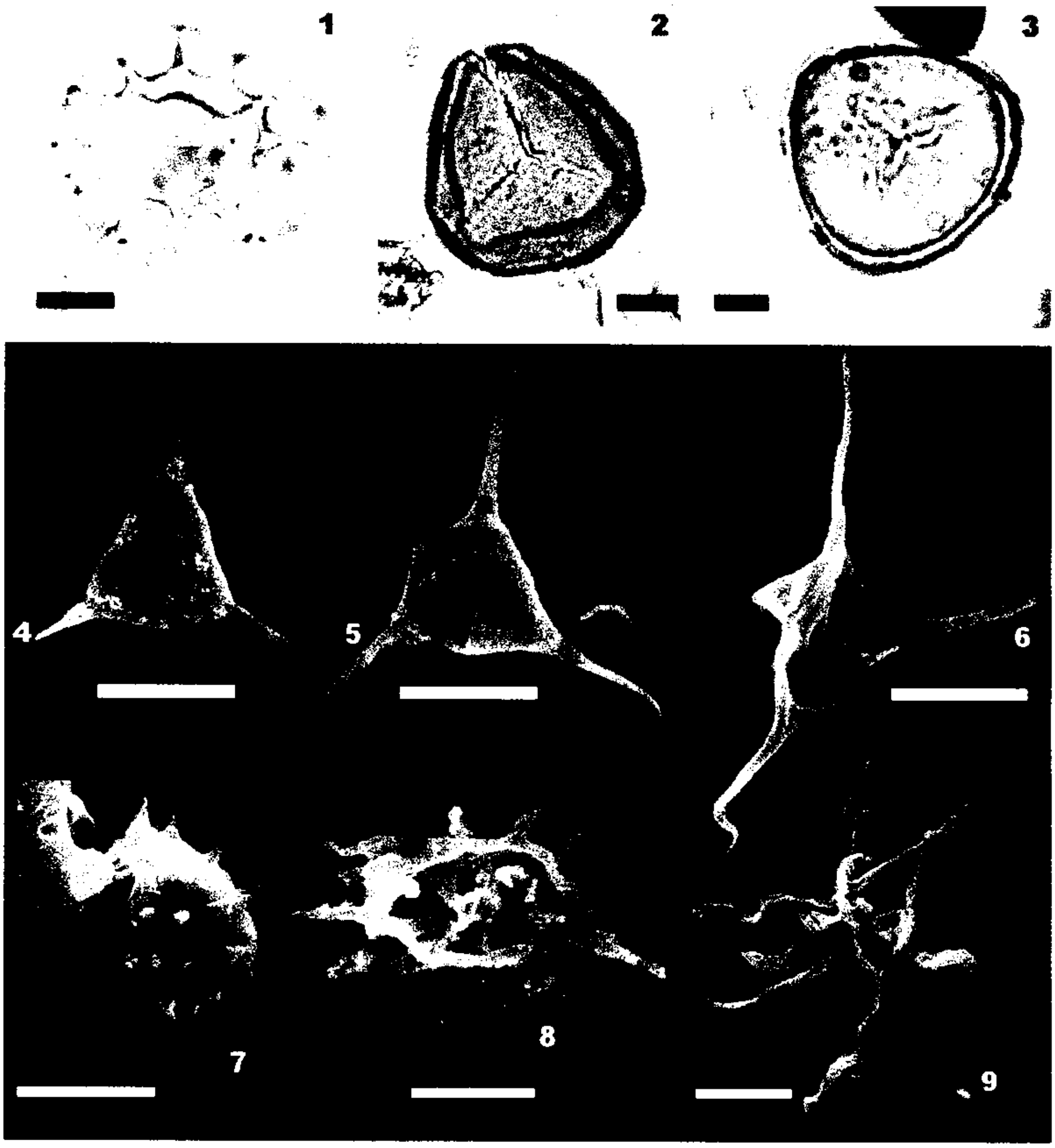
Plate III

1.*Duvernaysphaera aranaides* (Cramer 1964) Cramer & Díez 1972. Slide BOV1-3a. Boviken 1.

2.Spore attributable to *Ambitisporites* sp. Slide KUHL2-2a. Kuhlaken 2.

3.Spore attributable to *Ambitisporites* sp. Slide BOV3-1a. Boviken 3.

4.*Veryhachium reductum* Deunff 1958. Mount B1-16. Bodudd 1.



5.*Veryhachium trispinosum* Eisenack 1938. Mount B1-4. Bodudd 1.

6.*Dorsennidium europaeum* (Stockmans & Willière 1960) Sarjeant and Stancliffe 1994. Mount SN4-1. Snoder 4.

7.*Micrhystridium* morphotype with short processes, attributable to *Micrhystridium nannacanthum* Deflandre 1945. Mount SN4-1. Snoder 4.

8.*Micrhystridium* morphotype with short processes, attributable to *Micrhystridium parinconspicuum* Deflandre 1945. Mount B1-4. Bodudd 1.

9.*Micrhystridium* morphotype with long and ramified processes, attributable to *Micrhystridium imitatum* Deflandre 1945. Mount B1-4. Bodudd 1.

4.3 Distribution patterns in selected acritarch genera

4.3.1 Absolute abundances

The absolute abundances of the acritarch genera *Micrhystridium* (Pl. I 4-5; Pl. II 7-9), *Evittia* (Pl. I 1-3; Pl. IV 1), *Veryhachium* (Pl. I 7-8; III 4-5), *Dorsennidium* (Pl. I 10; Pl. III 6), *Multiplicisphaeridium* (Pl. II 1; Pl. IV 4-5), *Oppilatala* (Pl. I 6), *Percultisphaera* (Pl. IV 2-3), *Histopalla*, *Leiofusa* (Pl. I 9), and *Eupoikilofusa* (Pl. IV 8) show relatively strong variations during the pre-excursion interval of the examined succession (Fig. 6). The onset of the excursion is marked by a transient rise in absolute abundances in all genera. During the middle part of the excursion, all genera show reduced abundances, and it is only when $\delta^{13}C$ values approach pre-excursion levels that absolute abundances recover to values as they are encountered in the lower part of the section.

