Université des Sciences et Technologies de Lille 1

Ecole doctorale des Sciences de la Matière, du Rayonnement et de l'Environnement
Laboratoire « Géosystèmes » - UMR CNRS 8217

Thèse présentée pour obtenir le titre de Docteur de l'Université de Lille 1

Spécialité : « Géosciences, Ecologie, Paléontologie et Océanographie »

par

LAUREN POUILLE

Paléobiodiversité des Radiolaires du Paléozoique inférieur (Cambrien-Ordovicien). Aperçu à travers une étude des assemblages à radiolaires provenant des montagnes de l'Altai (Russie), d'Aksuran (Kazakstan), du bassin de Georgina (Australie) et de la Terre-Neuve occidentale (Canada)

Thèse dirigée par Taniel Danelian

Date de soutenance prévue de 12 Décembre 2012, à Villeneuve d'Ascq (59)

Devant le jury composé de :

Patrick DE WEVER	Muséum national d'Histoire Naturelle, France; *Rapporteur*
Paulian DUMITRICA	Université de Lausanne, Suisse ; *Rapporteur*
Jorg MALETZ	Université libre de Berlin, Allemagne ; *Examinateur*
Olga OBUT	Université de Novosibirsk, Russie; *Examinateur*
Martial CARIDROIT	Université de Lille 1, France; *Examinateur*
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Taniel DANELIAN	Université de Lille 1, France; *Directeur de thèse*

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Résumé

Notre compréhension de la structuration des chaînes trophiques pélagiques du Paléozoïque inférieur reste encore très fragmentaire. Nous nous intéressons ici à comprendre la paléobiodiversité des Radiolaires polycystines, composantes biotiques clefs du plancton hétérotrophe, dans le but de mieux comprendre le calendrier et la dynamique de diversification du plancton au cours du Paléozoïque inférieur. La découverte de représentants de la famille des Archéoentactinidae d'âge Botomien provenant des montagnes de l'Altaï (Sibérie) établit avec certitude la présence de radiolaires au Cambrien inférieur. L'étude des changements biotiques au sein des faunes à radiolaire menée sur notre matériel de Terre-Neuve nous permet de mettre en lumière l'existence de deux épisodes de changements fauniques intervenus au passage Cambrien-Ordovicien en relation avec des excursions isotopique négatives du δ13 Ccarb, comprenant pour le premier des événements d'extinction au niveau spécifique et une chute importante de la diversité au sein de certains genres et pour le second, des extinctions sélectives au niveau des genres mais aussi des renouvellements fauniques ainsi que des hausses importantes de diversité au niveau des espèces. Un échantillon d'Australie permet également de préciser la répartition paléogéographique des radiolaires au Cambrien supérieur (Jingshanien). Une étude taxonomique menée sur un échantillon provenant du Kazakhstan améliore notre compréhension de la structure interne des Inaniguttidae et nous permet d'identifier 30 nouveaux morphotypes (dont neuf nouvelles espèces), confirmant ainsi la présence d'un pic de diversité au sein des radiolaires au Darriwilien supérieur.

Mots clés: Polycystines Radiolaria, Cambrien, Ordovicien, Taxonomie, microsphere, Inaniguttidae, Plancton hétérotrophe, Terre-Neuve, Sibérie, Australie, Kazakhstan

Palaeobiodiversity of Early Paleozoic Radiolaria (Cambrian-Ordovician). Insights from a study of radiolarian assemblages from the Altai Mountains (Russia), Aksuran Mountains (Kazakhstan), Georgina Basin (Australia) and western Newfoundland (Canada).

Abstract

Our understanding of the structuration of Lower Paleozoic pelagic trophic chains during the 'Cambrian Explosion' and the 'Great Ordovician Biodiversification Event', which has lead to the establishment of modern marine ecosystems, is still very fragmentary. We are here interested in understanding the paleodiversity dynamics of polycystines Radiolaria planctonic group, a key biotic component of the heterotrophic plankton, in order get a better idea of the timing and dynamics of plankton diversification at the Lower Paleozoic. The discovery of new material from the Altai Mountains (Siberia) brings new data on the fossil record of the first biomineralized radiolarians with the identification of the oldest representatives of the Archeoentactinidae family dated of a Botomian age. Study conducted on Newfoundland and Australian material allowed us to characterize precisely the various biotic changes undergone by radiolarians during the Cambrian-Ordovician transition, at the dawn of the planktonic revolution but also to precise their paleogeographic distribution at the Late Cambrian. A detailed taxonomic study conducted on a Kazakhstanian sample has allowed us to describe a new radiolarian assemblage enriching considerably our knowledge on the radiolarian diversity at the middle Ordovician.

Key Words: Polycystines Radiolaria, Cambrian, Ordovician, Taxonomy, microsphere, Inaniguttidae, heterotrophic plankton, Newfoundland, Siberia, Australia, Kazakhstan.

SOMMAIRE

Introduction……………………………………………………………………………….. 9

I. Contexte macroévolutif et macroécologique général de l'étude………………. 11
II. Objectifs…………………………………………………………………………….. 15
III. Organisation du mémoire……………………………………………………… 19

Chapitre 1 : Radiolaires du Cambrien inférieur (Botomien) des montagnes de l'Altaï (Sibérie)………………………………………………………………………… 21

I. Etat de l'art ………………………………………………………………………. 23
II. Contexte géologique et stratigraphique………………………………………… 25
  II.1. Contexte géologique……………………………………………………….. 25
  II.2. Contexte stratigraphique……………………………………………………… 27
III. Matériel étudié.. 29
IV. Méthodes……………………………………………………………………….. 34
V. Résultats et discussion…………………………………………………………. 34
VI. Article 1 : Lower Cambrian (Botomian) polycystine Radiolaria from the Altai Mountains (southern Siberia, Russia)………………………………………….. 37

Chapitre 2 : Etude des assemblages à radiolaire provenant de Terre-Neuve et d'Australie à la transition Cambrien-Ordovicien……………………………….... 45

Partie 1. Etude des changements biotiques intervenus au sein des assemblages à radiolaires de Terre-Neuve (Canada) à la transition Cambrien/Ordovicien………….. 47

I. Etat de l'art …………………………………………………………………… 49
II. Contexte géologique et stratigraphique…………………………………………. 51
  II.1. Contexte géologique ....… 51
  II.2. Contexte stratigraphique (d'après James et Stevens, 1986)…………… 52
III. Matériel étudié……………………………………………………………………55
IV. Méthodes……………………………………………………………………… 67
V. Résultats et discussion……………………………………………………………67
VI. Article 2 : The pattern of radiolarian diversity changes during the Late Cambrian-Early Ordovician transition as recorded in the Cow Head Group of Newfoundland (Canada) ……………………………………………………………………… 73

Partie 2. Etude d'un assemblage à radiolaires d'Australie du Jingshanien (Cambrien supérieur) et comparaison avec le matériel de Terre-Neuve…………...107

I. Contexte géologique et stratigraphique……………………………………………109
II. Résultats……………………………………………………………………………110
III. Discussion…………………………………………………………………………..110

Chapitre 3 : Etude d'un nouvel assemblage à radiolaires du Kazkhstan d'intérêt majeur pour la compréhension de la diversité des radiolaires au Darriwilien supérieur (Ordovicien moyen)……………………………………………………………………..… 117

I. Etat de l'art…………………………………………………………………….. 119
II. Contexte géologique et stratigraphique…………………………………………… 122
III. Matériel …..………………………………………………………………………. 124
IV. Méthodes……………………………………………………………………….. 125
  IV.1. Technique de sectionnement des radiolaires (d'après De Wever *et al.*, 2001)…………………………………………………………………………126
  IV.2. Imagerie 3D par tomographie de rayons X……………………………127
V. Résultats et discussion…………………………………………………… 130
VI. Article 3 : New and revised Inaniguttid Radiolaria and associated trilobites from the upper Darriwilian (Ordovician) Shundy Formation of Kazakhstan................133
VII. Article 4 : A new diverse Radiolarian assemblage from the Upper Darriwilian (Ordovician) Shundy Formation of Kazakhstan: a key fauna to better evaluate Radiolarian diversity trends in the context of the Great Ordovician Biodiversification Event..179

Conclusion et perspectives…………………………………………………………218

Références bibliographiques……………………………………………………226

Annexes………………………………………………………………………………..244

Introduction

I. Contexte macroévolutif et macroécologique général de l'étude

Le Paléozoïque inférieur est caractérisé par des changements profonds dans la structure des communautés marines et par une croissance quasi-continue de la biodiversité entre les temps édiacariens et la crise biologique de l'Ordovicien terminal (Fig. 1), marquée par l'"Explosion cambrienne" (Bottjer *et al.*, 2000, 2001; Butterfield, 2001; Zhuravlev et Riding, 2001) et la "Grande Biodiversification Ordovicienne" (GOBE) (Miller, 2004; Webby *et al.*, 2004 ; Harper, 2006 ; Servais *et al.*, 2008, 2009).

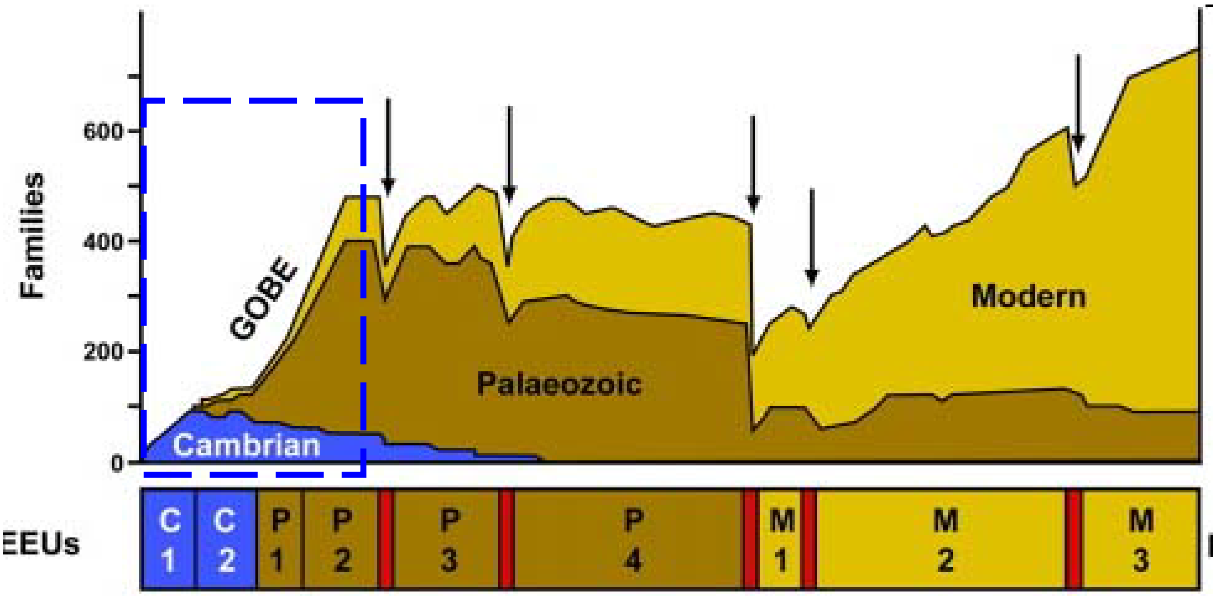


Figure. 1 : Evolution de la diversité de la biosphère marine au niveau taxonomique des familles (modifié d'après Servais *et al.*, 2010).

L'importante radiation de la vie marine qui a eu lieu au cours de l'« explosion Cambrienne » se fait dans un contexte paléogéographique d'éclatement du supercontinent Rodinia en de nombreux morceaux (Valentine et Moores, 1972 ; Butterfield, 2001). Le Cambrien inférieur est alors marqué par l'apparition de la majeure partie des embranchements qui constituent le règne animal actuel (Harper, 2006 ; Vannier *et al.*, 2009) et des premiers organismes à squelette biominéralisé (ex: spongiaires) ou sclérifiés (ex: arthropodes). L'explosion cambrienne voit également la mise en place de nouveaux plans d'organisation avec notamment l'apparition de la bilatéralisation, de nouvelles innovations évolutives (systèmes nerveux et digestifs plus complexes, apparition des premiers organes visuels, amélioration de la motricité…) ainsi que l'extinction progressive des animaux à corps mous composant les faunes édiacariennes (Conway Morris, 1998; Harper, 2006; Vannier, 2009). Cette explosion cambrienne est surtout connue au travers de rares “Lagerstätten”, des gisements à préservation exceptionnelle, tels que la faune de Burgess au Canada, la faune de Chengjiang en Chine ou encore la faune de Sirius Passet au Groenland (Servais *et al*., 2009, Rigby et Milsom, 2000). Le Cambrien inférieur est également marqué par l’apparition des premiers écosystèmes à structure trophique complexe à une période où la vie animale a probablement commencé à coloniser les milieux hyperbenthiques, dans la tranche d’eau située à proximité du fond, à l’interface eau-sédiment (Vannier, 2009).

Par la suite, une ‘révolution planctonique’ aurait entrainé la colonisation du domaine pélagique, d’abord par les organismes phytoplanctoniques à partir du Cambrien supérieur, suivis par les groupes zooplanctoniques au cours de l’Ordovicien, établissant ainsi une nouvelle chaine trophique pélagique à caractère moderne (Peterson, 2005 ; Signor et Vermeij, 1994 ; Vannier *et al*., 2003 ; Servais *et al*., 2008, 2009 ; Fig. 2).

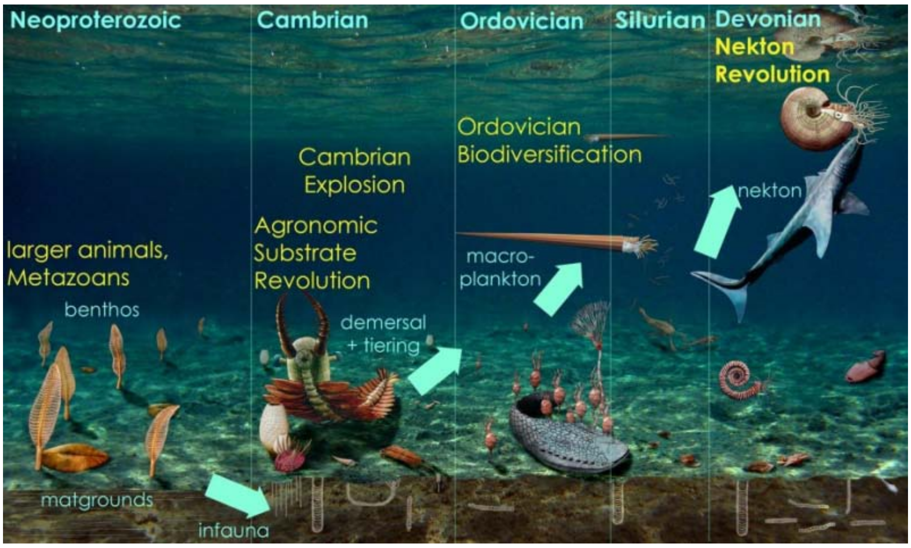


Figure. 2 : Changements macro-écologiques majeurs intervenus au cours de l’évolution de la chaine trophique marine au Paléozoïque (d’après Klug *et al*., 2010).

De plus, à la transition Cambrien-Ordovicien, de nombreuses larves de métazoaires benthiques développent une stratégie de planctotrophie et migrent dans la colonne d’eau pour échapper à une pression de prédation grandissante dans la zone hyperbenthique, due au développement important des suspensivores benthiques (Signor et Vermeij, 1994 ; Nützel et Frýda, 2003 ; Nützel *et al*., 2006). La colonisation du domaine pélagique opérée lors de cette ‘révolution planctonique’ pourrait trouver son origine dans des changements intervenus au sein de la chimie et de l'oxygénation des océans au cours du Paléozoïque inférieur (Saltzman, 2005 ; Saltzman *et al.*, 2011; Young *et al.*, 2009). En effet, des enregistrements montrant la présence d'une excursion isotopique positive du $\delta^{13}C_{carb}$ connue sous le nom de SPICE (Steptoean Positive Carbon Isotope Excursion) retrouvés dans de nombreux terrains (Amérique du Nord, Chine, Sibérie, Baltique, Australie, Kazakhstan) d'âge Steptoéen (zone à *Glyptagnostus reticulatus- Irvingella*, Paibien) indiquent une perturbation importante dans le cycle du carbone à l'échelle globale. D'après Saltzman *et al.* (2011), cette excursion isotopique positive du $\delta^{13}C_{carb}$ traduirait une augmentation majeure de l'O_2 atmosphérique au Steptoéen, susceptible d'avoir entrainé d'importants changements au niveau de la quantité de nutriments disponibles dans la colonne d'eau (phosphore, nitrogène..), et, par conséquent, une augmentation de la production primaire et de la diversité au niveau de la chaine trophique marine marquant ainsi le début de la révolution planctonique (Martin, 1996 ; Saltzman *et al.*, 2011 ; Fig. 3).