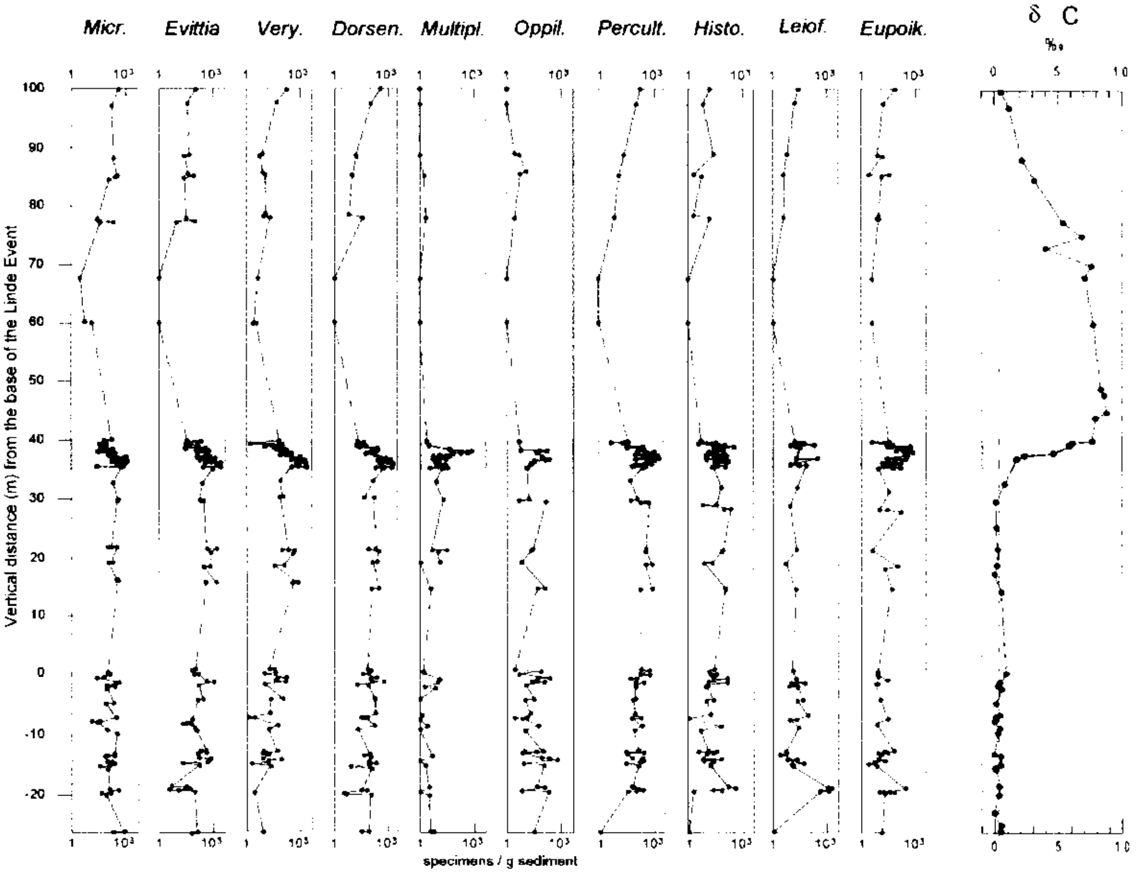


Fig. 6: Absolute abundances of selected acritarch genera throughout the sampled section. Note logarithmic scale of the X-axis. $\delta^{13}C$ data shown for comparison are from Samtleben et al. (2000). *Micr.* = *Micrhystridium*, *Very.* = *Veryhachium*, *Multipl.* = *Multiplicisphaeridium*, *Oppil.* = *Oppilatala*, *Percult.* = *Percultisphaera*, *Histo.* = *Histopalla*, *Leiof.* = *Leiofusa*, *Eupoik.* = *Eupoikilofusa*.

4.3.2 Relative abundances

With the exception of *Micrhystridium*, *Evittia*, *Veryhachium*, and *Eupoikilofusa*, all selected acritarch genera show reduced relative abundances during the δ^{13}C excursion (Fig. 7a). For the interval comprising the onset of the excursion, the selected acritarch genera reveal a succession of increased relative abundances (Fig. 7b). Specifically, a sequence of temporarily increased relative abundances of *Multiplicisphaeridium*, *Oppilatala*, *Percultisphaera*, *Histopalla*, *Leiofusa*, and *Eupoikilofusa* (in the order of appearances) can be observed.

4.4 Distribution patterns within the *Micrhystridium* and *Veryhachium* plexus

4.4.1 Absolute abundances

Morphotypes within the *Micrhystridium* plexus (i.e., morphotypes with short processes – *M. nannacanthum* and *M. parinconspicuum,* Pl. I 4, Pl. III-7 and Pl. III 8, respectively), *M. stellatum* sensu stricto (Pl. I 5), and morphotypes with long ramified processes – *M. imitatum* (Pl. III 9) show variations in absolute abundances before the onset of the δ^{13}C excursion, with absolute abundances mostly varying between 100 and 1.000 specimens per gram of sediment (Fig. 8a).

During the onset of the excursion when δ^{13}C changes are most rapid, *M. stellatum* sensu stricto and the morphotypes with long and ramified processes decline in abundances. They remain very low or are even absent during the middle part of the excursion. This only changes in the upper part of the excursion when δ^{13}C values decrease again and the abundances of both morphotypes recover to pre-excursion values. *Micrhystridium* morphotypes with short processes also show reduced absolute abundances during the isotope excursion, but the drop in values is less strong than in the other *Micrhystridium* morphogroups (Fig. 8a).

A slightly different picture emerges for morphotypes from the *Veryhachium* plexus. Both *V. reductum* (Pl. I 7; Pl. III 4 - short processes) and *V. trispinosum* (Pl. I 8; Pl. III 5 - short processes) are abundant elements of pre-excursion acritarch assemblages. During the onset of the excursion, they reach their highest absolute abundances within the entire succession. Later during the excursion, their abundances decline, and it is only towards the end of the excursion that pre-excursion abundances are regained.