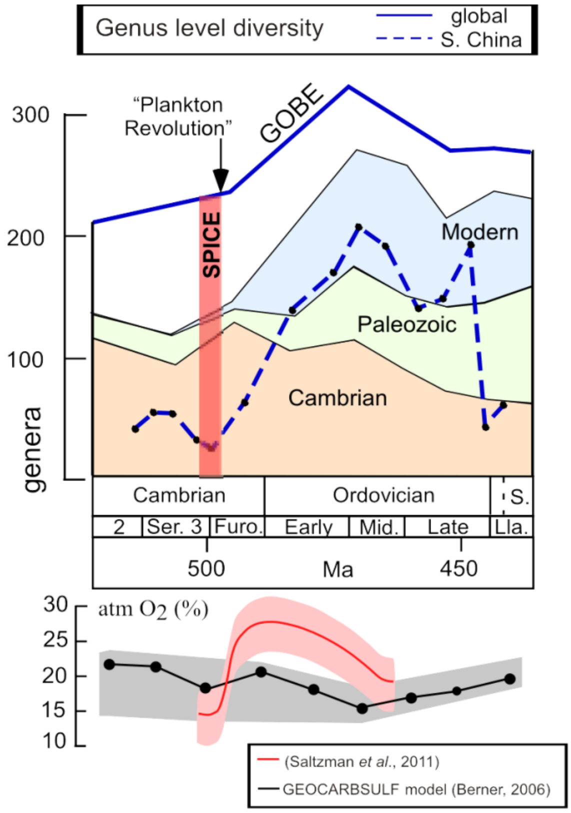


Figure. 3 (modifiée d'après Saltzman *et al.*, 2011) : Schéma compilant les courbes de l'évolution de la diversité des genres au Cambrien-Silurien (représentées ici par la courbe de la diversité des genres à l'échelle globale (d'après Alroy, 2010) et la courbe de la diversité des genres du Sud de la Chine (d'après Rong *et al.*, 2007), les positions du SPICE $\delta^{13}C_{carb}$, du GOBE et du début de la révolution planctonique ainsi que les changements intervenus au sein de l'O_2 atmosphérique (d'après les modèles de Saltzman *et al.*, 2011 et de Berner, 2006).

La conquête de l'ensemble du domaine pélagique par les organismes phytoplanctoniques pourrait avoir été un des facteurs déclencheur de la Grande Biodiversification Ordovicienne (Vecoli *et al*., 2005 ; Lehnert *et al*., 2007). En effet, il est fort probable que leur présence dans la colonne d'eau ait eut un impact majeur sur la diversification des suspensivores dans le milieu benthique et sur l'invasion des groupes zooplanctoniques et nectoniques dans la colonne d'eau (Vannier *et al*., 2003, Servais *et al*., 2008). La vie marine connaît alors de l'Ordovicien inférieur et l'Ordovicien moyen la plus importante période de radiation évolutive de son histoire qui se déroule en un temps relativement court (25 Ma ; Webby *et al*., 2004 ; Servais *et al*., 2009). Lors de cette « Grande Biodiversification Ordovicienne » (Webby *et al*., 2004), la faune Cambrienne (dominée par les trilobites) décline progressivement et est remplacée par une faune Ordovicienne (dominée par les organismes suspensivores) qui va atteindre une diversité (familles, genres, espèces) trois fois supérieure à celle-ci (Sepkoski, 1995 ; Harper, 2006 ; Servais *et al*., 2009). Cette période radiative résulte de la combinaison de nombreux paramètres biologiques intrinsèques (taux important d'innovations morphologiques) et physico-chimiques extrinsèques (Vecoli *et al*.,2005 ; Lehnert *et al*., 2007 ; Servais *et al*., 2008). En effet, l'Ordovicien est caractérisé par un très haut niveau marin avec des courants océaniques peu actifs (Barnes, 2004 ; Haq et Schutter, 2008), de larges mers épicontinentales, particulièrement au niveau des tropiques (Walker *et al*., 2002), une longue période de type « greenhouse » avec de faibles contrastes climatiques ainsi qu'un taux élevé de CO2 (Brenchley *et al*., 1994 ; Veiser *et al*., 2000 ; Berner et Kothavala, 2001 ; Barnes, 2004 ; Saltzman, 2005) et une forte activité volcanique entrainant une augmentation de la quantité de nutriments disponibles dans les océans (Bergström *et al*., 2004 ; Barnes, 2004 ; Servais *et al*., 2009). Le contexte paléogéographique (plaques continentales très dispersées) favorise également un haut degré d'endémicité faunique (Servais *et al*., 2003, 2005, 2008 ; Achab et Paris, 2007). La piste de potentiels impacts d'astéroïdes a également été proposée par Schmitz *et al*. (2008) comme possible évènement déclencheur de cette diversification. Cette période est suivie à l'Ordovicien supérieur d'un refroidissement rapide qui a donné naissance à la grande glaciation Hirnantienne (Saltzman et Young, 2005) ayant entrainé un événement d'extinction majeur se traduisant par une baisse très importante de la diversité et la disparition de 85% des espèces et 60% des genres (Jablonski, 1991 ; Sheehan, 2001).

II. Objectifs

Pour mieux comprendre certains des événements les plus importants de l'évolution de la Vie sur Terre ayant eu lieu durant cet intervalle comme l'« explosion cambrienne » et la « Grande biodiversification ordovicienne » il y a un besoin urgent d'obtenir des informations supplémentaires sur quelques composantes biotiques clefs des écosystèmes marins du Paléozoïque inférieur. Un exemple de composante écologique qui nécessite d'avantage de données est le plancton hétérotrophe, dont les Radiolaires polycyctines constituent un des principaux représentants. Par ailleurs, des phylogénies moléculaires récentes suggèrent que les Radiolaires polycyctines font partie de la branche la plus basale du supergroupe monophylétique de protistes Rhizaria, lequel comprend aussi les Foraminifères et les Cercozoaires (Bass *et al.*, 2005). Par conséquent, l'enregistrement fossilifère le plus ancien des Radiolaires polycystines est d'une importance particulière pour comprendre l'histoire évolutive des diverses lignées des Rhizaria. Il est donc primordial de bien connaître le timing et les modalités de cette invasion au Cambrien. Or, nos données actuelles sur les Radiolaires du Paléozoïque inférieur et notamment du Cambrien sont tellement rares que chaque découverte de matériel supplémentaire peut améliorer de façon significative notre connaissance de la biodiversité et des relations évolutives du groupe.

1) Les origines du plancton, et notamment des radiolaires polycystines, un composant majeur du plancton hétérotrophe, sont encore très énigmatiques. Bien que la plupart des auteurs s'accordent sur l'idée d'une origine planctonique des radiolaires (Anderson, 1983; Tappan, 1993), certains auteurs pensent qu'ils pourraient être issus d'ancêtres benthiques qui auraient migrés, comme les autres organismes unicellulaires, dans le domaine planctonique au cours de l'explosion Cambrienne (Petrushevskaya, 1977; Nazarov et Ormiston, 1985; Lipps, 1993; Rigby et Milsom, 2000). Jusqu'à récemment, la présence de radiolaires au début du Cambrien était encore incertaine (Lipps, 1992) mais la découverte en 1999 d'une faune à radiolaires très diverse et bien préservée dans des strates datant du Templétonien en Australie (Won et Below, 1999) témoigne de manière indiscutable de la présence ce groupe planctonique dans les écosystèmes marins du Cambrien moyen. Malgré de nombreuses similarités morphologiques entre ces faunes à radiolaires du Cambrien moyen et les spicules d'éponges (ex : spicules centrées sur un point et entrecroisées, éléments du squelette creux ; Won et Below, 1999), les arguments moléculaires ne montrent aucune relation

phylogénétique proche entre les deux lignées et indiquent que la biominéralisation siliceuse de leur squelette serait apparue de manière indépendante (Danelian et Morreira, 2004).

Une bonne connaissance des premiers enregistrements fossiles des radiolaires est également de la plus haute importance pour pouvoir calibrer l'arbre phylogénétique des Rhizaria et cerner au mieux leur histoire évolutive. Malheureusement, pour l'instant, tous les organismes retrouvés au Cambrien inférieur pouvant s'apparenter à des radiolaires se sont révélés trop abimés pour permettre une identification certaine et la présence non-ambigüe de radiolaires au Cambrien inférieur reste pour le moment encore douteuse (i.e. Maletz, 2011).

Dans la première partie de cette thèse, nous essaierons donc à améliorer nos connaissances sur l'enregistrement fossilifère des premiers radiolaires biominéralisés et à trancher sur la question de leur présence éventuelle au Cambrien inférieur. Pour ce faire, nous nous sommes tournés vers les séquences sédimentaires du Cambrien inférieur qui affleurent dans la région de Gorny Altai (Sibérie). En effet, la présence de radiolaires polycystines du Cambrien inférieur (Botomien) provenant de la localité 445 dans la région de Gorny Altai a été rapportée récemment par Obut et Iwata (2000). Cependant, leur mauvais état de préservation ne permet pas pour le moment une identification précise du matériel. Dans le cadre d'un projet franco-russe du CNRS portant sur « la biodiversité des écosystèmes pélagiques au Paléozoique inférieur » entre notre laboratoire « Géosystèmes » à Lille 1 et l'institut de géologie pétrolière et géophysique de Novosibirsk (« Trofimuk Institute of Petroleum Geology and Geophysics »), j'ai donc mené deux missions d'échantillonnage dans la région de Gorny Altai en collaboration avec une équipe russe menée par Olga Obut et Nikolay Sennikov avec l'objectif d'améliorer nos connaissances sur l'enregistrement fossile des radiolaires du Cambrien inférieur. Ces missions de terrain ont été consacrées principalement à un échantillonnage plus serré de la localité 445 sur la section de Kaspa qui a déjà révélé la présence de radiolaires potentiels (Obut et Iwata, 2000) et à l'élaboration d'un log plus détaillé de la coupe productive.

2) Notre compréhension de la structuration des chaînes trophiques pélagiques lors de la « révolution planctonique Ordovicienne », qui a abouti à la mise en place des écosystèmes marins à caractère moderne, est elle aussi très fragmentaire. Dans le but de mieux comprendre cette révolution planctonique, une comparaison des changements biotiques survenus à travers divers groupes fossilifères du plancton présent au Cambrien terminal ou à la base de l'Ordovicien, comme les Radiolaires polycystines (protistes hétérotrophes), les Acritarches (représentants du phytoplancton), les Chitinozoaires (œufs planctoniques de Métazoaires), les

Graptolites (plancton colonial) et les Conodontes (necton) est nécessaire. Un regard croisé sur tous ces groupes permettrait de développer une perspective sur les changements de la biodiversité et de productivité survenus à travers la chaîne trophique pélagique au passage Cambrien-Ordovicien. Si la biodiversité de la plupart de ces groupes planctoniques a été bien documentée, les données concernant le groupe des radiolaires restent encore très éparses à la transition Cambrien-Ordovicien. Il y avait donc un besoin pressant d'obtenir des données paléontologiques supplémentaires sur Radiolaires polycystines, composantes biotiques clefs du plancton hétérotrophe au paléozoïque, afin de décrypter le calendrier et la dynamique de diversification du plancton au passage Cambrien-Ordovicien.

Dans ce but, nous nous intéressons donc dans la deuxième partie de cette thèse à comprendre la dynamique de paléobiodiversité du groupe planctonique des Radiolaires polycystines ainsi que les changements biotiques intervenus au sein de ce groupe au cours de l'intervalle d'intérêt. Afin de répondre à ces questions, j'ai effectué deux missions de terrain en 2010 et 2011 en Terre Neuve occidentale afin d'échantillonner quatre sections du Groupe Cow Head, qui constitue actuellement un chantier privilégié pour l'étude intégrée de plusieurs groupes planctoniques présents au cours de l'intervalle temporel concerné. J'ai également eu l'opportunité d'observer des radiolaires provenant d'un échantillon du Cambrien supérieur d'Australie.

3) L'évènement de Grande Biodiversification Ordovicienne a entrainé de profonds bouleversements des communautés marines à l'Ordovicien. Pour comprendre ces changements, une étude comparative de l'évolution de divers groupes représentatifs du plancton est essentielle. Elle permettrait de développer une bonne perspective des changements de la biodiversité et de productivité survenus à travers la chaîne trophique pélagique au cours de la Grande Biodiversification Ordovicienne. En ce sens, les courbes de diversité de nombreux groupes planctoniques bien documentés ont été étudiés tels que les acritarches, les graptolites ou encore les chitinozoaires. Les courbes de diversité de tous ces groupes planctoniques montrent un pic de diversité maximale au Darriwilien (Servais *et al*., 2008, 2009 ; Fig. 4). La diversité des radiolaires a également été étudiée par Noble et Danelian (2004) et semble montrer aussi la présence d'un pic de diversité au Darriwilien (Fig. 4). Cependant les études portant sur les assemblages à radiolaires de l'Ordovicien sont encore assez fragmentaires et des études supplémentaires seraient aujourd'hui nécessaires pour améliorer nos connaissance sur la diversité des radiolaires à l'Ordovicien et confirmer la présence d'un pic de diversité maximale au Darriwilien (Servais *et al*., 2008).

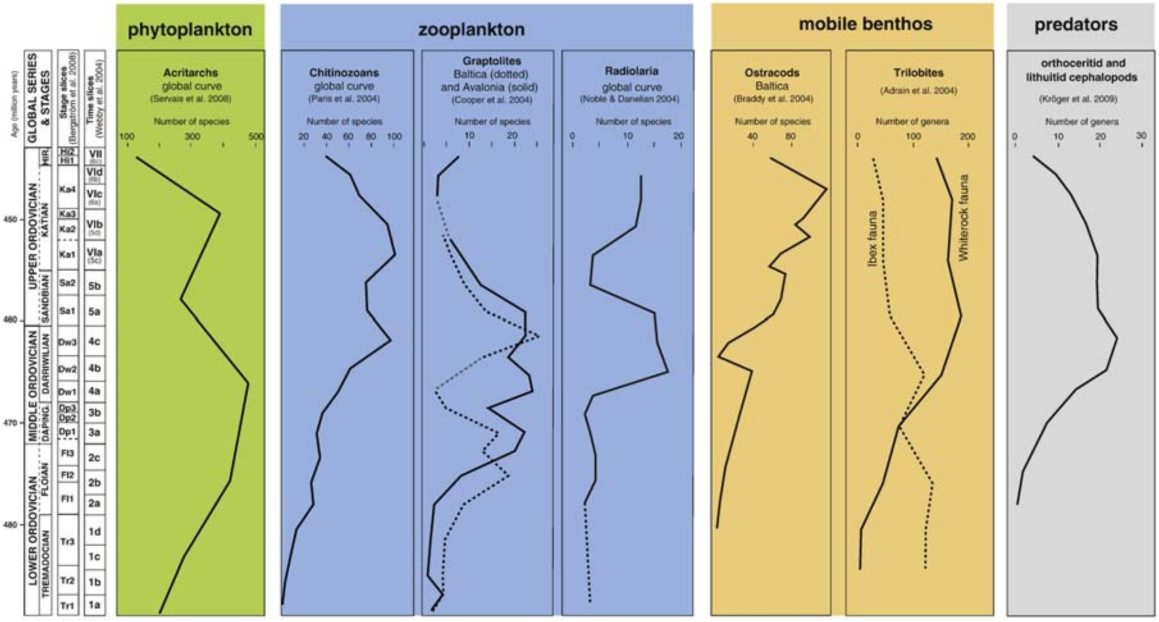


Figure 4 : Evolution de la diversité des groupes fossiles majeurs dans la colonne d’eau au cours de la « Grande Biodiversification Ordovicienne" (extrait de Servais *et al*., 2010).

Nous nous intéressons donc dans la troisième partie de cette thèse à comprendre la biodiversité des radiolaires à l’ordovicien et, plus particulièrement au Darriwilien où elle semblerait avoir atteint son niveau maximal. Pour ce faire, j’ai donc étudié un échantillon provenant de la région Atasu-Zhamshy au Kazakhstan qui s’est, jusqu’à présent, révélé être un chantier très productif pour l’étude des radiolaires ordoviciens. En effet, une grande partie des assemblages à radiolaires connus à l’Ordovicien inférieur et moyen ont été découverts dans des terrains du Kazakhstan (i.e : Danelian et Popov, 2003 ; Nazarov et Popov, 1976, 1980 ; Nazarov et Ormiston, 1986, 1993, Nazarov *et al*., 1977; Nazarov, 1975, 1977, 1988). Cependant, malgré de nombreuses études taxonomiques menées par Nazarov sur ces assemblages, il est encore difficile d’avoir une bonne idée de la structure interne de la plupart de ces radiolaires, et notamment des Inaniguttidae qui dominent les assemblages à radiolaires de l’Ordovicien moyen. L’étude de cet échantillon, daté du Darriwilien supérieur, nous permettrait donc d’approfondir nos connaissances sur la taxonomie de radiolaires de l’Ordovicien moyen et sur leur diversité à une période où elle semblerait atteindre son niveau maximal.