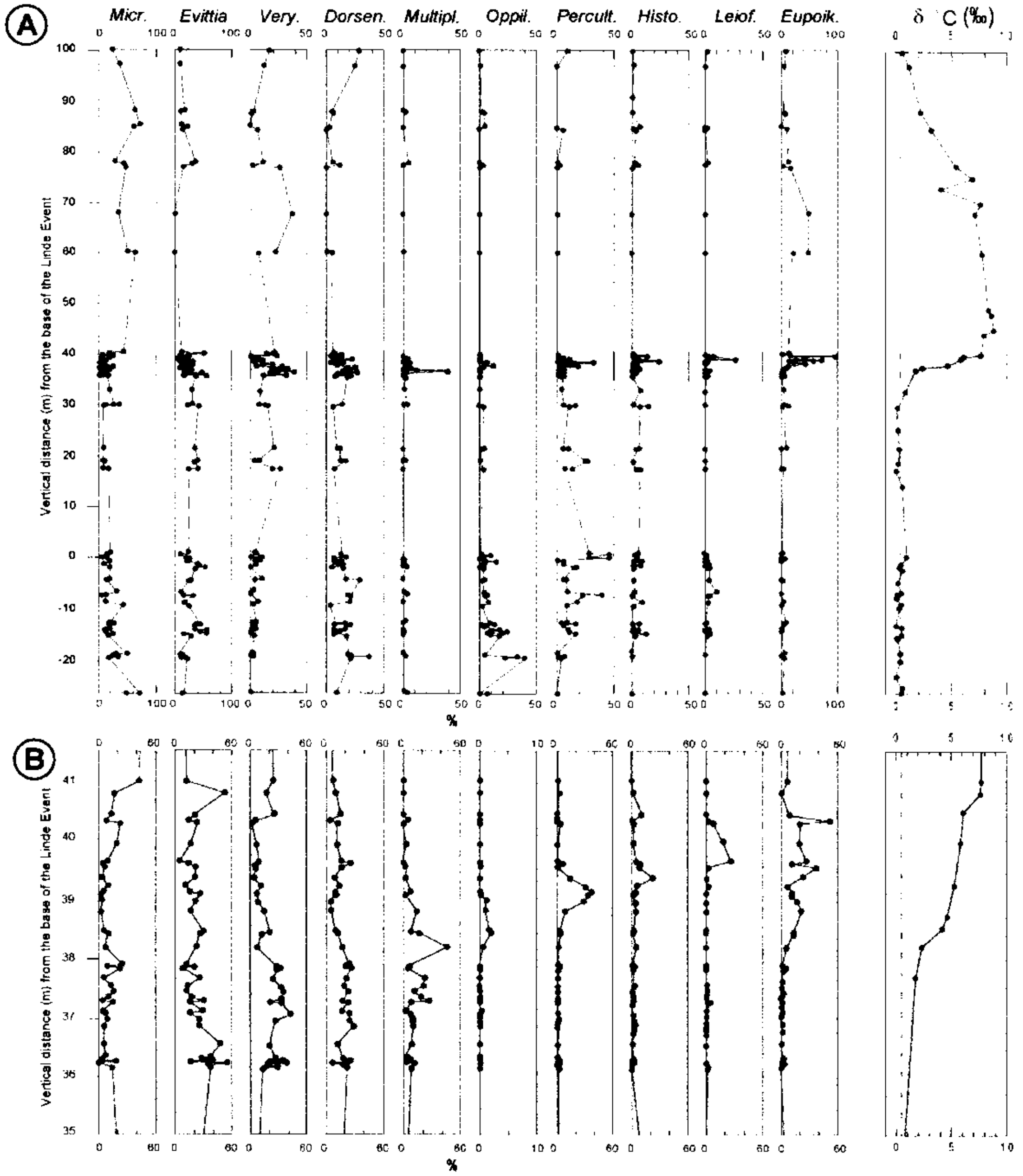


Fig. 7: Relative abundances of selected acritarch genera (A) throughout the sampled section and (B) during the interval of strongest $\delta^{13}C$ shifts. δ ^{13}C data shown for comparison are from Samtleben et al. (2000). *Micr.* = *Micrhystridium*, *Very.* = *Veryhachium*, *Multipl.* = *Multiplicisphaeridium*, *Oppil.* = *Oppilatala*, *Percult.* = *Percultisphaera*, *Histo.* = *Histopalla*, *Leiof.* = *Leiofusa*, *Eupoik.* = *Eupoikilofusa*.

4.4.2 Relative abundances

Within the *Micrhystridium* plexus, the relative abundances of morphotypes with short processes and *M. stellatum* sensu stricto show inverse distribution patterns (Fig. 8b). The relative abundances of morphotypes with short processes mirror the isotope excursion by strongly increasing during the onset of the excursion, remaining on a high level in the middle part of the excursion, and declining when $\delta^{13}C$ return to pre-excursion values. The relative abundances of *M. stellatum* sensu stricto show an opposite trend. Within the *Veryhachium* plexus, relative abundances of *V. reductum* roughly mirror the isotope excursion, whereas relative abundances of *V. trispinosum* exhibit an inverse pattern (Fig. 8b).

5. Discussion

The Late Ludlow is characterised by global changes in biota, facies development, and the development of stable carbon and oxygen isotopes (Bickert et al. 1997, Jeppsson 1998, Jeppsson and Aldridge 2000, Samtleben et al. 2000, Jeppsson et al. 2002, Munnecke et al. 2003). The strongest $\delta^{13}C$ excursion of the entire Phanerozoic is observed on a global scale in this time interval. It has been termed "upper Ludfordian A-period" (Bickert et al. 1997) owing to the strong palaeoclimatic/-oceanographic changes that have been postulated by these authors. According to Bickert et al. (1997), an arid climate prevailed in the low latitudes during this time, resulting in low terrestrial nutrient input into the marine realm.

Very similar isotope excursions, also associated with facies changes and extinction events, are observed not only in the Silurian, but also in the Cambrian and Ordovician, and are likewise interpreted as times of arid climate (Fig. 1; see summary in Munnecke et al. 2003). The strong similarities of these events indicate similar steering mechanisms. The conclusions derived from the present study, therefore, probably are transferable to the other A-periods in the Early Palaeozoic.

5.1 Productivity changes and $\delta^{13}C$ values

In Mesozoic and Cenozoic sediments, positive excursions of $\delta^{13}C$ values often can be attributed to enhanced bioproductivity and/or enhanced deposition of organic matter (black shales; e.g., Berger and Vincent 1986; Kump and Arthur 1999; Herrle et al. 2003). These explanations can be ruled out for the upper Ludfordian A-period for three reasons:

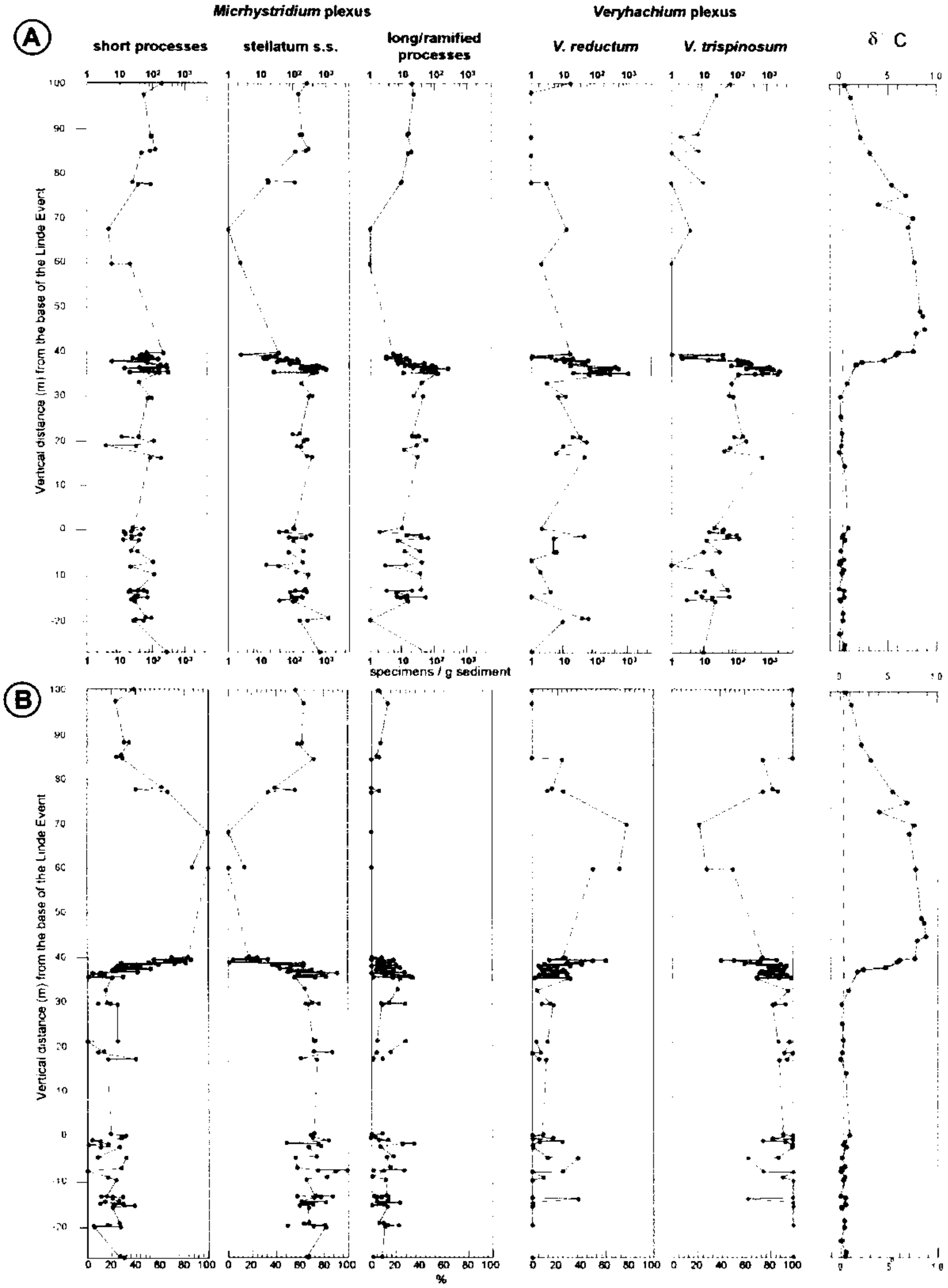


Fig. 8. Absolute (A) and relative abundances (B) of different morphotypes in the *Micrhystridium* and *Veryhachium* plexus throughout the sampled section. Note logarithmic scale of the X-axis in Fig. 8A. $\delta^{13}C$ data shown for comparison are from Samtleben et al. (2000).