Les objectifs principaux de ce travail de thèse sont donc :

(1) Améliorer nos connaissance sur l'enregistrement fossilifère des premiers radiolaires biominéralisés et à trancher sur la question de leur présence éventuelle au Cambrien inférieur.

(2) Comprendre la dynamique de paléobiodiversité ainsi que les changements biotiques intervenus au sein des assemblages à radiolaires au cours de l'intervalle critique qu'est la transition Cambro-Ordovicienne, correspondant à l'aube de la « révolution planctonique ».

(3) Approfondir nos connaissances sur la taxonomie et la diversité des radiolaires au Darriwilien supérieur, période à laquelle de nombreux groupes planctonique atteignent leur pic de diversité.

III. Organisation du mémoire

Afin de répondre au mieux aux objectifs posés, ce manuscrit est divisé en trois chapitres. Ils se déclinent de la façon suivante : nous présentons d'abord « l'état de l'art des connaissances sur les assemblages à radiolaires de la période étudiée », nous présentons ensuite le « contexte géologique et stratigraphique » de l'étude puis nous présentons le « matériel étudié » et les « méthodes » employées. La partie « résultats et discussion» présente succinctement les principaux résultats obtenus, ainsi que quelques discussions supplémentaires, qui n'ont pas été traitées dans les différents articles. Cette partie est plus étoffée dans les articles joints (publiés, soumis ou en préparation). Il est à noter que les parties « contexte géologique et stratigraphique » et « matériel étudié » des différents chapitres sont également reprises dans les différents articles présentant les résultats. Elles permettent toutefois d'aborder le contexte géologique et stratigraphique de nos différentes études de manière plus détaillée et plus approfondie que dans les articles et permettent surtout l'ajout de nombreuses précisions permettant une vision plus détaillée du travail d'échantillonnage mené au cours des différentes missions de terrain.

Dans le premier chapitre, nous présentons la découverte de nouveaux Radiolaires polycystines du Cambrien inférieur (Botomien) provenant du matériel échantillonné dans les montagnes de l'Altaï (Sibérie méridionale, Russie).

Le second chapitre est consacré à l'étude de la paléobiodiversité et des changements biotiques intervenus chez les radiolaires de Terre-Neuve durant la transition Cambrien supérieur-Ordovicien inférieur. Il se décline en deux parties. La première est consacrée à l'étude du matériel que nous avons pu échantillonner en Terre-Neuve, la seconde décrit très succinctement les premiers résultats liés à l'étude d'un échantillon d'Australie daté du Cambrien supérieur.

Le troisième chapitre a pour objet une étude taxonomique détaillée d'un assemblage à radiolaires du Darriwilien supérieur provenant du Kazakhstan. Elle permet notamment de définir un nouvel assemblage à radiolaire composé de nombreuses nouvelles espèces nous permettant de mieux comprendre la diversité des radiolaires à l'Ordovicien moyen.

Enfin, une dernière partie conclut ce travail de thèse (« Conclusion et perspectives ») en proposant une synthèse de la répartition stratigraphique des familles et genres à Radiolaires au cours du Cambrien et de l'Ordovicien, ainsi que des perspectives scientifiques possibles pour enrichir ces données nouvellement acquises.

La section « annexes » qui clôt ce manuscrit présent deux articles auxquels j'ai contribué et qui s'intègrent dans notre problématique de thèse, traitant de l'importance biostratigraphique et paléoenvironnementale des Trilobites du Botomien de la coupe d'Ak-Kaya dans l'Altaï et de la distribution paléogéographique des radiolaires ordoviciens.

Chapitre 1 :

Radiolaires du Cambrien inférieur (Botomien) des montagnes de l'Altaï (Sibérie)

I. Etat de l’art

L’enregistrement fossile des radiolaires du Cambrien inférieur au Cambrien moyen est encore très fragmentaire et la détermination précise des radiolaires provenant du Cambrien inférieur était jusqu’à présent encore très ambigüe (Fig. 1). En effet, de nombreux organismes sphériques découverts au Cambrien inférieur par le passé ont été mal identifiés et attribués au groupe des radiolaires par erreur comme ce fut le cas pour les genres *Aetholicopalla*, classé par la suite dans le groupe des microfossiles problématiques Cambroclaves (Elicki et Wotte, 2003) et *Blastulospongia*, aux affinités encore incertaines (Pickett et Jell, 1983, Conway Morris, 1990; Conway Morris et Chen, 1990).

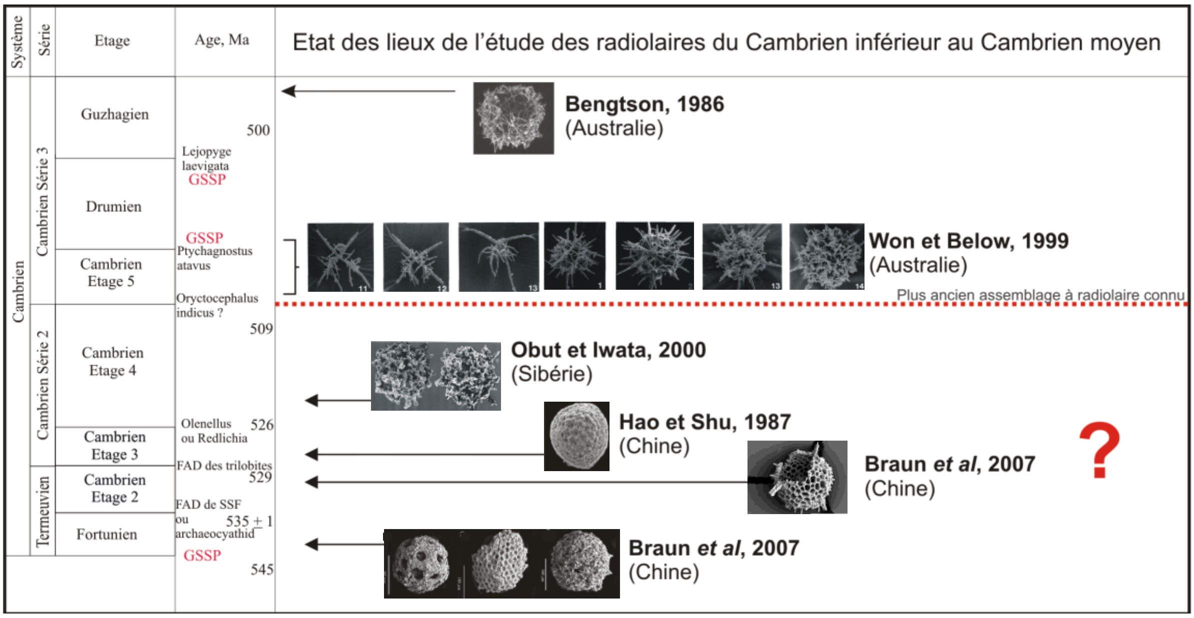


Figure 1 : Schéma récapitulatif des enregistrements à radiolaires connus actuellement au Cambrien inférieur et au Cambrien moyen ainsi que leur provenance géographique. Les flèches indiquent l’âge exact de ces faunes à radiolaires. Echelle chronostratigraphique d’après Peng et Babcock, 2011.

Les plus anciens organismes fossiles appartenant potentiellement au groupe des radiolaires connus actuellement ont été découvert en Chine par Braun *et al*. (2005, 2007) dans des terrains datés du Précambrien supérieur au Cambrien basal. Quatre spécimens présentant une coque sphérique ont été extraits de cherts localisés en dessous de la zone à *Anabarites* et *Protohertzinia* (Fortunien) de la Formation de Kuanchuanpu, dans la province de Shaanxi. Ces organismes ont été attribués par Braun au groupe des radiolaires malgré une très mauvaise préservation rendant toute identification précise impossible. Un radiolaire unique, très bien préservé et presque complet, a également été retrouvé dans des concrétions carbonatés de la Formation de Hetang dans la province de Zhejiang, daté du Meishucunien (zone à *Anabarites* et *Protohertzinia* ; Etage 2 du Cambrien inférieur). Il présente cependant une morphologie très similaire à celle des Inaniguttidae que l'on retrouve à partir de l'Ordovicien moyen et une possible contamination n'est donc pas à exclure. Hao et Shu (1987) décrivirent également un certain nombre de radiolaires de la Formation de Shuijingtuo dans province de Shaanxi en Chine provenant de la zone à *Eoredlichia* (Adtabanien, Serie 2 du Cambrien) qui furent identifiés par la suite comme appartenant au groupe des Lobopodiens (Ramsköld, 1992 ; Zhang et Aldridge, 2007). La présence très controversé de radiolaires du Cambrien inférieur (Atdabanien) provenant de matériel de Batenev Ridge, dans la partie ouest de la Sibérie a été rapporté en 1973 par Nazarov. Cependant, la présence réelle de ces radiolaires n'a jamais pu être confirmée (Obut et Iwata, 2000). En 2000, Obut et Iwata et décrivirent des radiolaires fortement recristallisés provenant d'un niveau siliceux daté du Botomien (Série 2 du Cambrien inférieur) dans la Formation de Shashkunar dans la région de Gorny Altai en Sibérie. Ces radiolaires, attribués par Obut et Iwata (2000) à deux nouveaux genres et trois nouvelles espèces (*Archaeocenosphaera muricata*, *Altaiesphaera acanthophora* et *Altaiesphaera sparsispinosa*), présentent une coque poreuse et sphérique pourvues d'épines mais dont la structure interne n'a pas été préservée leur attribution précise reste délicate.

Les premiers radiolaires identifiés avec certitude et bien documentés ont été découverts par Won et Below (1999) dans des concrétions carbonatées du Cambrien moyen (Série 3, étage 5) provenant du basin de Georgina dans la région du Queensland en Australie. Ce matériel a été prélevé dans des séries d'âge Templétonien à l'Undillien (Cambrien étage 5, Fig. 1). Avec la présence de deux nouvelles familles (Archeoentactiniidae et Palaeospiculidae), six nouveaux genres (*Archeoentactinia*, *Fungomacula*, *Spongomassa*, *Palaeospiculum*, *Aitchisonellum* et *Protobiramus*) et 18 nouvelles espèces, cette faune à radiolaire très diversifiée constituait jusqu'à récemment le plus ancien assemblage à radiolaire connu. Cette faune présente la particularité de posséder exclusivement des spicules centrés sur un point et des radiolaires dont les éléments squelettiques sont constitués de tubes creux. Ces deux caractéristiques se retrouvent également chez les éponges siliceuses, cependant, les taxons attribués à la famille des Palaeospiculidae se différencient des éponges par leur spicules divisées en une partie apicale et une partie basale (Won et Below, 1999). Enfin, les plus anciens Echidninides, considérés comme des radiolaires primitifs (Dumitrica *et al.*, 2000), sont décrits pour la première fois par Bengtson (1986) parmi un assemblage de microfossiles siliceux contenant un nouveau genre (*Echidnina*) et une nouvelle espèces (*Echidnina runnegari*). Cet assemblage, extrait de roches calcaires de la région du Queensland en Australie nord-orientale, est daté du Mindyallien (dernier étage du Guzhangien, cf. Fig. 1) basé sur la présence de Trilobites correspondant à la Zone à *Cyclagnostus quasivespa*.

II. Contexte géologique et stratigraphique

II.1. Contexte géologique

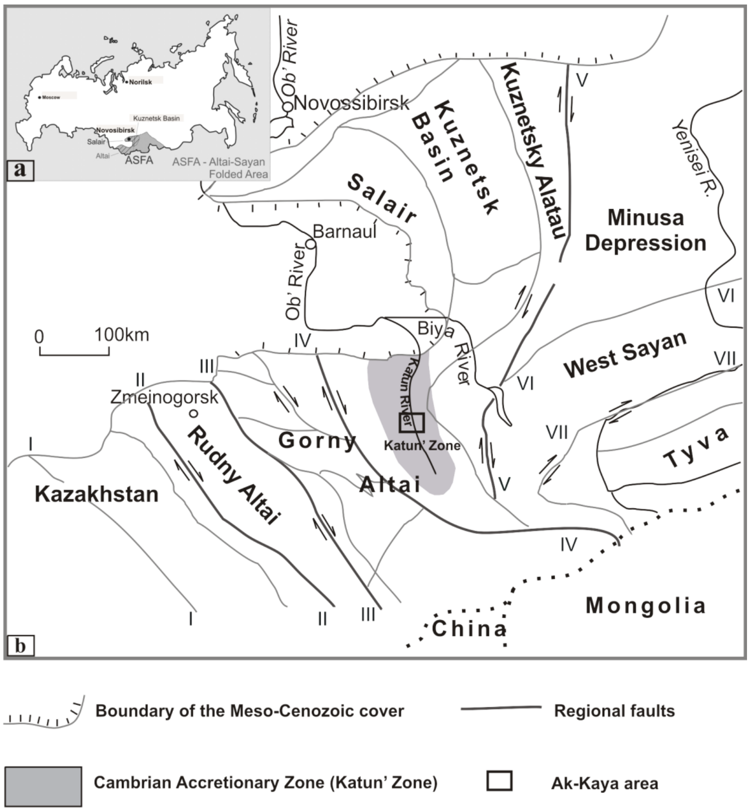


Figure 2 : a) Carte géographique de la Russie avec la région de l'Altai Sayan Folded Area représentée en gris, incluant la région détaillée dans la figure Fig. 2 b) (hachuré). b) Carte tectonique simplifiée de la région de l'Altai-Sayan Folded Area (modifié d'après Yolkin *et al*., 1994). Les zones de cisaillement majeures du Pz-Mz et de chevauchement montrent les directions de mouvement des blocs. I - Chara, II - Irtysh, III - Northeastern, IV - Charysh-Terekta, V - Kuznetsk-Altai, VI - West Sayan; VII- Kurtushiba (d'après Pouille *et al*., 2011)

La région Gorny Altai est située au sud-ouest de la Sibérie (entre 51 et 53° Nord / 80-86° Est) à environ 500km de Novosibirsk (Fig. 2). Elle fait partie d'une structure tectonique complexe nommée l'Altai-Sayan Folded Area (ASFA). La région de Katun' ('Katun' zone) situé au nord de Gorny Altai s'étend sur plus de 120km le long de la rivière Katun (Dobrestov *et al*., 2004). Elle est formée d'un ancien complexe d'accrétion composé de fragments d'îles océaniques ou monts sous-marins et d'arc insulaires formés au cours du Vendien-Cambrien inférieur. A la suite de l'ouverture de l'océan paléo-asiatique (900-830 Ma), une activité volcanique intense de type point chaud au début du Cambrien fut responsable de la formation d'un certain nombre de plateaux basaltiques et d'îles océaniques situés entre l'océan paléo-asiatique et le continent Sibérien (Safonova *et al.*, 2011). Le complexe d'accrétion de Katun' a été formé au cours du Cambrien inférieur à moyen, suite à la subduction de la croute océanique paleo-asiatique sous le craton sibérien entrainant l'accrétion d'îles océaniques existantes et notamment du large plateau océanique de Katun, avec l'arc insulaire de Kuznetsk-Altay situé sur la marge Sud-Est du continent Sibérien (Buslov *et al.*, 1993; Buslov *et al.*, 2001; Dobrestov *et al.*, 2004) (Fig.3).

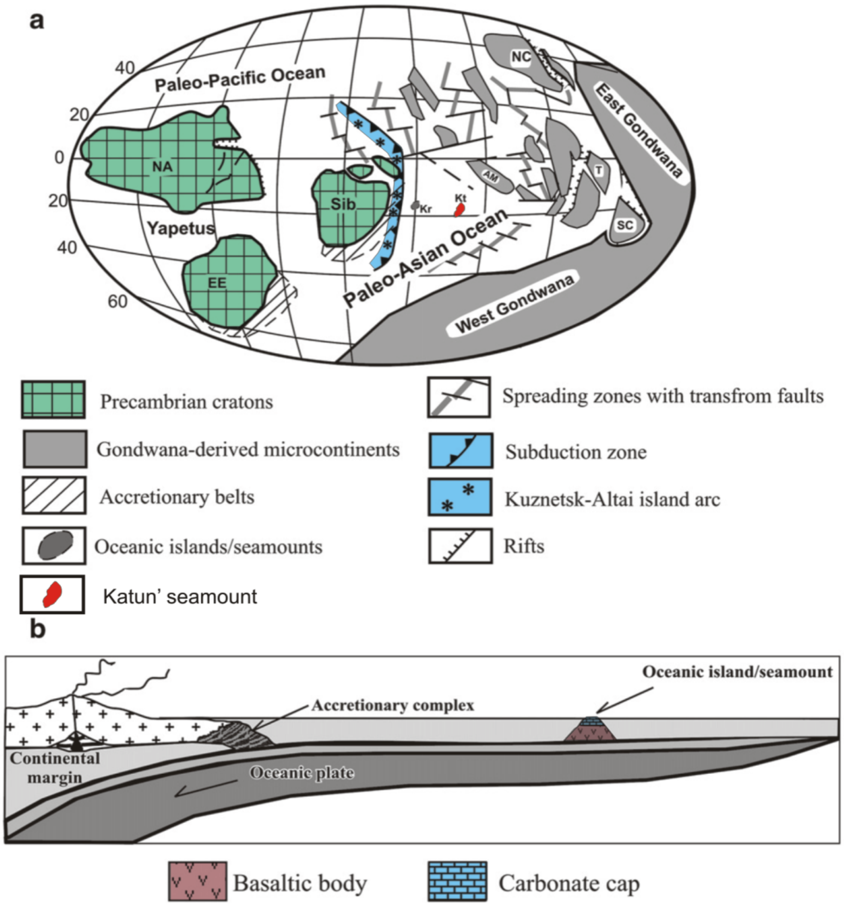


Figure 3: a) Reconstruction paléogéographique donnant la position du plateau océanique de Katun' et de l'arc insulaire de Kuznetsk-Altay au sein de l'océan Paléo-asiatique à la transition Néoproterozoique–Cambrien. Abréviations utilisées pour désigner les blocs continentaux: NA — Amérique du Nord, EE — Europe de l'Est, Sib — Sibérie, AM — Altai–Mongolie, T — Tarim, NC —Chine du Nord, SC —Chine du Sud. Monts sous-marins: Kr— Kurai, Kt — Katun. B) Schéma simplifié montrant la façon dont les îles océaniques et monts sous-marins ont été accrétés à la marge continentale du craton Sibérien (modifié d'après Safonova *et al.*, 2009).