(1) The absolute abundance of marine phytoplankton (acritarchs) decreases, indicating reduced planktic productivity;

(2) The extreme amplitude of nearly 10‰ in $\delta^{13}C$ values on Gotland is by far too high to be explained by productivity changes (see discussion in Bickert et al. 1997);

(3) oxygenated deep shelf sediments of this time period do not indicate an increased, but a reduced deposition of organic matter (Wenzel, 1997).

Therefore, the results presented here, i.e. that the absolute abundance of organic-walled phytoplankton is reduced during the isotope excursion, confirm the interpretation of Jeppsson (1990) and Bickert et al. (1997) who assume the upper Ludfordian to represent a time of reduced bioproductivity. The extreme amplitude of $\delta^{13}C$ values is probably caused by changes between estuarine and anti-estuarine circulation in the ocean (Bickert et al. 1997). During the Silurian, euxinic conditions prevailed below the surface waters in the pelagic ocean, resulting in a strong fractionation in carbon isotopic composition between surface and deep waters produced by the settlement and deposition of ^{12}C-rich organic material in deep-sea sediments (black shales). Under arid climate conditions (A-periods), the formation and downwelling of saline surface water caused an anti-estuarine circulation pattern in shallow seas and ^{13}C-enriched open ocean surface water reached the shelf areas, resulting in high $\delta^{13}C$ values.

During humid conditions (H-periods), upwelling of ^{12}C-enriched deep-water lead to low $\delta^{13}C$ values. This upwelling of nutrient-rich deep water as well as input of terrigenous nutrients resulted in abundant and diverse acritarch communities. During A-periods terrestrial nutrient input was low and upwelling ceased, resulting in impoverished acritarch communities.

It is, however, important to note that the change in phytoplankton bioproductivity obviously did not considerably change the carbon isotopic composition of the seawater, because times of high productivity are correlated with low $\delta^{13}C$ values and vice versa. The probable reason for this observation is that the difference between a biological pump with maximum activity and a strangelove ocean state is only on the order of 2 to 3‰ in $\delta^{13}C_{DIC}$ (Berger and Vincent, 1986) This is less than one third of the amplitude observed, and is considerably lower than the effect of varying input of ^{12}C-enriched subsurface water or an influx of ^{13}C-enriched surface water.

Plate IV

1. *Evittia denticulata* (Cramer 1970) Le Hérissé 1989. Mount B1-4. Bodudd 1.

2. *Percultisphaera stiphrospinata* Lister 1970. Mount B1-4. Bodudd 1.

3. Detailed view of the wall structure of the specimen in 2.

4. *Multiplicisphaeridium pardaminum* Díez & Cramer 1976. Mount B1-41. Bodudd 1.

5.*Multiplicisphaeridium saharicum* Lister 1970. Mount B1-41. Bodudd 1.

6.Sphaeromorph, attributable to *Leiosphaeridia* sp. Mount SNV1-2. Snauvalds 1.

7.*Cymatiosphaera mariae* Cramer, Díez, Rodriguez & Fombella 1976. Mount SNV1-2. Snauvalds 1.

8.*Eupoikilofusa tenuistriata* Pothé de Baldis 1975. Mount B1-41. Bodudd 1.

5.2 Timing and causes of biotic changes

All of the isotope excursions summarised in Fig. 1 coincide with biotic extinction events. The strongest faunal changes in hemipelagic organisms (e.g. conodonts, graptolites) are observed at the beginning or even prior to the increase of δ^{13}C values (see summary in Munnecke et al., 2003; Jeppsson et al., 2002). Organisms thriving in shallow-water environments, e.g., reefs, were only little affected. Therefore environmental changes that are directly connected with the stable isotopic composition of the sea water (e.g. growth if ice caps, temperature and sea-level changes) can be excluded to be responsible for the early extinctions. Obviously, the most strongly affected area during that time was the outer shelf area, whereas shallow-water communities are less affected (see discussion in Munnecke et al. 2003). Munnecke et al (2003) have speculated that the extinctions were caused by an influx of euxinic deep-water masses in peripheral marine areas resulting from the breakdown of the front between oxygenated surface water and anoxic deeper water during the turnover from an estuarine to an anti-estuarine circulation. Such a scenario would have affected not only benthic organisms on the deep shelves, but also the deep migrating zooplankton and nekton (e.g. conodonts, graptolites), whereas phytoplankton should have been less affected. Sedimentologically, this hypothesis is corroborated by the lamination in the upper Hemse Beds, which also indicate anoxic or disoxic bottom water conditions.

Our results show that the distribution patterns of all marine palynomorph groups are closely correlated with the carbon isotope development. For the interval of increased carbon isotope values, acritarchs generally show a strong decrease in absolute abundances (Figs. 4a, 5a, 6). A similar picture emerges for sphaeromorphs, prasinophytes, chitinozoans, and scolecodonts (Fig. 4a). Moreover, a pronounced turnover in the composition of acritarch assemblages can be observed (Figs. 4 to 8). This turnover is strongest during the initial rise of carbon isotope values and thus postdates the extinction events in conodonts. Obviously, the phytoplankton was affected later by the oceanographic/climatic changes than deeper-water organisms. A similar behaviour is known from the Ireviken Event close to the Llandovery/Wenlock boundary. Here, a turnover of the acritarch assemblages occurs in the Upper Visby Beds contemporaneous to the ascent of carbon isotope values, but clearly after the extinction event of conodonts, graptolites, and trilobites (Le Hérissé, 1989; Jeppsson, 1997a,c; Gelsthorpe, 2002).

The reduction in marine palynomorph abundances during the isotope excursion could be explained by a low-latitude climatic shift from relatively humid to more arid conditions, which decreased the chemical weathering on the continents, and consequently led to a reduction in the input of terrestrial nutrients. The succession of several distinct maxima in the abundance of different acritarch genera during the initial increase of $\delta^{13}C$ values (Fig 7) indicates continuously changing environmental conditions in the photic zone, with optimum ecological conditions for single genera often being restricted to less than one meter of strata, and thus only lasting for a relatively short time interval. This sequence of blooms in different acritarch genera is best visible in the distribution pattern of *Multiplicisphaeridium*, *Oppilatala*, *Percultisphaera*, *Histopalla*, *Leiofusa*, and *Eupoikilofusa* (Fig. 7b). These genera probably exploited specific palaeoenvironmental conditions. As many acritarchs probably represent the Palaeozoic equivalents of Meso- and Cenozoic organic-walled dinoflagellate cysts (e.g., Servais et al. 1997, Moldowan & Talyzina 1998, Talyzina et al. 2000), the observed blooms may well be the results of environmental changes as they are known to affect Meso- and Cenozoic organic-walled dinoflagellate cyst assemblages. Hence, it may be speculated that the blooms were controlled by changes in productivity, temperature, salinity, oxygen availability, and/or stratification in the surface waters (compare Pross et al. in press, and Slujis et al. subm., for reviews on the ecology of cyst-forming dinoflagellates).

5.3 Morphological variation in acritarchs, acritarch ecophenotypism, and surface water properties

The time of elevated isotope values probably represents a period of arid climate in low latitudes. This is well documented by the high $\delta^{18}O$ values of the upper Ludfordian A-period measured in diagenetically unaltered brachiopod shells (Fig. 3; Samtleben et al. 1996, 2001). The shift of about 4‰ in $\delta^{18}O$ values is too high to be explained by decreasing temperatures because it requires a temperature drop in low-latitude surface waters of about 16°C, a value that is totally unrealistic (Samtleben et al. 1996, Bickert et al. 1997). Thus, salinity changes must be taken into account to explain the large $\delta^{18}O$ amplitude observed. Independent evidence for enhanced salinity is provided by the widespread occurrence of calcareous cyanobacteria on Gotland, in Scania (Sweden), in the Holy Cross Mountains (Poland), and in Australia (Cherns, 1983, Wigforss-Lange 1999, Samtleben et al. 2000, Jeppsson et al. 2002, Kozlowski 2003), typically favouring elevated salinity. However, because salinity changes were obviously the dominant factor influencing the $\delta^{18}O$ development, even increased sea-surface temperatures during the upper Ludfordian A-period cannot be ruled out.

Acritarch genera that are normally abundant in distal environments on Gotland (i.e. *Evittia*, *Percultisphaera*) are almost absent during the upper Ludfordian A-period, whereas genera typical for proximal environments (e.g., *Veryhachium*, *Micrhystridium*, *Leiofusa*) are more frequent during that time (Stricanne et al. in press). This observation is in accordance with the lithological development on western Gotland. Sediments deposited during this time are composed of shallow-water carbonates, (i.e. reefs, reef-related strata, foreshore sandstones, oncolitic limestones, and proximal shelf deposits), whereas the preceding lower Ludfordian H-period is strongly characterized by open-marine distal shelf deposits.

Our acritarch data show a marked shift within the *Micrhystridium* and *Veryhachium* plexus. In the lower Ludfordian H-period specimens with long and ramified processes prevail, whereas in the upper Ludfordian A-period a dominance of specimens with short processes is observed (Fig. 8). In a previous study of the present authors (Stricanne et al. in press) it is shown that *Micrhystridium* morphotypes with short processes show a decline in relative abundance from proximal to distal environments in the lower Hemse Beds on Gotland, and specimens with long and ramified processes become more abundant towards the distal shelf environments. The shifts observed in the *Micrhystridium* and *Veryhachium* plexus in the present study are much more pronounced than those of the inshore-offshore transect mentioned above, and the *Micrhystridium stellatum* population, which does not show significant differences in relative abundance in the inshore-offshore transect, shows a strong decrease during the isotope excursion. Therefore, these shifts cannot be explained solely by decreasing water depth. Instead, they may be connected with the physical properties of the ambient sea water. Whereas it is unknown if temperatures during the A-period were higher or lower compared to the preceding H-period (see above), the salinity and therefore also the density of the surface waters was most probably higher. If an analogy of Palaeozoic acritarchs to Meso- and Cenozoic organic-walled dinoflagellate cysts is assumed (see above), our findings on acritarch process lengths are compatible with the environmental changes inferred from the oxygen isotope records. According to studies on fossil and recent organic-walled dinoflagellate cysts, some taxa develop a reduced ornamentation in water of higher temperature (Wall et al., 1973; Wall and Dale, 1974; Turon, 1984; Kokinos and Anderson, 1995; Hallett, 1999). Moreover, laboratory experiments show a reduction in process length in dinoflagellate cysts under elevated as well as under reduced salinity (Ellegaard et al., 2002).

However, as the exact systematic position of acritarchs is yet unclear, the function of their processes remains speculative. It may be hypothesized that the function of the processes was related to the buoyancy of the surrounding waters. In that case, the reduction in process length during the upper Ludfordian A-period might represent an adaptation to higher-density waters.

5.4 The terrestrial signal

Both the absolute and relative abundances of terrestrial palynomorphs (cryptospores and trilete spores; compare with Hagström, 1997) closely mirror the $\delta^{13}C$ curve (Fig. 4a, b). The strong negative correlation of absolute spore and marine palynomorph abundances indicate that both the marine and terrestrial realms were synchronously affected by the environmental changes that also caused the isotope excursion. The following explanations are possible:

1) Sea-level change. The high absolute abundance of miospores might be the result of a sea-level drop. Such a drop would drain large shallow-water settings, thus providing extended areas for colonisation by early land plants. At the same time, the increased proximity of the depositional setting would favour the deposition of miospores as these have a relatively low buoyancy and therefore are predominantly deposited in near-shore settings (e.g. Holmes, 1994; Traverse 1994). However, in a previous study on palynomorphs from the lower Ludlow on Gotland no increase of spore abundances toward shallow environments has been observed (Stricanne et al. in press). Additionally, the lithological development on Gotland indicates an increase in water depth during deposition of the Burgsvik and Hamra/Sundre Beds (Samtleben et at. 2000).
2) Humid climate. An increase of humidity on the continents would not only have improved environmental conditions for early land plants, but would also have led to increased fresh water runoff by rivers. At the same time, a humid climate would have increased chemical weathering and thus the influx of clay and nutrients into the marine realm. However, carbonate facies development, stable isotope geochemistry, and acritach abundances argue against this scenario. The carbonate sediments of the upper Ludfordian A-period are characterised by clay-poor shallow-water carbonates, and the $\delta^{18}O$ development indicates arid climate conditions (Fig. 3; Samtleben et al. 1996, Bickert et al. 1997). Moreover, acritarch abundances are likely to have increased in the case of higher nutrient availability.

Our data show that this is not the case. Instead, absolute acritarch abundances decline during the isotope excursion.

The only major clastic influx on Gotland during the upper Ludfordian A-period is represented by the Burgsvik Sandstone which is composed of well-sorted, mostly medium-grained foreshore sandstones and is overlain by oolites. The source area for this sandstone may be sought in the rising Caledonides. Additionally, the uplift of the Caledonides may have accelerated continental run-off into the Baltic epicontinental seas. However, the co-occurrence of sandstones and oolites was also observed far offshore in the Holy Cross Mountains of Poland (Kozlowski 2003) and also in Australia during that time (Jeppsson et al. 2002). This might indicate that global low-latitude weathering conditions on the continents were favourable for the formation of sand; an arid climate as proposed by Bickert et al. (1997) with significant diurnal temperature variations could have led to breaking up of rocks through thermal expansion and contraction. In this respect, the frequent occurrence of sandstones and siltstones in A-periods (see summary in Munnecke et al. 2003) could be taken as an argument for an arid climate in the low latitudes. At the same time, the oligotrophic conditions in the marine realm favoured the formation of oolites.

Generally, spores are silt-sized components and are brought into the marine system predominantly by rivers (Holmes, 1994; Traverse 1994). On the other hand, well-sorted sandstones normally are devoid of palynomorphs because of their different hydrodynamic behaviour compared to the quartz grains (Holmes, 1994). Surprisingly, the marine Burgsvik Sandstones on Gotland contain high absolute abundances of spores (Fig. 4). This indicates a different transport mechanism for the spores such as possibly aeolian input through strong winds. In accordance, the hiatus observed in shallow-water settings at the beginning of the upper Ludfordian A-period (and also of most A-periods summarised in Fig 1) could be interpreted as the result of a deepening of the wave base due to increasing wind energy, resulting in submarine erosion in shallow-water settings (see discussion in Munnecke et al. 2003, page 120). Stronger winds could have originated, e.g., from an intensification of the Hadley cell. Alternatively, if A-periods represented intervals of cooler high-latitude temperatures, stronger winds could have resulted from increased atmospheric heat transport from low to high latitudes. The fact that at least one of the A-periods is associated with polar glaciation (Hirnatian glaciation, Late Ordovician) might support this assumption (Munnecke et al. 2003). However, these scenarios are currently highly speculative, and exceptionally well-dated material from high palaeo-latitudes has to be investigated before a global climatic model can be solidly established.