II.2. Contexte Stratigraphique

Les différents terrains affleurant dans la région de Katun' sont composés essentiellement d'épaisses séquences de roches sédimentaires carbonatées et biogéniques s'étendant du Vendien au Cambrien moyen qui se sont accumulées dans un environnement peu profond sur les flancs d'un plateau basaltique (Fig. 3) et qui ont été incorporés suite à une subduction au complexe d'accrétion de Katun (Dobretsov *et al.*, 2004; Uchio *et al.*, 2004, Safonova *et al.*, 2011). Ces séquences carbonatées sont divisées en six formations distinctes, du plus ancien au plus récent (Fig. 4):

- La Formation de Baratal, la plus ancienne, pouvant atteindre une épaisseur de 1000 mètres, est constituée essentiellement de bancs calcaires épais en partie stromatolitques et de schistes noirs à sa base. Cette Formation est datée grâce à la présence de microphytolites d'âge Vendien (Buslov *et al.*, 1993; Zybin et Sergeev, 1978). La Formation d'Eskongo remplace la Formation de Baratal dans certaines localités. Elle est constituée de dolomites sombres et de bancs calcaires intercalés avec des niveaux schisteux et des intercalations siliceuses. Elle contient des microphytolites, des algues calcaires et des microfossiles à paroi squelettique caractéristiques du Vendien-Tommotien (Terleev, 1991) ainsi que des spicules d'éponge (Protospongia. Chancelloria, Monaxonellida, Hexactinellida et Tetraxonida) provenant des niveaux schisteux de la Formation (Zybin *et al.*, 2000).

- La Formation de Manzherok recouvre la séquence du Vendien-Cambrien de manière discordante ; elle est constituée d'une épaisse séquence de laves basaltiques pouvant atteindre jusqu'à 1250 mètres et contenant par endroit des blocs de roches carbonatées brêchés et silicifiés, témoins d'une accumulation de dépôt caractéristique d'un contexte de pente. Elle contient des algues, des microphytolites et des spicules d'éponge caractéristique du Cambrien inférieur (Safonova *et al.*, 2011; Zybin *et al.*, 2000).

- La Formation de Shashkunar, épaisse d'environ 500 mètres, recouvre la Formation de Manzherok de manière discordante. Elle possède à sa base une épaisse séquence de conglomérats, superposés par de fins bancs de calcaires gris et noirs avec des nodules siliceux plus fréquents vers le sommet. L'âge Botomien de la Formation de Shashkunar est contraint par les trilobites appartenant à la biozone à *Parapagetia*-*Serrodiscus*, identifiés par Repina et Romanenko en 1978. La présence d'archaeocyathes et d'algues dans les calcaires, ainsi que la présence de spicules d'éponges et de protoconodontes, caractéristiques des étages Botomien et Atdabanien, retrouvés dans les nodules siliceux de cette Formation confirment cet âge (Zybin *et al.*, 2000).

- La Formation de Cheposh, épaisse de 700 mètres, est composée de calcaires massifs composés de biohermes à Archaeocyathes. Les associations de trilobites contenues dans cette Formation appartiennent à la zone à *Parapoliella-Onchocefalina* daté du Toyonien inférieur. Les archaeocyathides et brachiopodes retrouvés dans la Formation suggèrent, quand à eux, un âge s'étendant du Botomien au Toyonien (Zybin *et al.*, 2000).

- La Formation de Barangol est constituée d'une alternance de bancs calcaires et de marnes datés du Toyonien supérieur sur la base des associations à trilobites, des algues calcaire et des archaeocyatides (Zybin *et al.*, 2000).

- La dernière Formation est la Formation de Ust'-Sema. Elle est constituée d'une épaisse séquence basaltique de 1000 mètres d'épaisseur surmontant d'épais conglomérats à sa base et renfermant des blocs de calcaires par endroit. Elle contient une faune similaire à celle contenue dans la Formation de Cheposh (Zybin *et al.*, 2000) et chevauche cette dernière de manière discordante. Elle s'étend du Cambrien inférieur au Cambrien moyen.

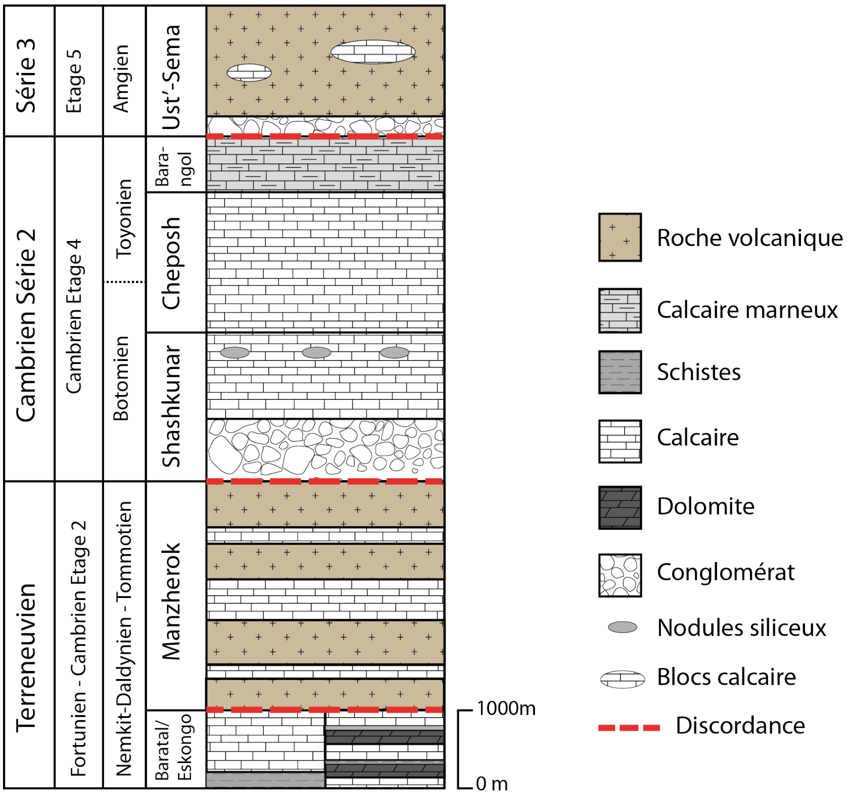


Figure 4 : Colonne lithostratigraphique représentant les différentes formations rencontrées sur le complexe d'accrétion de Katun', Gorny Altaï, Sibérie méridionale. La formation d'Eskongo remplace celle de Baratal dans certaines localités.

III. Matériel étudié

La section "Kaspa" étudiée ici est située dans les gorges de Ak-Kaya, sur la rive gauche de la rivière Katun', au nord de Gorny Altai, près de la rivière Kaspa, à 60 km du village de Ust'-Sema (Fig. 5). Cette section est composée des Formations de Manzherok, Shashkunar et Cheposh. Nos échantillons ont été collectés au sommet de la Formation de Shashkunar, autour de la localité 445 (N°51 08' 20,1'' E086° 09' 21,7'') à environ 160 mètres de la base de la Formation et à 740 mètres d'altitude (Fig. 5). Cette séquence de 500 mètres d'épaisseur est constituée majoritairement de mudstone siliceux entrecoupés de niveaux à carbonates ou de schistes. Outre ces faciès siliceux, témoignant d'un milieu de dépôt profond, elle présente également des traces d'épanchement volcanique avec la présence par endroit d'inclusions de cendres ou de tuffs suggérant un environnement de dépôt situé en base de pente d'un plateau océanique (Fig. 6)

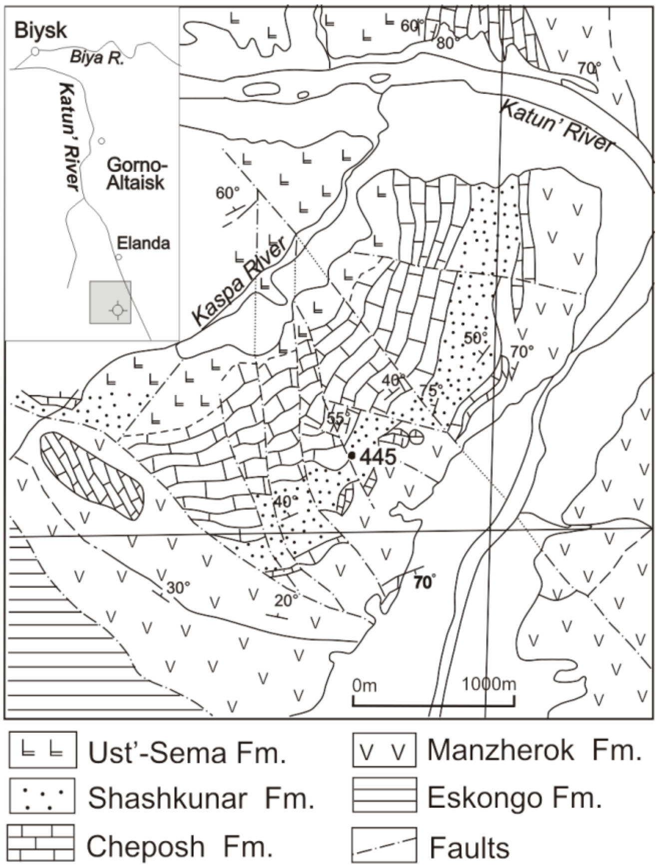


Figure 5. Carte géologique des gorges de Ak-Kaya, dans la région interfluviale de Katun'-Kaspa au nord de Gorny Altaï avec localisation de la localité 445, sur la section 'Kaspa' (d'après Pouille *et al.*, 2011).

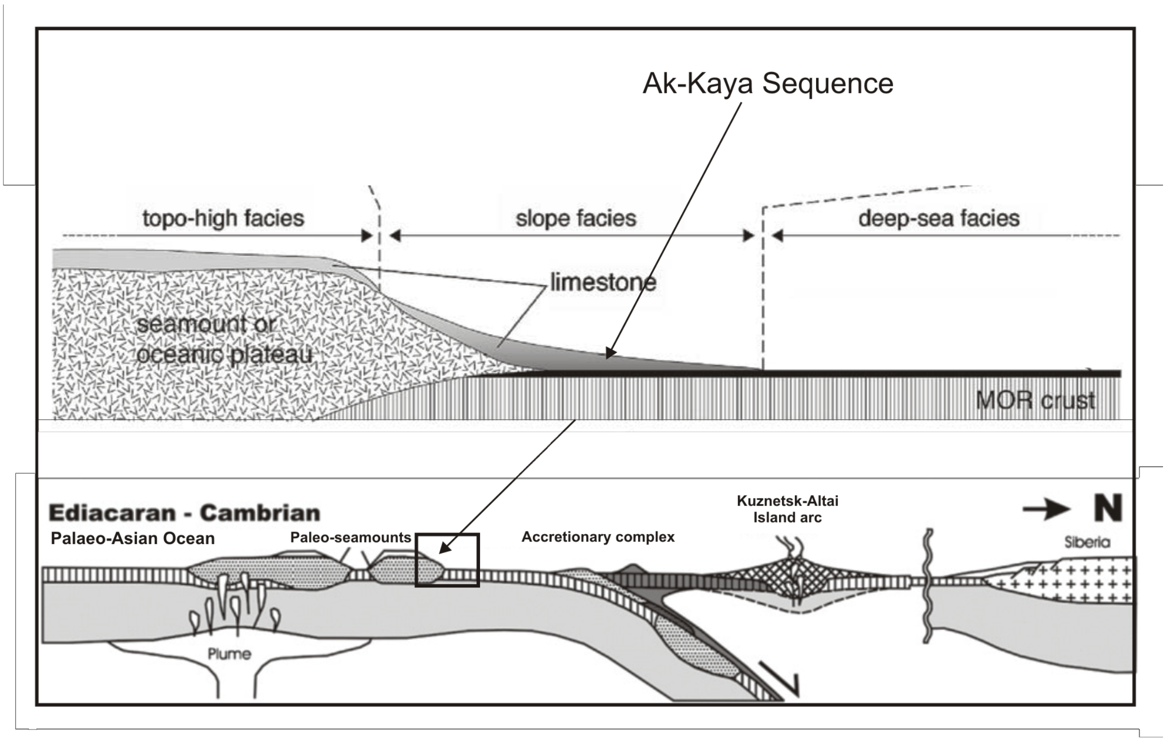


Figure 6: Schéma illustrant la configuration du système d'arc insulaire de Kuznetsk-Altay à l'Ediacarien-Cambrien (en-dessous) ainsi qu'une illustration des différents faciès calcaires déposés sur ou autour du plateau océanique, incluant la position du faciès caractérisant la région d'Ak-Kaya (au-dessus) (modifiée d'après Ota *et al*., 2007 et Glorie *et al*., 2011).

Les affleurements au sommet de la Formation de Shashkunar près de la localité 445 sont pour la plupart plissées, avec de nombreuses failles et sont constitués de nodules siliceux finement lités de couleur grise, verte ou rouge intercalés dans des bancs calcaires. Les trilobites trouvés quelques dizaines de mètre sous ce niveau lors de notre deuxième mission d'échantillonnage, identifiés par le Dr. Igor Korovnikov, ont été déterminés comme appartenant à *Calodiscus resimus* Repina, *Serrodiscus fossuliferus* Repina et *Alacephalus* aff. *contortus* Repina, confirmant avec certitude un âge Botomien inférieur (Korovnikov *et al*., 2012). Un total de 17 échantillons ont été prélevés au cours de ces deux missions de terrain (5 lors de la 1ère mission, 12 lors de la seconde) dans les niveaux à nodules siliceux de l'unité 34 s'étendant sur 8 mètres d'épaisseur. La figure 7 ci-dessous fournit une représentation détaillée de l'échantillonnage et la planche 1 illustre la coupe et les affleurements échantillonnés.