6. Conclusions

-The development of acritarch communities in the Ludlow of Gotland is closely correlated with the stable isotope development. High stable isotope values are correlated with low abundances of acritarchs, and vice versa. A similar pattern is known for conodonts (Jeppsson and Aldridge, 2000). This clearly shows that an increase in marine palaeoproductivity cannot have been considered as reason for the positive $\delta^{13}C$ excursion.

-The results are in good accordance with those climatic models for the Silurian that assume alternating humid and arid climatic conditions in low latitudes (Jeppsson 1990, Bickert et al. 1997). Times of high isotope values correspond to arid climatic conditions in low latitudes, with low input of terrestrial nutrients resulting in impoverished acritarch (and conodont) communities. During times of low $\delta^{13}C$ and $\delta^{18}O$ values, humid climate prevails, and the input of terrestrial nutrients resulted in abundant and diverse phytoplankton communities.

-The major turnover of the composition of the acritarch communities took place during the increase of the isotope values after hemipelagic planktic or nektonic organisms like graptolites and conodonts have been affected. A similar pattern is observed at the Ireviken Event close to the Llandovery-Wenlock boundary. This indicates that environmental changes connected with the isotope excursions at first affected deeper-water settings, and only later influenced the photic zone.

-The dominance of acritarchs with short, non-ramified processes during the upper Ludfordian A-period might be the result of enhanced water density caused by higher salinity.

-The abundance of terrestrial spores closely mirrors the marine stable isotope development indicating that both realms are synchronously affected by the climatic changes. The high abundance of spores during the upper Ludfordian A-period could be explained by an increased aeolian input.

Article VI – *"Assessing mechanisms of global change in the Late Silurian: Palynological data from Gotland, Sweden", submitted to* ***Palaeogeography, Palaeoclimatology, Palaeoecology****, Elsevier Publisher, Amsterdam, The Netherlands.*

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Appendix (next page)

Quantitative table showing absolute abundances (part. per g / sediment) of all palynomorphs groups and acritarch species through the profile. For convienience, the samples of the first row are indicated by the first letters of the locality name followed by a locality number X (see Laufeld, 1974, and Samtleben et al, 2000 for explanations and position of the samples) and sample number Y: SP X-Y – Sproge; SN X-Y – Snoder; LA X-Y – Lakskär; BOV X-Y – Bovik; SM X-Y – Smissarve; VAK X-Y – Vakten; A X-Y – Alsvik; MI X-Y – Mickels; LU X-Y – Lukse; KR X-Y – Krokvät; NIS X-Y – Nisse; SNV X-Y – Snauvalds; DR X-Y – Drakarve; SNI X-Y – Snippsnyte; V X-Y – Vaktård; K X-Y – Klasård; B X-Y – Bodudd; NÄ X-Y – Näs; TOM X-Y – Tomsarve; KULH X-Y – Kulhaken; UD X-Y – Uddvide; RI X-Y – Rivet; RIV X-Y – Rivviken; BAR X-Y – Barshageudd; KLE X-Y – Klehammarsård.

Article VI – "*Assessing mechanisms of global change in the Late Silurian: Palynological data from Gotland, Sweden*", *submitted to* ***Palaeogeography, Palaeoclimatology, Palaeoecology****, Elsevier Publisher, Amsterdam, The Netherlands.*

	SP6-1	SP6-2	SN4-1	SN4-2	SN4-3	SN4-4	SN4-5	SN4-11	SN4-12	LA1-4	LA1-14	BOV1-3	BOV1-11	BOV1-15	BOV1-22
Acritarchs / g.sed	399	927	557	489	610	946	603	1707	1614	700	182	1163	1340	1732	1639
Sphaeromorphs / g.sed	169	577	118	178	286	229	196	348	306	286	108	247	406	506	523
Prasinophytes / g. sed	0	20	4	9	5	8	18	34	6	57	27	16	79	27	40
Scolecodonts / g. sed	38	115	26	11	48	51	13	116	44	35	11	4	42	27	12
Chitinozoans / g. sed	3	13	0	13	17	8	13	212	38	41	28	60	299	110	81
Spores / g. sed	0	0	0	0	0	0	0	20	6	8	72	36	84	82	69
Ammonidium microcladum	0	0	2	0	0	28	0	0	0	0	0	0	0	0	0
Baltisphaeridium muricatum	12	0	0	0	0	3	0	0	0	0	0	0	0	0	0
Comasphaeridium brevispinosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Cymbosphaeridium pilaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dilatisphaera laevigata	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0
Dilatisphaera tubula	0	0	0	0	0	0	0	0	8	0	0	0	5	0	0
Dorsennidium europaeum	18	82	98	143	195	196	110	314	391	123	14	92	126	123	86
Dorsennidium inflatum	24	16	38	28	67	106	29	123	75	19	0	24	19	103	69
Eisenackidium wenlockensis	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eupoikilofusa striatifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eupoikilofusa tenuistriata	2	10	17	4	5	0	4	68	50	5	2	4	14	0	0
Evittia denticulata	80	131	127	82	60	144	81	232	0	207	36	629	639	787	869
Evittia sanpetrensis	0	23	0	0	0	0	0	20	0	0	0	0	0	0	0
Gorgonisphaeridium succinum	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
Hapsidopalla jeandeunffii	0	0	0	0	0	0	0	0	0	0	0	0	14	0	23
Helosphaeridium latispinosum	0	0	2	0	0	8	0	0	0	0	15	0	0	0	0
Histopalla margarita	2	0	0	0	0	0	4	7	0	19	20	24	28	7	75
Leiofusa bernesgae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leiofusa parvitatis	0	0	0	0	0	0	0	0	0	11	10	40	19	14	6
Leoniella carminae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micrhystridium imitatum	2	52	12	20	38	28	25	55	58	14	0	12	9	48	6
Micrhystridium nannacanthum	0	26	0	2	0	0	0	0	0	0	4	0	0	0	0
Micrhystridium parinconspicuum	56	147	5	11	48	8	31	164	275	22	14	28	42	21	23
Micrhystridium stellatum	128	426	74	77	89	156	139	389	891	71	26	92	89	137	127
Multiplicisphaeridium arbusculum	12	7	0	0	2	11	4	0	0	0	0	4	0	0	0
Multiplicisphaeridium forquillum	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
Multiplicisphaeridium pardaminum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Multiplicisphaeridium saharicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neoveryhachium carminae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onondagaella asymmetrica	0	0	0	0	0	0	0	0	8	0	0	8	0	0	0
Onondagaella deunffii	0	0	0	0	0	0	0	0	0	0	0	0	9	14	0
Oppilatala frondis	4	0	14	0	0	0	0	0	0	3	0	0	0	0	0
Oppilatala septispinosa	20	0	120	118	82	170	112	61	0	74	13	56	163	240	121
Percultisphaera stiphrospinata	0	0	22	18	5	40	34	41	8	106	31	131	145	171	161
Pulvinosphaeridium pulvinellum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Quadraditum fantasticum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salopidium wenlockensis	36	0	24	2	2	40	27	157	0	0	0	0	0	41	0
Schismatosphaeridium rugulosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tunisphaeridium parvum	0	0	0	0	0	0	0	14	0	3	0	0	0	0	0
Veryhachium lairdi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veryhachium reductum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veryhachium trispinosum	0	0	0	0	10	0	0	61	50	25	3	20	19	27	69
Visbysphaera gotlandica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Visbysphaera microspinosa	0	0	0	0	7	3	0	0	0	0		0	0	0	0
Visbysphaera pirifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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BOV1-27	BOV3-1	BOV3-7	BOV3-11	BOV3-17	BOV2-1	BOV2-5	SM3-2	VAK1-1	A4-1	A4-2	A4-3	MI1-1	LU1-2	LU1-4	KR5-1	KR5-5	KR4-2
547	489	1109	526	573	863	1135	729	858	234	182	326	812	681	1122	551	549	2495
200	110	211	134	89	158	314	274	274	51	36	121	306	256	444	362	260	778
28	6	58	25	20	52	49	16	33	19	12	18	3	30	18	22	6	76
2	8	12	8	0	5	9	13	23	1	2	18	35	22	27	35	0	68
54	41	46	21	31	30	76	13	164	2	5	33	44	44	27	91	30	178
54	66	46	31	9	49	31	129	67	0	1	0	0	16	18	120	11	34
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0	0	0	0	9	0	0	0	6	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
0	0	4	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
68	97	70	54	70	63	63	24	187	20	19	56	171	161	144	94	19	313
35	19	12	0	39	8	45	0	6	37	17	4	47	76	81	0	13	135
0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	9	17	10	15	16	49	5	23	0	0	0	0	8	0	0	0	0
196	168	501	235	224	390	494	171	152	75	30	40	85	177	341	198	288	964
0	6	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	42
0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	76
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	13	21	13	4	38	13	5	70	0	1	0	19	11	27	11	13	169
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	3	4	8	0	8	4	21	23	7	9	15	85	22	45	22	6	8
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	6	8	10	20	3	36	34	0	3	0	17	38	11	36	7	11	59
0	6	0	0	0	0	0	13	0	0	0	0	6	8	0	0	0	0
26	9	46	19	44	16	27	80	18	0	0	0	66	19	18	29	11	0
61	56	170	80	86	133	162	200	82	25	16	31	148	52	153	72	75	144
0	0	0	0	0	0	9	0	0	1	5	0	0	0	0	14	4	17
0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	18	1	6	20	0	0	0	0	0	0
0	0	8	0	0	0	0	0	0	2	2	0	0	11	0	0	0	0
0	13	0	0	0	0	0	0	12	0	0	0	0	0	0	4	0	0
0	0	0	0	0	0	0	8	0	4	4	13	0	0	0	0	0	0
57	9	37	10	37	65	58	3	41	4	1	0	19	11	27	14	0	59
50	26	186	77	24	93	99	63	152	51	65	126	73	60	72	79	68	178
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	8	0	0	9	0	0	0	0	0	0	0	0	0	0	0
0	19	0	0	0	0	0	100	0	0	1	0	16	16	18	0	0	118
4	0	0	4	0	0	0	0	0	0	0	0	0	3	0	0	0	0
0	0	0	0	0	0	0	0	0	0	2	0	0	0	9	0	0	0
0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	9	0	0	0	0	0	0	6	1	1	1	8	16	18	0	0	0
9	16	12	10	11	22	63	21	58	2	2	0	19	16	126	0	13	144
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	4	0	0	0	0	0	12	0	1	0	0	0	0	7	0	68
0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0