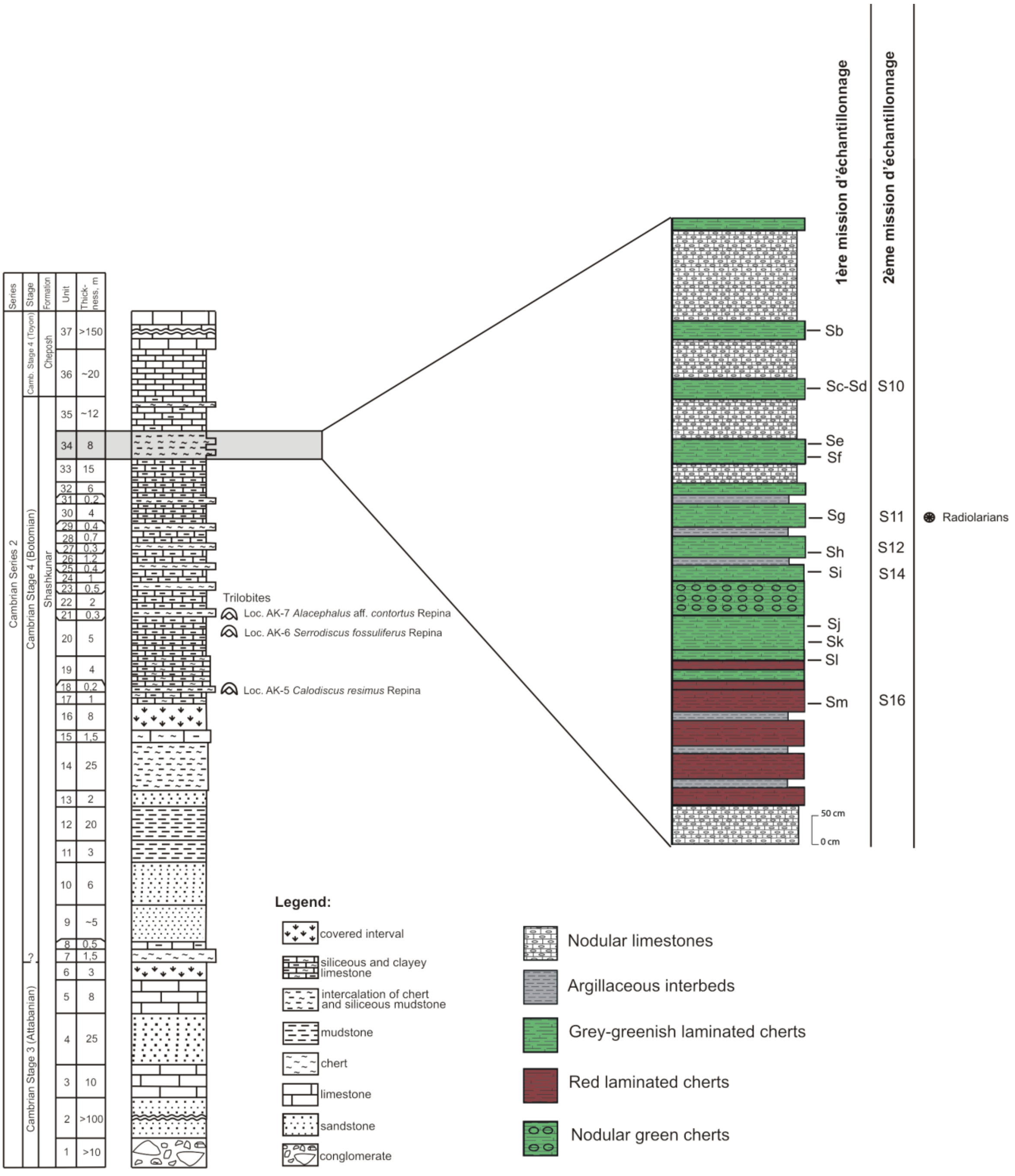


Fig. 7. Colonne lithostratigraphique représentant les formations de Shashkunar et Cheposh de la section Kaspa avec la localisation des trilobites identifiés par Korovnikov *et al*. (2012) lors de notre mission de terrain (à droite) ainsi qu'une colonne lithostratigraphique représentant les niveaux à nodules siliceux de l'unité 34 avec localisation des échantillons prélevés lors des deux missions d'échantillonnage et notamment de l'échantillon S11 dont ont été extraits les radiolaires (à gauche) (modifiée d'après Korovnikov *et al*., 2012 ; voir Annexe 1).

Planche 1:

SECTION DE KASPA – REGION AK-KAYA

1) et 2) Photographie des gorges de Ak-Kaya, le long de la rivière Katun, dans la région de Katun', au nord de Gorny Altai en Sibérie méridionale.

3) Photographie de la section Kaspa dans les gorges de Ak-Kaya. La flèche indique l'emplacement de la localité 445. La limite entre les formations de Shashkunar et de Cheposh est marquée par un trait de couleur jaune.

4) La localité 445, au sommet de la Formation de Shashkunar est localisé par un carré rouge. La limite entre les formations de Shashkunar et de Cheposh est marquée par un trait de couleur jaune.

5) et 9) Photographie des niveaux à nodules siliceux de l'unité 34 s'étendant sur 8 mètres d'épaisseur, situé au sommet de la section de Kaspa.

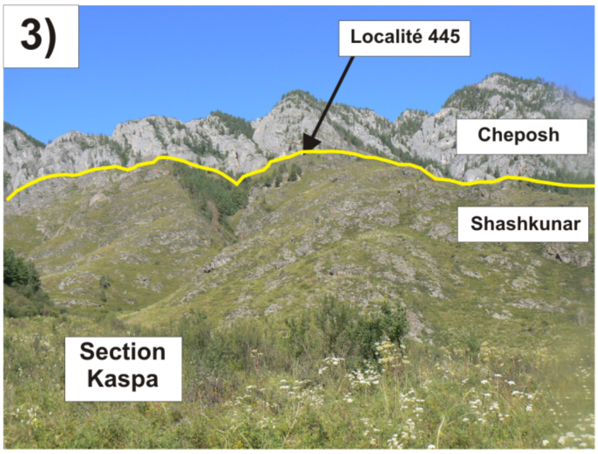
6) Photographie du niveau de transition entre les niveaux à schistes rouges et les niveaux à schistes verts à environ 2 mètres de la base de l'unité 34. L'emplacement des échantillons Sm et Sl est indiqué par une flèche.

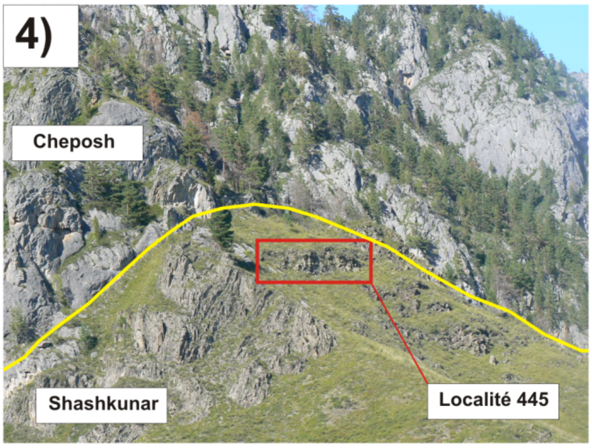
7) Emplacement de l'échantillon Si, prélevé quelques centimètres en dessous du niveau à radiolaire dans des schistes gris-verts laminés en bancs de 2 à 5 centimètres.

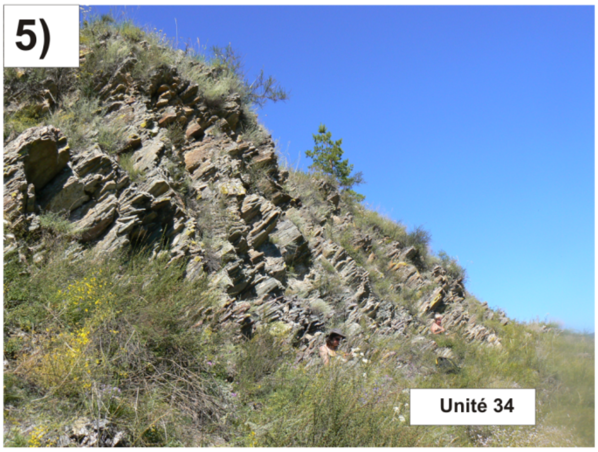
8) Emplacement de l'échantillon S11, échantillon productif, prélevé dans le niveau à radiolaire composé de schistes gris-verts laminés en bancs de 2 à 5 centimètres avec la présence de quelques interlits argileux.

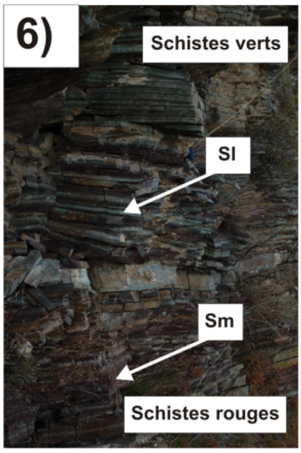

1)
Gorges de Ak-Kaya

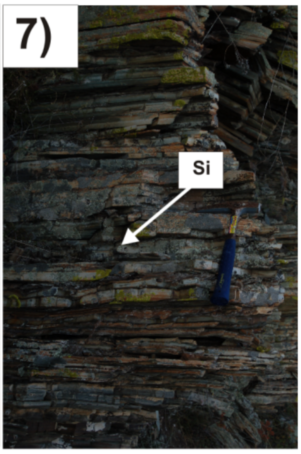

2)
Gorges de Ak-Kaya

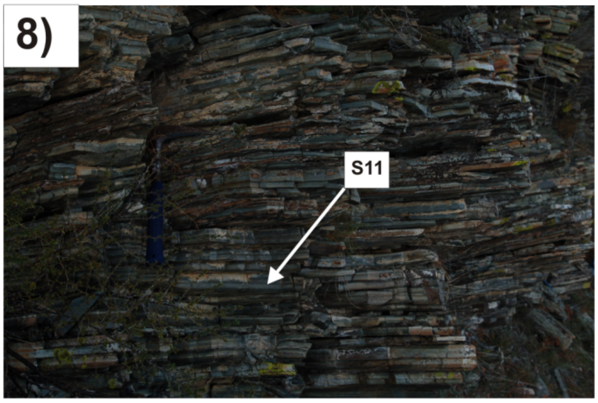

3)
Localité 445
Cheposh
Shashkunar
Section Kaspa

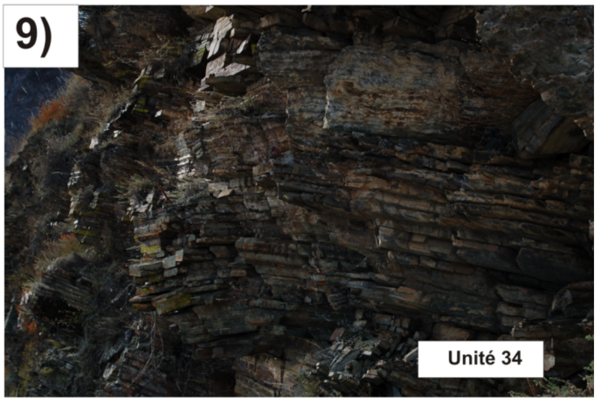

4)
Cheposh
Shashkunar
Localité 445


5)
Unité 34


6)
Schistes verts
Sl
Sm
Schistes rouges


7)
Si


8)
S11


9)
Unité 34

IV. Méthodes

Les différents échantillons ont été d'abord lavés et brossés puis rincés à l'eau distillée et séchés avec un pistolet à air. La roche a été ensuite concassée au marteau en petits fragments de 1-3 cm afin de faciliter les attaques acides et homogénéiser l'échantillon. L'échantillon a été attaqué une première fois avec de l'acide chlorhydrique (HCl) concentré à 10 %, jusqu'à la fin de la réaction. Il a été ensuite rincé à l'eau distillée plusieurs fois et le résidu récupéré par un tamis de maille 50µm.

L'échantillon a été ensuite attaqué avec de l'acide Fluorhydrique (HF) concentré à 4% pendant une période de 8 à 12 heures. Puis il a été rincé plusieurs fois à l'eau distillée et le résidu récupéré par un tamis de maille 50µm. L'opération a été répétée jusqu'à destruction totale de la roche (le processus peut durer entre 2 semaines et 1 mois). A chaque opération, l'échantillon a été rincé à l'eau distillée et le résidu récupéré par un tamis de maille 50µm. Le rinçage fût fait toujours à l'aide d'un léger courant d'eau afin de ne pas détruire le squelette du radiolaire par une trop forte pression.

Une fois les échantillons calcaires et siliceux préparés, le résidu présent dans le tamis a été ensuite récupéré à l'aide d'une pissette d'eau distillée dans un filtre pour préparation palynologique de 15 µm. Ce filtre a été placé dans un entonnoir permettant de laisser le surplus d'eau s'évacuer et de laisser le résidu sécher à l'air libre.

Une fois sec, le résidu a été récupéré dans un petit flacon en verre pour le tri des radiolaires sous la loupe binoculaire à l'aide d'un cil monté sur une tige. Afin d'être observés au Microscope Electronique à Balayage (MEB), les radiolaires ont été posés sur un plot métallique recouvert d'une pastille carbone adhésive.

V. Résultats et discussion:

La section Kaspa a révélé la présence de radiolaires (*Archeoentactinia* ?) datant du Botomien d'une très bonne qualité de préservation et ayant pu être attribué à la famille des Archeoentactiniidae (voir Article 1, partie 4. « Systematic palaeontology »), encore jamais observés jusqu'à présent dans des terrains aussi anciens.

Cette découverte nous a permis d'étendre l'extension stratigraphique de cette famille jusqu'au Cambrien inférieur (Botomien) mais nous permet également d'affirmer que la lignée des polycystines était présente avec certitude dans le plancton du Cambrien inférieur au moins depuis le Botomien, dans des environnements de type plateforme externe (voir Article 1, partie 5. « Discussion »). Elle nous permet également de confirmer que la famille des Archeoentactiniidae constitue une des familles les plus primitives de la lignée des radiolaires. Or, les Archeospicularia, qui possèdent un squelette formé de nombreux spicules, sont considérés par Dumitica *et al*. (2000) comme le groupe le plus ancien des radiolaires du Paléozoïque inférieur. Dumitica *et al*. (2000) suggèrent également que les radiolaires auraient évolué au cours du temps dans le sens d'une réduction du nombre de spicules. Cette hypothèse a été remise en question (Maletz, 2011) après la découverte d'une faune à radiolaires datant du Cambrien moyen (Won et Below, 1999) formés pour la plupart d'un à deux spicules (*Archeoentactinia*, *Spongomass*a, *Fungomacula* et *Paleospiculum*). Si une attribution de la famille des Archeoentactiniidae à l'ordre des Archeospicularia peut être discutée, notre découverte de radiolaires datés du Botomien (Cambrien inférieur) dont le squelette ne possède qu'un seul spicule confirme que la possession d'un squelette formé de nombreux spicule n'est pas un caractère propre aux radiolaires primitifs. Nous pouvons donc affirmer que les radiolaires les plus primitifs de la lignée des polycystines possédaient rarement plus de deux spicules et appuyer l'hypothèse de Maletz (2011) qui estime qu'une évolution des radiolaires primitifs vers une réduction des spicules initiaux ne se serait produite qu'en marge de l'histoire évolutive générale des radiolaires.

Article 1:

Lower Cambrian (Botomian) polycystine Radiolaria from the Altai Mountains (southern Siberia, Russia)

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Lower Cambrian (Botomian) polycystine Radiolaria from the Altai Mountains (southern Siberia, Russia)

Radiolaires polycystines du Cambrien inférieur (Botomien) des montagnes de l'Altaï (Sibérie méridionale, Russie)

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ABSTRACT

Relatively well-preserved polycystine Radiolaria are here described from Lower Cambrian (Botomian) strata of the Shashkunar Formation, Altai Mountains in southern Siberia (Russia). These radiolarians display a test formed of a disorderly and three-dimensionally interwoven meshwork of numerous straight and curved bars branching from a five-rayed point-centered spicule located within the inner shell surface. The shell structure allows their assignment to the family Archeoentactiniidae, thus extending the known age range of the family down to the Lower Cambrian. The Botomian age is based essentially on trilobites (*Parapagetia–Serrodiscus* zone), but also on archaeocyathids identified in earlier publications. The study of the radiolarian-bearing sedimentary sequence confirms the presence of polycystine radiolaria in the external platform environments of Lower Cambrian ecosystems.

RÉSUMÉ

Nous décrivons ici des radiolaires polycystines provenant des niveaux du Cambrien inférieur (Botomien) de la Formation de Shashkunar des Montagnes de l'Altaï en Russie méridionale. Ces radiolaires montrent un test construit par un réseau tridimensionnel constitué de nombreuses barres droites ou courbées, entrecroisées de manière désordonnée. Ces barres se développent à partir d'un spicule formé de cinq épines centrées sur un point situé à l'intérieur de la coque. Cette structure particulière suggère leur appartenance à la famille des Archeoentactiniidae. L'âge Botomien de ces niveaux est contraint par des Trilobites (*Parapagetia–Serrodiscus* zone) et des Archéocyathes déterminés dans des travaux antérieurs. L'étude de la série sédimentaire comprenant les radiolaires confirme la présence des Radiolaires polycystines dans des environnements de plate-forme externe des écosystèmes du Cambrien inférieur.

1. Introduction

The earliest radiolarian record is difficult to decipher (see Maletz, in press, for a recent review) and until recently

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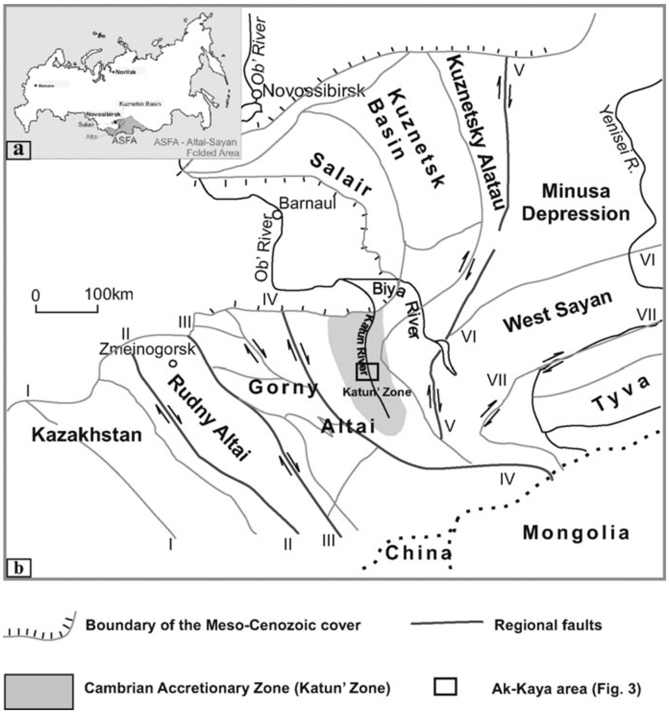

Fig. 1. a: geographic map of Russia with the Altai Sayan Folded Area (in grey), including the area detailed in Fig. 1 b (stripped); b: simplified tectonic map of the Altai-Sayan Folded Area. Major Pz-Mz shear-zones and shear overthrusts, showing directions of block movements: I: Chara; II: Irtysh; III: Northeastern; IV: Charysh-Terekta; V: Kuznetsk-Altai; VI: West Sayan; VII: Kurtushiba.

Fig. 1. a : carte géographique de la Russie avec la région de l'Altai Sayan Folded Area (en gris), incluant la région détaillée dans la figure Fig. 1 b) (hachuré) ; b : carte tectonique simplifiée de la région de l'Altai-Sayan Folded Area. Les zones de cisaillement majeures du Pz-Mz et de chevauchement montrent les directions de mouvement des blocs. I : Chara ; II : Irtysh ; III : Northeastern ; IV : Charysh-Terekta ; V : Kuznetsk-Altai ; VI : West Sayan ; VII : Kurtushiba.

Modified from Yolkin et al., 1994.

the presence of the clade in the Cambrian was still questionable (Lipps, 1992). The discovery of a well-preserved and diverse fauna from Templetonian strata of Australia (Won and Below, 1999) established the undisputable presence of this plankton group in Middle Cambrian marine ecosystems. In spite of a number of morphological similarities of this primitive fauna with sponge spicules (i.e., interlocked point-centered spicules; skeletal elements consisting of hollow tubes; Won and Below, 1999) molecular arguments suggest that siliceous biomineralisation took place independently in the two eukaryote lineages (Danelian and Morreira, 2004). In addition, molecular phylogenies indicate that polycystine radiolarians are one of the deepest lineages of the Rhizaria supergroup (Bass et al., 2005). Therefore, knowledge of the earliest radiolarian fossil record is of prime importance to calibrate the Rhizarian phylogenetic tree, but also to understand their early evolutionary history.

An early controversial report on Cambrian radiolarians from Russia was published by Nazarov (1973), based on Lower Cambrian (Atdabanian) material from the Batenev Ridge, West Siberia (Russia). However, subsequent efforts to replicate or to confirm the presence of unambiguous radiolarians from these strata remained without any successful result (Obut and Iwata, 2000). More recent investigations by Obut and Iwata (2000) unveiled the presence of spherical Radiolaria with a porous cortical shell from the Lower Cambrian Shashkunar Formation of the Altai Mountains, south of West Siberia. However, the internal structure was not able to be observed in any of the described material and their unambiguous assignment to polycystine radiolarians was questioned in a recent review of the Cambro-Ordovician radiolarian record (Maletz, in press).

In the framework of a recent French-Russian collaborative project, we undertook new field and laboratory work in the Altai Mountains with the objective to improve the fossil record of Cambrian radiolarians. We have discovered additional material from the same locality reported by Obut and Iwata (2000), which allows to observe new morphological and structural details of the test. We here report on preliminary results that improve our understanding of the skeleton structure of these radiolarians. We also stress on the available biostratigraphic constraints for the age of the radiolarian-bearing strata and on the depositional environnements in which they were found.

2. Geological and stratigraphic framework

The Gorny Altai region is situated in the southern part of West Siberia and is part of a complicated tectonic structure of the Altai-Sayan Folded Area (ASFA) (Fig. 1). The Katun' zone of Gorny Altai stretches over 120 km along the Katun' River (Fig. 1; Dobretsov et al., 2004). It is formed of an ancient accretionary complex composed of several Upper Neo-Proterozoic–Lower Palaeozoic island arcs and oceanic island fragments (Dobretsov et al., 2004). During the Vendian–Early Cambrian, a complex system of island arcs (Kuznetsk-Altay island arc system) was situated at the margin of the Siberian continent (Dobretsov et al., 2004; Safonova et al., 2011). Early Cambrian hot spot activity was responsible for the formation of a number of oceanic seamounts situated between the Palaeo-Asian Ocean and the Siberian continent (Safonova et al., 2011). The Katun' accretionary complex was formed following the subduction of the Palaeo-Asian oceanic crust beneath the Siberian craton and the accretion of existing paleo-islands (seamounts) to the Kuznetsk-Altay island arc (Buslov et al., 1993; Buslov et al., 2001; Dobretsov et al., 2004).

The Vendian-Cambrian sequence that crops out along the Katun' River (northern Gorny Altai, Katun' zone) is mainly composed of a thick sequence of biogenic carbonate sedimentary rocks that accumulated on shallow marine depositional environments of a basaltic plateau. They belong to two laterally coeval formations, which may reach 1000 m in thickness: the Baratal Formation, made essentially of thick-bedded partly stromatolitc limestones, underlain by black shales, and the Eskongo Formation, made of dark colored dolomites and limestones with some intercalations of chert (Fig. 2). These oldest parts of the Katun sedimentary sequence are considered as Vendian to Early Cambrian (Tommotian) in age; the Baratal Formation contains microphytolites of a Vendian age (Buslov et al., 1993; Zybin and Sergeev, 1978). The Eskongo Formation contains microphytolites, calcareous algae and shelly microfauna characteristic of a Vendian-Early Cambrian age (Terleev, 1991). A lot of sponge spicules (*Protospongia* sp. and *Chancelloria* sp. and specimens of Monaxonellida, Hexactinellida and Tetraxonida) were also identified in the siliceous levels of this Formation (Zybin et al., 2000). The Manzherok Formation is essentially a thick (up to 1,250 m) sequence of Lower Cambrian basaltic lavas that overly unconformably the Baratal Formation. Blocks of brecciated silicified carbonate rocks which reflect accumulation in a slope depositional environment are present in places. They contain algae, microphytoliths and sponge spicules (Safonova et al., 2011; Zybin et al., 2000). The Shashkunar Formation, a 500 m thick Lower Cambrian sequence of essentially carbonate rocks, overlies unconformably the Manzherok Formation and displays at its base a thick sequence of conglomerates. It is composed essentially of thin-bedded grey to dark grey limestones with interbedded nodular chert levels which become more frequent towards the top of the Formation. Trilobites of the Botomian *Parapagetia–Serrodiscus* zone were identified in the 1970s (Repina and Romanenko, 1978; see Zybin et al., 2000 for further details). In addition to the trilobites, archaeocyathids and algae of an Early Cambrian age were also found in these limestones. Moreover, sponge spicules and protoconodonts, characteristic of the Upper Atdabanian and Botomian stages, as well as radiolarians were found in the siliceous mudstone lenses of this formation (Obut and Iwata, 2000; Zybin et al., 2000).

The up to 700-m-thick Cheposh Formation, composed of massive limestones made of archaeocyathid biohermes, overlies conformably the Shashkunar Formation. Trilobite associations found in this Formation belong to the

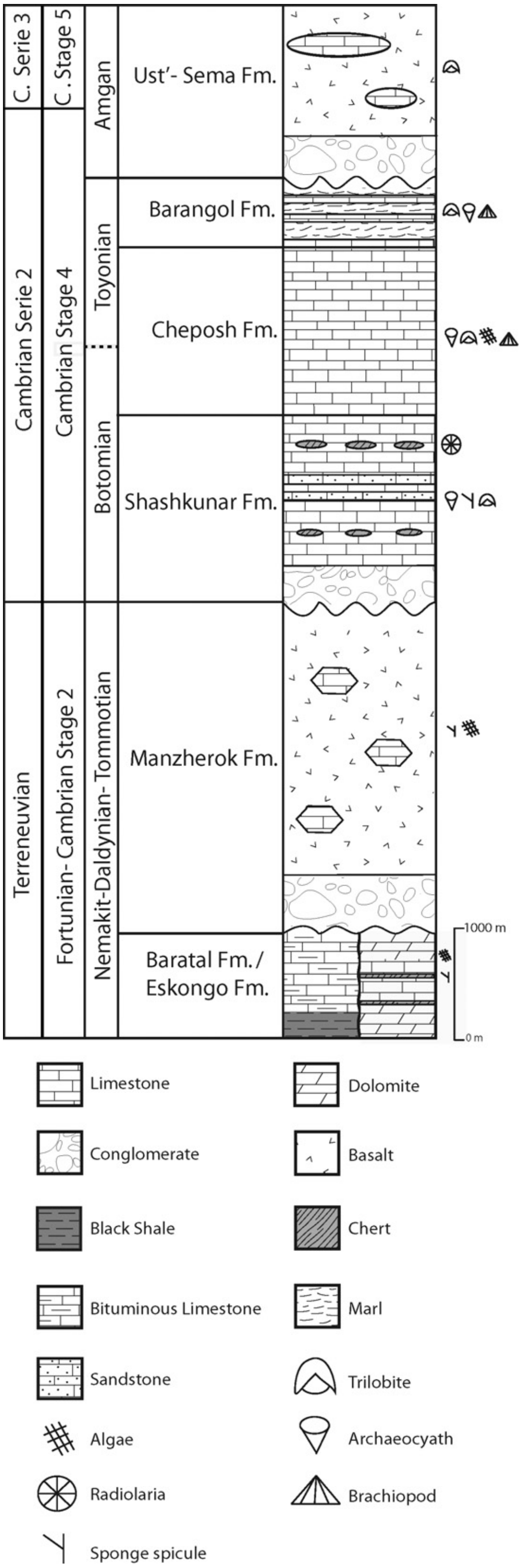

Fig. 2. Generalised stratigraphic column of the Vendian-Cambrian Katun' Zone, Gorny Altai, southern Siberia.

Fig. 2. Colonne stratigraphique générale de la « Katun' Zone » au Vendien-Cambrien, Gorny Altaï, Sibérie méridionale.

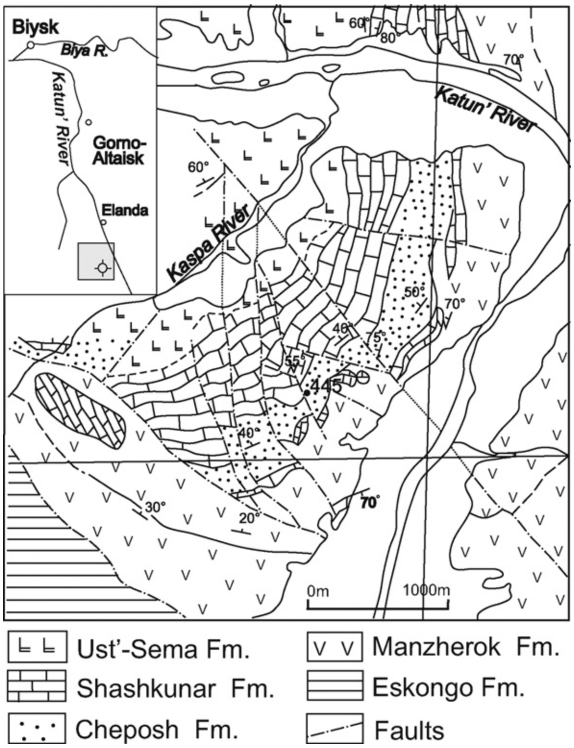

Fig. 3. Geological sketch-map of the Katun'-Kaspa interfluvial area (northern Gorny Altai).

Fig. 3. Carte géologique de la région interfluviale de Katun'-Kaspa (au nord de Gorny Altaï).

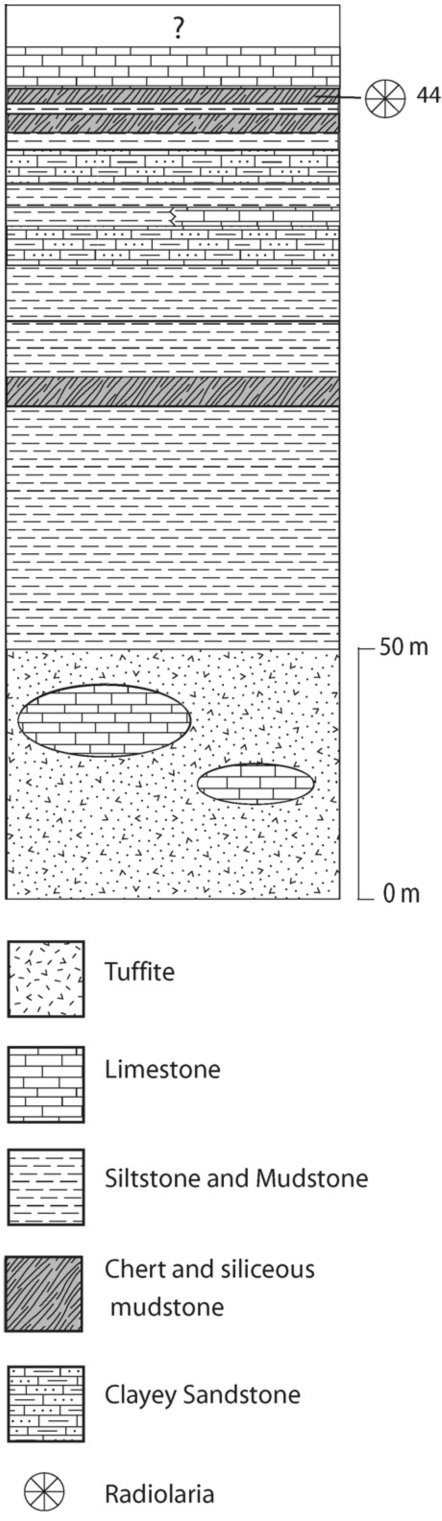

Fig. 4. Detailed stratigraphic column of the Lower Cambrian Shashkunar Formation in the studied "Kaspa" section, Ak-Kaya area, northern Gorny Altai.

Fig. 4. Colonne stratigraphique détaillée du Cambrien inférieur de la formation de Shashkunar dans la section « Kaspa » située dans la région de Ak-Kaya au nord de Gorny Altaï.

Modified from Zybin et al., 2000.

Lower Toyonian *Parapoliella–Onchocefalina* zone. Archaeocyathids and brachiopods found in this formation suggest a wider, but compatible, Botomian to Toyonian age (Zybin et al., 2000). The Lower Cambrian carbonate sequence ends with the 160-m-thick Upper Toyonian Barangol Formation, the age which is based on calcareous algae, archaeocyatids and trilobites (Zybin et al., 2000). It is uncorformably overlain by the Ust'-Sema Formation, a 1,000-m-thick basaltic sequence displaying thick conglomerates at its base, containing blocks of limestones with a similar fauna to the one identified in the Cheposh Formation (Zybin et al., 2000).

All these carbonate sequences were probably accumulated on the slope of a mid-oceanic basaltic seamount, formed by a mantle plume event (Safonova et al., 2011); they were later incorporated in the Katun' accretionary complex (Dobretsov et al., 2004; Uchio et al., 2004).