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KR4-4	KR3-4	KR3-6	KR2-2	KR2-3	KR1-4	KR1-9	NIS5-1	NIS5-2	SNV1-1	SNV1-2	DR6-1	DR5-2	SNI2-1	SNI2-4	SNI2-6	V6-3	V6-1
1195	1499	1845	684	482	837	527	1987	4016	1007	2150	2529	4622	4131	823	2016	1081	1258
504	267	689	301	204	369	293	455	1628	282	385	786	1887	1444	406	814	242	305
145	90	41	25	31	59	27	94	16	34	80	9	51	233	82	150	38	134
37	9	46	3	5	20	2	0	32	8	32	54	153	31	3	16	11	24
75	75	145	145	80	33	84	94	379	31	104	515	2737	1708	179	71	71	63
5	90	81	88	17	129	36	86	458	19	48	9	204	202	53	277	21	107
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	12	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0
0	0	0	0	0	0	0	20	0	8	0	0	17	100	13	28	11	8
75	108	214	49	77	120	68	127	332	179	282	262	483	249	75	225	64	170
65	23	23	5	17	7	15	20	0	11	13	90	17	25	22	56	0	32
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	5	6	22	0	0	2	39	16	0	0	0	224	75	3	131	11	32
528	333	307	178	99	89	129	480	1692	355	883	903	1587	1642	173	553	257	403
0	14	23	0	0	0	2	10	0	0	13	0	17	75	3	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	37	35	8	0	3	0	0	0	0	0	0	0	0	16	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	117	29	38	21	17	30	147	142	8	26	108	293	299	122	234	27	8
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	17	0	0	10	0	0	16	4	0	18	0	0	0	0	0	8
0	0	0	0	0	0	0	10	0	0	0	0	0	25	0	0	5	0
37	14	35	0	2	0	8	29	0	11	26	54	17	25	31	19	27	47
0	5	0	0	0	0	0	0	0	0	0	0	34	0	0	0	0	0
19	23	12	11	17	38	19	59	111	4	26	0	69	75	9	28	75	55
51	225	243	27	42	82	70	254	174	95	128	145	283	199	72	113	311	233
0	23	0	0	0	3	0	0	0	0	26	0	0	0	9	0	0	44
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	10	0	0	0	18	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	12	5	2	0	0	10	0	8	0	45	121	25	6	9	27	20
0	42	17	0	0	0	0	39	79	0	13	27	103	100	6	19	0	0
23	70	110	0	7	48	4	0	0	8	0	0	0	0	0	0	0	71
75	370	371	315	140	364	154	137	538	267	537	262	241	423	132	263	86	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0
5	5	6	0	0	3	2	0	0	0	0	0	0	0	0	0	11	0
14	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0
121	0	0	0	5	0	0	0	0	0	0	0	0	25	0	0	0	0
0	9	12	0	0	0	0	0	16	0	0	9	0	0	0	0	0	12
0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	9	0	0
0	5	41	0	9	0	2	69	47	0	13	18	138	124	19	47	21	8
61	86	122	16	42	48	23	528	822	50	166	580	966	597	110	263	118	107
0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	11	0	0	0	0	0	0	0	0	0	0		19	5	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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K1-1	B1-1	B1-2	B1-3	B1-4	B1-5	B1-6	B1-7	B1-10	B1-12	B1-14	B1-16	B1-17	B1-19	B1-20	B1-21	B1-23	B1-25
1046	3462	1945	2970	2407	5444	10344	4030	4897	6915	8994	3125	3709	6064	4686	5594	4257	2009
509	2103	483	1087	335	1388	4737	2148	1743	2183	2266	675	672	1004	1690	2007	841	864
210	325	110	165	54	427	516	213	401	194	70	163	238	235	1157	1004	959	450
18	46	15	29	36	43	32	107	17	0	0	44	126	0	73	0	13	14
121	93	29	485	54	235	677	640	349	108	623	218	224	107	312	278	302	274
32	58	29	19	18	0	32	107	70	0	35	11	56	0	92	192	26	26
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	12	0	10	72	43	97	0	0	43	0	0	0	21	0	21	39	11
14	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0
171	558	307	223	443	1153	1643	800	540	1837	1987	642	482	1132	753	918	736	292
25	174	37	39	109	192	226	80	52	151	209	98	154	214	73	192	223	97
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	97	0	0	86	35	11	0	256	55	0	53	0
28	0	7	49	9	43	32	53	17	0	0	0	42	0	0	21	0	0
310	1336	687	1650	389	2178	2985	1441	2336	1794	2336	512	1078	982	1378	939	552	259
14	0	0	0	0	0	0	53	0	0	0	0	0	0	0	64	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0	0	27	0	129	40	35	173	174	33	42	0	18	43	0	32
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	70	29	10	0	0	0	0	0	0	0	0	0	21	18	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	116	22	10	72	0	97	40	87	43	70	44	0	256	55	43	105	22
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
28	105	15	0	18	43	193	53	35	43	105	11	14	107	37	85	158	97
121	279	95	19	299	192	354	213	157	324	662	185	140	577	147	470	434	130
14	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	13	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	35	7	19	0	43	0	0	0	43	35	0	0	21	0	19	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	35	37	126	36	258	387	294	296	151	314	76	70	64	238	64	39	11
0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	197	124	243	54	85	548	67	279	519	628	152	84	320	863	726	328	292
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	64	0	0	0	0	0	0	0	0	21	26	43
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	21	0	0
14	105	15	10	9	64	0	0	0	0	35	11	0	43	0	0	26	54
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	302	66	68	45	21	1063	187	209	86	139	152	308	192	220	534	263	140