3. Material and methods

The studied "Kaspa" section is situated in the Ak-Kaya Gorge, in the middle reaches of the Katun' River (left bank), northern Gorny Altai, 60 km south from Ust'-Sema Village (Fig. 3). A full description of the studied section is provided by Zybin et al. (2000; Fig. 3). Our samples were collected from the top of the Shashkunar Formation, around locality 445 (N51° 08′ 20, 1′′ E086° 09′ 21, 7′′), from member 7 of the subsection, about 159 m above the base of the Formation. Grey, greenish or reddish thin-bedded centimetric nodular siliceous beds crop out along with bedded nodu-

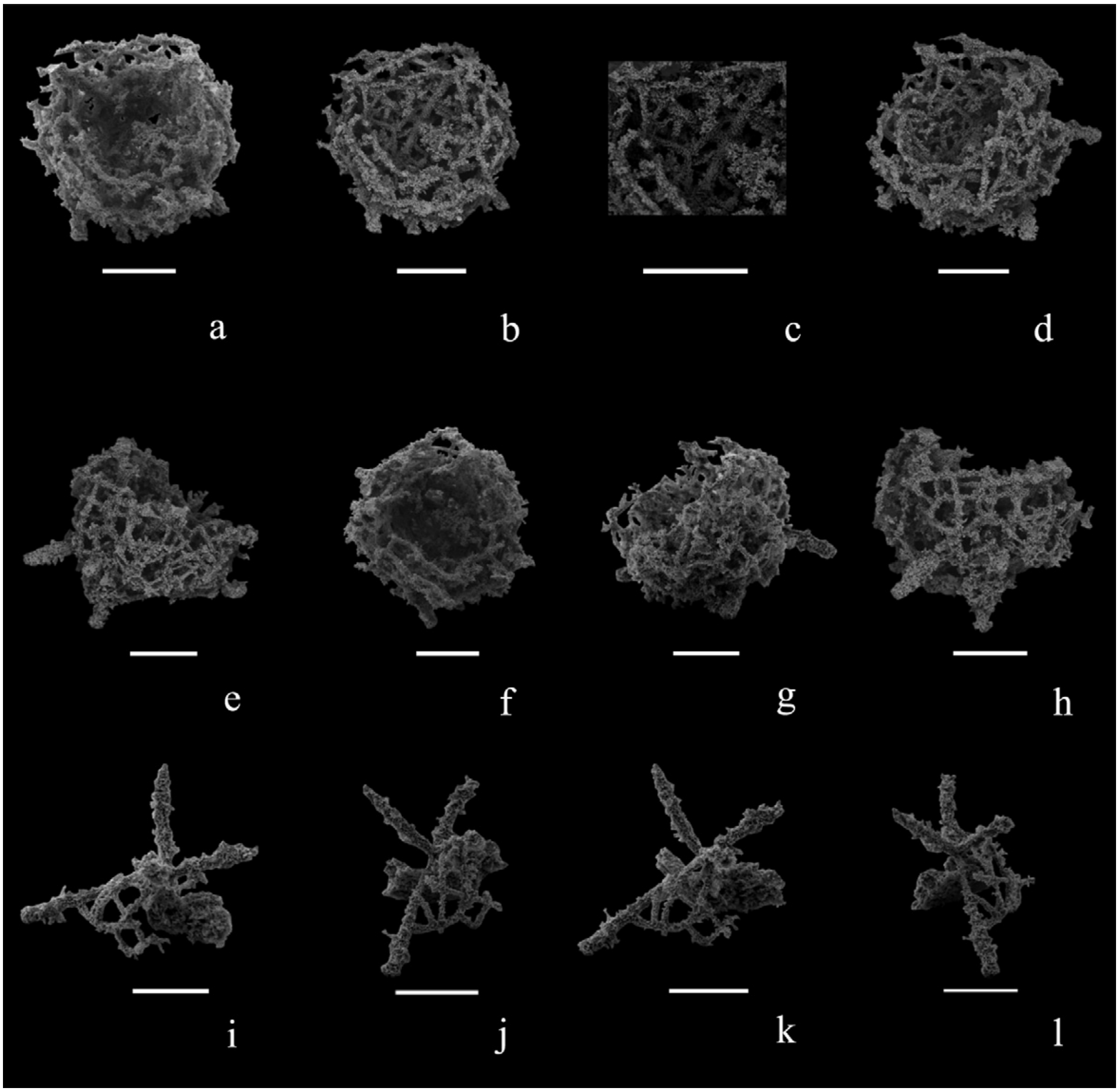

Fig. 5. Scanning Electron Micrographs of the two radiolarian specimens yielded from locality 445, Shashkunar Formation, "Kaspa" section. Bar scale corresponds to 100 μm on all figures. **a–l** *Archeoentactinia?* sp.A.; **a-e**: well-preserved specimen; **a, f**: secondary electron images allowing to observe a single double-layered shell; **b-e**: backscattered electron images allowing to observe the internal structure of the shell, the primary spicule (see detail on the magnified Fig. 5, c) and a number of spines on the external part of the shell; **i-l**: very incomplete specimen (juvenile?), displaying the primary spicule and the innermost part of a three-dimensional shell with the emergence of curved bars branching from the primary spicule.

Fig. 5. Photographies prises en microscopie électronique à balayage des deux spécimens de radiolaires provenant de la localité 445 dans la formation de Shashkunar sur la section « Kaspa ». La barre d'échelle correspond à 100 μm sur toutes les images. **a–l** : *Archeoentactinia* ? sp. A. ; **a–e** : spécimen bien préservé; **a, f** : images prises sous faisceau d'électrons secondaires permettant d'observer une coque à double couche; **b-e** : images prises sous faisceau d'électrons rétrodiffusés permettant d'observer la structure interne de la coque, un spicule initial (voir détails sur la figure agrandie Fig. 5, c) et des épines sur la surface externe de la coque; **i-l** : spécimen très incomplet (juvénile ?), montrant un spicule initial et l'ébauche de la partie la plus interne d'une coque en trois dimensions avec l'émergence de barres courbées ramifiées à partir du spicule initial.

lar limestones (Fig. 4). Radiolarians were extracted from greenish-grey laminated cherts level, the same bed as the one described by Obut and Iwata (2000). Five samples were studied from this bed. Microfossils were removed from the samples by using a standard hydrofluoric acid treatment: samples were crushed into 1 to 3 cm fragments and processed in a plastic beaker filled with 4% diluted hydrofluoric acid. The sample was washed every 8 to 12 h and the residue was then sieved and dried. Only two radiolarian specimens were found so far in the examined residue.

4. Systematic palaeontology

Superorder POLYCYSTINA Ehrenberg, 1838

Family ARCHEOENTACTINIIDAE Won and Below, 1999

Genus ***Archeoentactinia*** Won and Below, 1999

Type species: *Archeoentactinia incaensis* Won and Below, 1999

Archeoentactinia? sp. A

Fig. 5, a-l

***Description**:* The skeleton consists of an irregularly sub-spherical shell made of a three-dimensionally and disorderly interwoven meshwork formed by numerous straight or curved bars. The central part of the shell is a hollow cavity and the surface of the shell is uneven and angular. The three-dimensional arrangement of the bars is organised in two distinctive layers that gives the impression of a two-shelled skeleton. However, the two shell-layers are so closely interconnected that it is more appropriate to describe them as a single two-layered shell. The curved bars emerge from a prominent structure composed of five massive rays originating from a central point (Fig. 5, b-c). This five-rayed spicule is located eccentrically within the inner surface of the shell wall. It is the most robust and thickest element of the shell skeleton. Therefore it can be considered as the primary spicule *sensu* Maletz and Bruton (2007). Seven spines emerge from the shell surface. Since nearly half of the skeleton is broken, it is likely that the total number of spines emerging from the shell is in fact more important. Five of these spines protrude from the primary spicule

***Measurements* (in μm)**:

Diameter of shell: 290–260; length of primary rays: 90–170; thickness of primary rays: ca. 20–25.

Material: Two specimens

Remarks:

Our material differs from the genera *Archaeocenosphaera* and *Altaiesphaera* described by Obut and Iwata (2000) by its bigger skeleton size (260–290 μm, as opposed to 80–160 μm) and by the presence of a large polygonal pore frame (as opposed to small rounded pores). Further comparison with the material of Obut and Iwata (2000) is hampered because their internal structure is unknown. Our material is also characterised by the presence of a main pentactine spicule that is grown attached to the internal side of the cortical shell and which appears to have been formed at an early stage of the shell development.

Occurrence: Lower Cambrian (Botomian) of the Shashkunar Formation, Sanashtykgol Horizon, Ak-Kaya section, near locality 445 mentioned by Zybin et al., 2000. Left bank of Katun' river, 60 km from Ust'-Sema Village, northern Gorny Altai, SW Siberia

5. Discussion

Our specimens display strong affinities with representatives of the Archeoentactiniids known from Middle Cambrian strata of Australia (Won and Below, 1999), which are characterized by a skeleton made of a disorderly, three-dimensionally interwoven meshwork with one or more four to six-rayed point-centered spicules (Won and Below, 1999). More particularly, our specimens are morphologically close to the genus *Archeoentactinia* which is characterized by a large empty space in the central cavity of the shell and only one (or two) point-centered primary spicules positioned very close to the shell wall. Moreover, the type-species *Archeoentactinia incaensis* displays also some rare individuals with a five-rayed spicule, the intersection point of which is positioned very close to the inner surface of the shell wall. Therefore, the material obtained from Altai attests that the earliest representatives of the family Archeoentactiniidae originated during or before the Botomian. Cambrian Radiolaria are best known from Middle Cambrian shallow-water carbonate environments (i.e., the Middle Cambrian strata; Won and Below, 1999), but they are also known Upper Cambrian in deep-sea deposits (Tolmacheva et al., 2001). The facies of the siliceous limestones of the Shashkunar Formation, in which radiolarians were found, reflect an upper slope depositional environment which was present at the flank of an oceanic plateau. This is of particular importance because it establishes the presence of polycystine Radiolaria in the open marine environments of Lower Cambrian ecosystems.

6. Conclusions

New microfossil material from nodular cherts of Botomian slope carbonates of the Shashkunar Formation can be assigned to the Archeoentactiniid family. The previously known age range of the family Archeoentactiniidae can be therefore extended to the Lower Cambrian (Botomian). Our new discovery establishes firmly the presence of polycystine Radiolaria in outer shelf environments of the Early Cambrian marine ecosystems.

Acknowledgments

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Chapitre 2

Etude des assemblages à radiolaires provenant de Terre-Neuve et d'Australie à la transition Cambrien-Ordovicien

Partie 1

Etude des changements biotiques intervenus au sein des assemblages à radiolaires de Terre-Neuve (Canada) à la transition Cambrien-Ordovicien

I. Etat de l'art

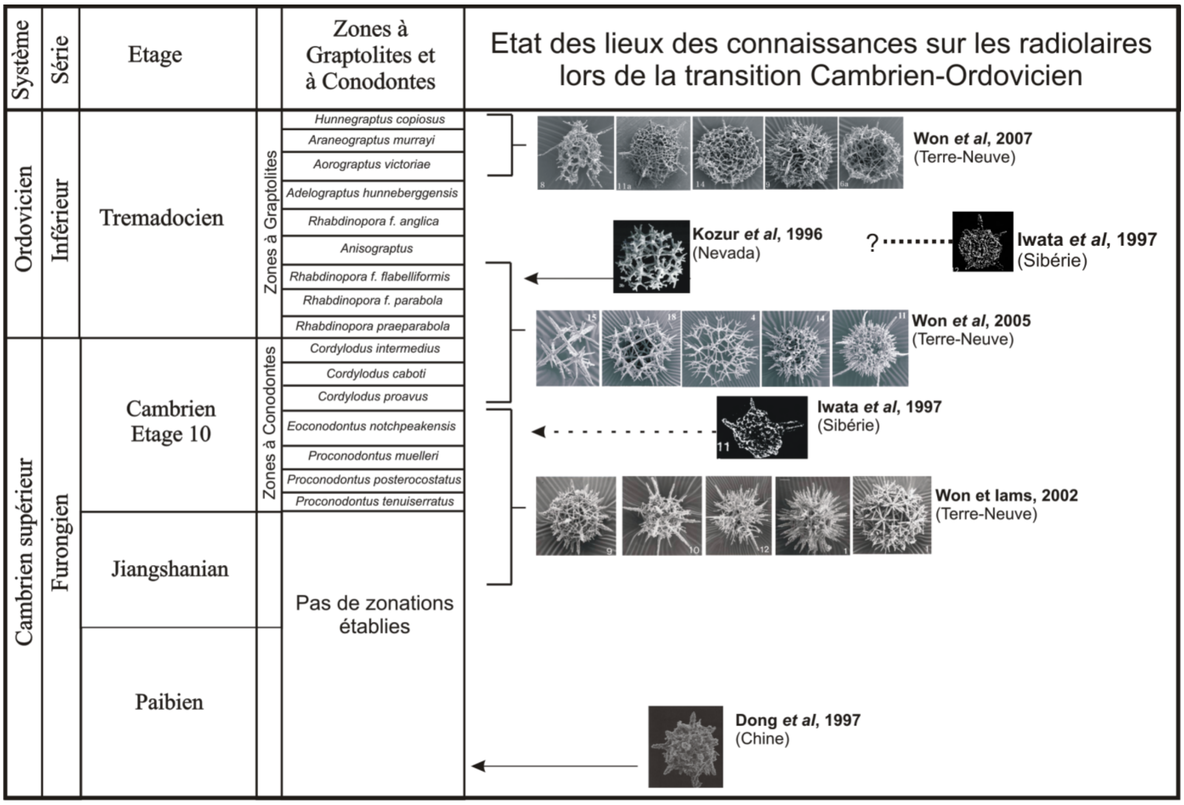


Figure 1 : Schéma récapitulatif des enregistrements à radiolaires connus actuellement au passage du Cambrien supérieur à l'Ordovicien inférieur ainsi que leur provenance géographique. Les flèches indiquent l'âge exact de ces faunes à radiolaires. Les zones à graptolites et conodontes ont été compilées d'après les travaux de Maletz, 2011 et Barnes, 1988.

Les premiers Polyentactinidae, représentés par *Polyentactinia hunanensis,* apparaissent à la base du Furongien dans un assemblage provenant de la région de Hunan en Chine décrit par Dong *et al*. (1997). Cet assemblage, extrait de roches micritiques de la Formation de Bitiao, est daté de la base du Paibien par la présence de trilobites appartenant à la Zone à *Glyptagnostus reticulatus*.

Cependant l'enregistrement fossile à radiolaire le plus complet retrouvé au Furongien, décrit par Won et Iams (2002), provient du groupe de Cow Head en Terre-Neuve occidentale (Fig. 1). Il contient des assemblages à radiolaire très bien préservés s'étendant du Jiangshanien à l'étage 10 du Furongien. Cette faune, très diversifiée, voit l'apparition de deux nouvelles familles (Echidninidae et Protoentactiniidae), sept nouveaux genres (*Subechidnina*, *Curvechidnina*, *Ramuspiculum*, *Grosmorneus*, *Echidnina*, *Pararcheoentactinia* et

Protoentactinia) et 32 nouvelles espèces. Les radiolaires du Furongien sont caractérisés principalement par des formes pourvues de spicules qui peuvent être centrés en un point, comme les formes du Cambrien moyen, mais aussi centrés sur une barre médiane ou une micro-barre. Won *et al.* (2005) décrit également quelques rares radiolaires provenant du Cambrien supérieur (Zone à *Cordylodus proavus*). Des radiolaires du Cambrien supérieur ont également été observés par Iwata *et al.* (1997) dans la localité 4400 dans la région de Gorny Altai. Ces radiolaires très mal préservés, provenant de la Zone à *P.muelleri- P.notchpeakensis* (étage 10 du Furongien) ont été identifiés comme de possibles *Inanibigutta* mais leur état de préservation ne permet pas une identification certaine. La présence de radiolaires provenant de la localité 95071901 dans la région de Gorny Altai a également été mentionnée par Iwata *et al.* (1997) à l'Ordovicien inférieur. De possibles *Inanigutta* et *Praespongocoelia* ont été observés mais leur attribution précise reste toutefois incertaine de même que l'âge exact de leur localité (entre le Tremadocien supérieur et le Floian). Des assemblages très bien préservés et très diversifiés provenant du groupe de Cow Head en Terre-Neuve occidentale, s'étendant du Trémadocien inférieur au Trémadocien moyen (Zones à *Cordylodus lindstromi, Cordylodus angulatus* et *Rossus manitouensis*) ont été décrits par Won *et al.* (2005). Ils présentent cinq familles différentes (Archeoentactiniidae, Echidninidae, Palaeospiculidae et Protoentactiniidae et Aspiculumidae) dont quatre étaient déjà présentes au Cambrien supérieur et deux au Cambrien moyen, ainsi que dix genres et 24 espèces. A partir du Trémadocien inférieur, les faunes à radiolaires se distinguent des faunes cambriennes par la présence de nombreux Echidninidae et Protoentactiniidae, présentant la particularité de posséder des spicules fusionnées ou modifiées ainsi qu'une cavité interne bien distincte (Won *et al.*, 2005). Kozur *et al.* (1996) décrit également un assemblage à radiolaires provenant de la Formation de Windfall dans le Nevada datant du Trémadocien inférieur (Zones à *Cordylodus angulatus*) composé de deux familles (Echidninidae et Protoentactiniidae), quatre genres (*Parechidnina*, *Echidnina*, *Protoentactinia* et *Nobella*) et cinq nouvelles espèces. Enfin, des radiolaires du Trémadocien supérieur (Zone à conodontes apparentant à « l'intervalle de faible diversité », Zone à *Macerodus dianae* et Zone à *Paraoistodus proteus*) provenant du groupe de Cow Head en Terre-Neuve ont été décrits par Won *et al.* (2007). Cette faune comprend sept nouveaux genres (*Neopalaeospiculum*, *Protospongentactinia*, *Archeoproventocitum*, *Protoproventocitum*, *Westernbrookia*, *Aspiculum*, *Cowheadia*) et présente des Echidninidae, Palaeospiculidae et Protoentactiniidae pourvus d'un squelette sphérique unifié, constitué de spicules entièrement ou en grande partie fusionnés.

II. Contexte géologique, paléogéographique et stratigraphique

II.1. Contexte géologique

Le groupe de Cow Head, situé dans la grande Péninsule du Nord, au nord du 50^{e} parallèle, à l'extrémité ouest de la Terre-Neuve (Canada), est une séquence de 300 à 500 mètres d'épaisseur déposée dans un environnement marin profond. Cette séquence, datée du Cambrien moyen à l'Ordovicien moyen représente une séquence d'accumulation transgressive déposée à faible latitude, à la base d'un talus de marge continentale située à l'extrémité sud de la Laurentia (Fig. 2 ; James et Stevens, 1986). Elle présente une alternance de bancs calcaires et de schistes argileux intercalés ponctuellement par des conglomérats calcaires et de grès représentant une coupe du talus continental. Cette séquence est disposée en une série de tranches de nappes de charriage empilées au sein de l'extrémité nord de l'allochtone de Humber Arm située à l'ouest de la Terre-Neuve (Fig. 3 ; James et Stevens, 1986; Cooper *et al.*, 2001). Elle présente l'avantage de contenir un nombre significatif de groupes fossiles du Paléozoïque inférieur. Le groupe de Cow Head peut être subdivisé en cinq périodes de dépôt qui reflètent des intervalles de changements de sédimentation survenus sur cette plateforme (James et Stevens, 1986).