93	139	497	495	823	1131	2449	881	802	1621	2266	1198	1232	1858	772	1366	1261	519
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	13	17	0	0	0	42	0		43	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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B1-27	B1-31	B1-32	B1-33	B1-39	B1-41	B1-42	B1-46	B1-52	B1-56	B1-58	B1-59	B1-63	B1-67	B1-68	B1-69	B1-73	B1-74
5988	2704	4433	1671	1699	2040	1779	1299	3011	2106	3029	1829	1726	1004	1072	811	225	188
1760	1016	1794	657	660	530	1081	564	1642	1532	2038	1545	1378	938	1342	1022	280	292
777	350	621	406	316	152	310	258	252	173	194	85	196	128	142	105	56	51
17	9	17	11	0	11	7	5	11	0	46	21	19	0	21	34	3	8
345	105	690	149	109	518	224	281	274	90	216	57	101	425	489	533	21	6
121	26	224	37	34	73	79	18	55	62	137	28	78	4	17	6	39	8
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	52	0	6	23	40	0	77	0	57	0	6	0	0	3	0	10
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	96	103	21	0	0	0	0	11	0	0	0	0	0	0	3	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1070	656	845	331	247	180	145	50	109	166	262	208	120	87	214	101	8	26
224	44	103	64	40	82	33	23	11	42	11	62	32	69	69	24	0	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	15	0	87	142	220	8	2
121	70	241	21	109	276	244	285	482	250	376	116	367	289	0	0	38	0
1450	236	673	203	356	485	514	213	788	588	410	131	348	127	129	42	34	38
69	0	155	0	17	45	13	9	33	7	80	77	19	98	21	0	13	5
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	59	0	21	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	44	138	11	80	23	33	54	68	28	114	108	392	81	111	38	6	5
0	0	0	0	0	0	0	0	0	0	0	0	0	12	172	175	0	37
9	0	9	0	9	0	8	0	0	0	0	31	6	0	4	38	30	11
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	70	17	37	11	45	7	9	0	14	11	8	6	6	13	3	4	8
0	0	0	0	0	0	0	0	0	0	0	31	0	29	13	24	13	15
104	131	138	101	63	45	46	5	44	28	68	69	19	17	30	38	24	17
173	429	345	283	52	101	53	23	88	26	91	62	44	12	0	10	15	2
0	9	0	11	6	39	0	0	0	7	23	0	0	0	30	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	9	0	0	0	6	0	0	0	0	0	0	0	0	4	0	0	6
0	0	52	0	6	34	33	113	810	700	1116	533	234	0	26	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0
138	18	17	21	17	56	46	68	22	62	34	85	44	12	0	0	8	2
0	0	0	0	11	0	92	36	99	7	0	0	0	0	0	0	0	0
0	0	0	0	17	124	0	0	0	0	0	0	0	0	0	0	0	1
880	79	155	98	534	237	99	140	131	28	159	69	32	17	4	0	6	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0
0	26	0	0	0	0	13	0	11	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	5	6	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	17	0	0	0	0	0	23	0	6	34	14	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
380	210	121	123	17	17	46	41	44	28	11	62	6	23	39	21	6	0
1104	578	1276	342	103	225	323	154	208	125	205	139	57	35	17	52	9	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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B2-7	B2-10	NÄ1	TOM1-4	KUHL2-2	KUHL2-4	UD3-2	RI2-0	RI2-1	RI2-18	RIV2-1	RIV2-9	RIV2-18	RIV1-1	RIV1-4	BAR6-1	KLE3-1
858	326	362	371	26	14	253	626	379	111	205	433	437	321	325	490	1455
1188	522	177	454	68	52	118	362	333	181	265	282	181	218	203	319	1259
344	124	118	87	4	3	8	12	65	7	17	36	20	18	17	44	132
70	29	32	35	10	3	8	15	55	36	33	54	24	12	25	58	236
63	100	46	87	4	3	8	12	102	104	174	274	95	77	73	124	306
397	209	44	143	144	102	164	120	84	66	54	73	53	67	61	195	184
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	11	2	0	0	9	0	6	0	0
0	0	0	0	0	0	0	0	0	0	0	0	4	20	8	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	4	0	9	0	0	0	0	0	0	0	0	0	12	6	0	0
32	0	26	44	0	0	0	0	38	7	0	12	11	18	17	142	485
0	0	14	0	0	0	0	0	8	0	0	0	2	2	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
433	37	0	0	0	1	43	75	8	0	0	0	0	0	0	0	0
0	0	3	26	0	0	0	0	0	7	10	24	2	12	7	15	57
104	65	191	18	0	0	0	70	101	40	31	91	51	34	56	38	133
16	16	9	26	0	0	0	67	8	0	0	4	0	4	1	9	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
8	45	6	0	0	0	0	0	19	2	7	2	30	0	0	9	19
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	6	0	6	0	0	0	2	0	4	0	8	0	8	19
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	5	0	0	0	0	0	10	0	0	16	19	14	15	23	19
8	0	17	53	8	0	0	77	14	2	10	2	7	16	11	0	0
40	24	29	79	3	2	21	70	51	17	24	62	78	52	53	41	133
24	4	15	26	0	1	0	62	88	12	87	183	208	114	127	110	190
0	0	3	0	0	0	0	0	0	5	0	0	0	4	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	4	1	0	0	0	0	3	8	4	0	0	20	0
8	4	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
0	0	0	0	0	0	0	0	5	0	0	8	12	10	4	3	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	6	0	10	0	0	0	0	0	133
88	8	0	9	0	0	0	0	0	0	7	0	0	0	0	0	0
0	4	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	8	17	18	4	6	150	77	2	2	3	0	0	0	0	0	48
16	73	46	53	4	2	39	87	11	12	10	10	0	6	8	67	219
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
0	0	0	9	0	0	0	0	0	0	0	8	0	2		12	0
0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0

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