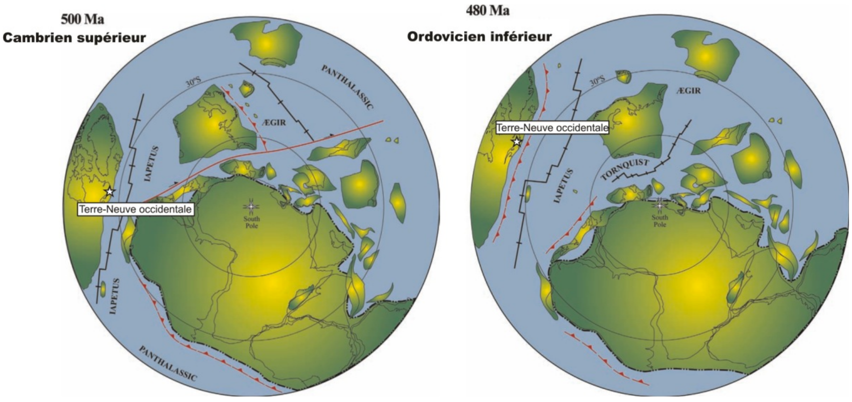


Figure 2 : Reconstitutions paléogéographique du Cambrien supérieur et de l'Ordovicien inférieur avec localisation de la Terre-Neuve occidentale située le long de la marge laurentienne. (modifié d'après Cocks et Torsvik, 2006).

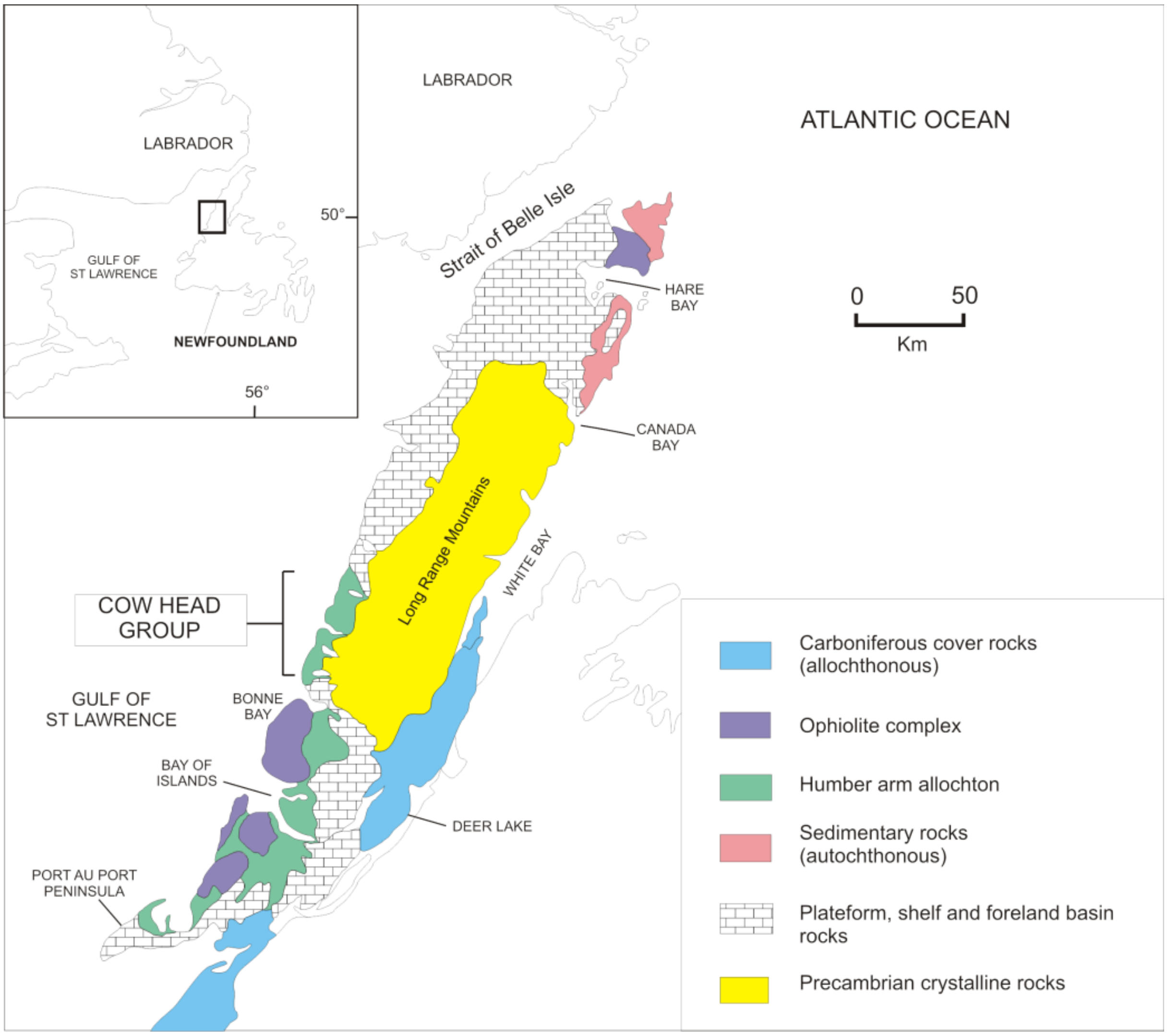


Figure 3 : Carte géologique montrant la distribution des différents terrains géologiques en Terre-Neuve occidentale ainsi que la localisation des morceaux de l'allochtone de Humber arm et l'emplacement du Groupe de Cow Head (modifiée d'après James et Stevens, 1986).

II.2. Contexte Stratigraphique (d'après James et Stevens, 1986)

Le groupe de Cow Head est divisé en deux formations contemporaines: Les formations de Shallow Bay et de Green Point, elles-mêmes divisées respectivement en quatre et trois membres (Fig. 4). Il existe une polarité distincte du nord-ouest au sud-est avec d'une part la séquence de la Formation de Shallow Bay représentant des faciès proximaux à grain grossier opposé aux faciès distaux à grain fin de la Formation de Green Point qui représente l'équivalent distal de la Formation de Shallow Bay.

La Formation de Shallow Bay est une séquence à grain grossiers et à conglomérats dont l'épaisseur varie de 100 à 300 mètres et qui est divisée en quatre membres :

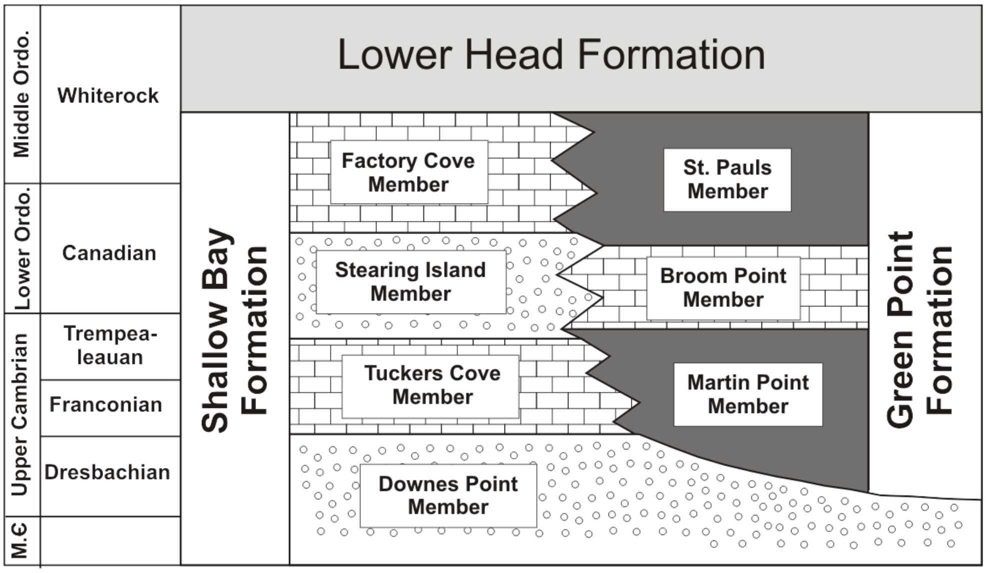


Figure 4 : Schéma simplifié illustrant les différentes unités stratigraphiques (formations et membres) composant le Groupe de Cow Head (modifiée d'après James et Stevens, 1986)

- Le membre de Downes Point, situé à la base de la Formation, est composé d'une série conglomératique avec des intercalations de calcaires laminaire à rubané et de calcarénites. Cette unité de 100 mètres d'épaisseur s'étend de la fin du Cambrien moyen jusqu'au début du Cambrien supérieur.
- Le membre de Tuckers Cove représente une série de 60 mètres d'épaisseur de conglomérats à fragments de calcarénite quartzeuse avec la présence de quelques calcaires laminaire à rubané, de grès, d'aleuréolites et de schistes argileux. L'enregistrement fossile à trilobites suggère une extension temporelle allant du Cambrien moyen au Cambrien supérieur.
- Le membre sus-jacent est le membre de Stearing Island qui représente une série de mégaconglomérats entrecoupés par de rares calcaires laminaire à rubané, de calcarénites quartzeuses et de schistes argileux. D'après l'enregistrement fossile à graptolites, cette unité de 80 mètres d'épaisseur s'étendrait du Cambrien supérieur à l'Ordovicien inférieur (Trémadocien).
- Le dernier membre, situé au sommet de la Formation, appelé membre de Factory Cove, représente une unité de 100 mètres d'épaisseur constituée de calcaires laminaire à rubané ainsi que de rares bancs de schistes argileux entrecoupés de petits blocs

conglomératiques et de mégaconglomérats. L'enregistrement à graptolites suggère ici un âge Ordovicien moyen (Dapingien à Darriwilien).

La Formation de Green Point est contemporaine de la Formation de Shallow Bay. Elle représente une épaisse séquence de 400 à 500 mètres d'épaisseur composée d'un facies à grains fins et comprend trois membres :

- Le membre de Martin Point, situé dans la partie inférieur, est une séquence de 100 à 150 mètres d'épaisseur composée principalement de schistes argileux verts et noirs, de calcaires laminaire à rubané, d'aleuréolite, de grès calcaire et de rare bancs de conglomérats. Cette unité est datée du Cambrien supérieur par l'enregistrement fossile à graptolites et conodontes. Le membre de Martin Point est l'équivalent distal du membre de Tuckers Cove (proximal) de la Formation de Shallow Bay.
- Le membre intermédiaire, appelé membre de Broom Point, représente une séquence épaisse de 80 mètres dominé par des calcaires laminaire à rubané avec la présence de rares aleuréolites, de grès et de conglomérats. Les graptolites et conodontes contenus dans cette unité suggèrent un âge Trémadocien inférerieur. Le membre de Broom Point est l'équivalent distal du membre de Stearing Island (proximal) de la Formation de Shallow Bay.
- Le membre de St. Pauls, situé dans la partie supérieur de la Formation est composé de schistes argileux rouges, verts et noirs, ainsi que de calcaires laminaire à rubané, de conglomérats calcaires, d'aleuréolite et de dolomie. Cette unité de 130 à 150 mètres d'épaisseur est datée du Trémadocien moyen/supérieur au Dapingien inférieur par l'enregistrement à graptolites et conodontes.

Les membres de la Formation de Green Point Formation chevauchent à certains endroits les membres inférieurs de la Formation de Shallow Bay (Fig. 4), comme dans les sections de Broom Point et de Martin Point. En effet, dans les sections de Broom Point North et Broom Point South, le membre de Broom Point de la Formation de Green Point chevauche le membre de Tuckers Cove de la Formation de Shallow Bay et dans la section de Martin Point South, le membre de Martin Point chevauche le membre de Tuckers Cover.

Le groupe de Cow Head représente une localité clé pour l'étude intégrée de divers groupes fossiles puisque la majeure partie des groupes planctoniques et benthiques existant lors de la transition Cambro-Ordovicienne (radiolaires, graptolites, conodontes, trilobites, brachiopodes, fossiles coquillers…) est retrouvé dans les strates de Cow Head (James et Stevens, 1986). Des études biostratigraphiques détaillées de certains groupes tels que les graptolites, conodontes (Fig. 5) ou encore trilobites ont permis d'établir un cadre temporel très bien défini pour les sections de Cow Head et de définir de manière très précise la limite Cambrien-Ordovicien.

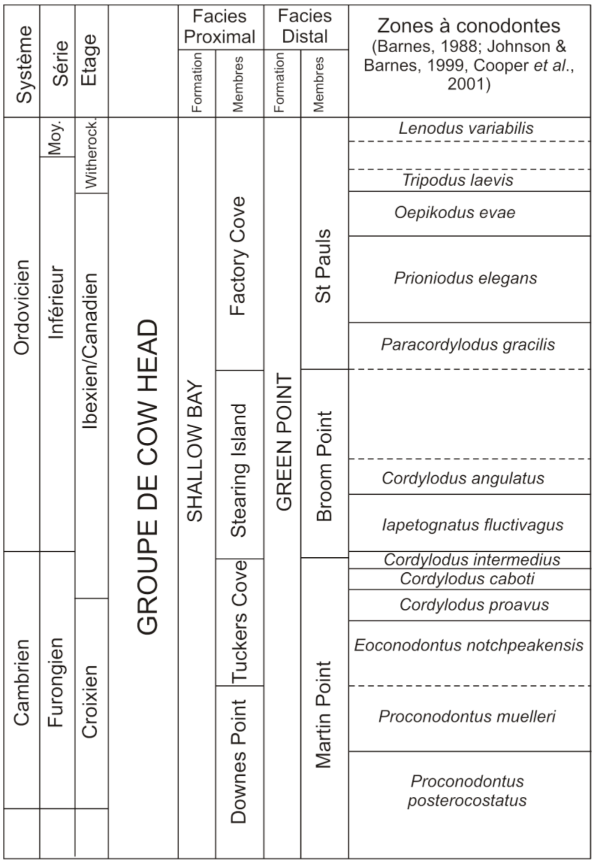


Fig. 5 : Echelle chronostratigraphique et biostratigraphique des zones à conodontes corrélées avec les différentes unités stratigraphiques du Groupe de Cow Head en Terre-Neuve occidentale (modifiée d'après Zhang et Barnes, 2004).

III. Matériel étudié

Deux missions de terrain menées en Terre-Neuve en collaboration avec Jörg Maletz ont permis un échantillonnage important dans des séries sédimentaires très bien décrites du Groupe de Cow Head (cf. James et Stevens, 1986). Lors de la première mission nous avons surtout échantillonnés des niveaux du Cambrien moyen et supérieur. Pour la deuxième mission, nous avons surtout mis l'accent sur un échantillonnage serré de l'intervalle situé autour de la limite Cambrien-Ordovicien. Nous avons donc échantillonné en détail le passage Cambrien supérieur/Ordovicien inférieur sur la coupe de Green Point, définie comme le GSSP (Global Boundary Stratotype Section and Point) de la base de l'Ordovicien. Nous avons également échantilloné trois autres coupes ayant enregistré des environnements plus proximaux par rapport au stratotype de Green Point et s'étendant du Cambrien moyen au Cambrien supérieur : les coupes de Martin Point South, de Broom Point North et de Broom Point South. Un total de 82 échantillons ont été collectés sur les quatre coupes selon la répartition suivante :

- 38 échantillons ont été collectés sur la coupe de Broom Point South (BPS) dans les unités 3, 5, 7, 8 et 10 du membre de Downes Point Membre et dans les unités 21, 22, 24, 35, 36 et 40 du membre de Tuckers Cove de la Formation de Shallow Bay ainsi que dans les unités 45, 46, 48, 50, 54, 55, 60 et 62 du membre de Broom Point de la Formation de Green Point (Fig. 6).

- 17 échantillons ont été collectés sur la coupe de Broom Point North (BPN) dans les unités 78, 82, 87 et 94 du membre de Broom Point de la Formation de Green Point (Fig. 6).

- 24 échantillons ont été collectés sur la coupe de Green Point (GP) dans les unités 3, 10, 13, 16, 17, 18, 20, 21 et 22 du membre de Martin Point et dans les unités 23, 25 et 26 du membre de Broom Point de la Formation de Green Point (Fig. 7).

- 3 échantillons ont été collectés sur la coupe de Martin Point South (MP) dans l'unité 23 du membre de Tuckers Cove de la Formation de Shallow Bay, et de l'unité 36s du membre de Broom Point de la Formation de Green Point (Fig. 7). Les figures 6 et 7 ci-dessous fournissent une représentation plus détaillée de l'échantillonnage.

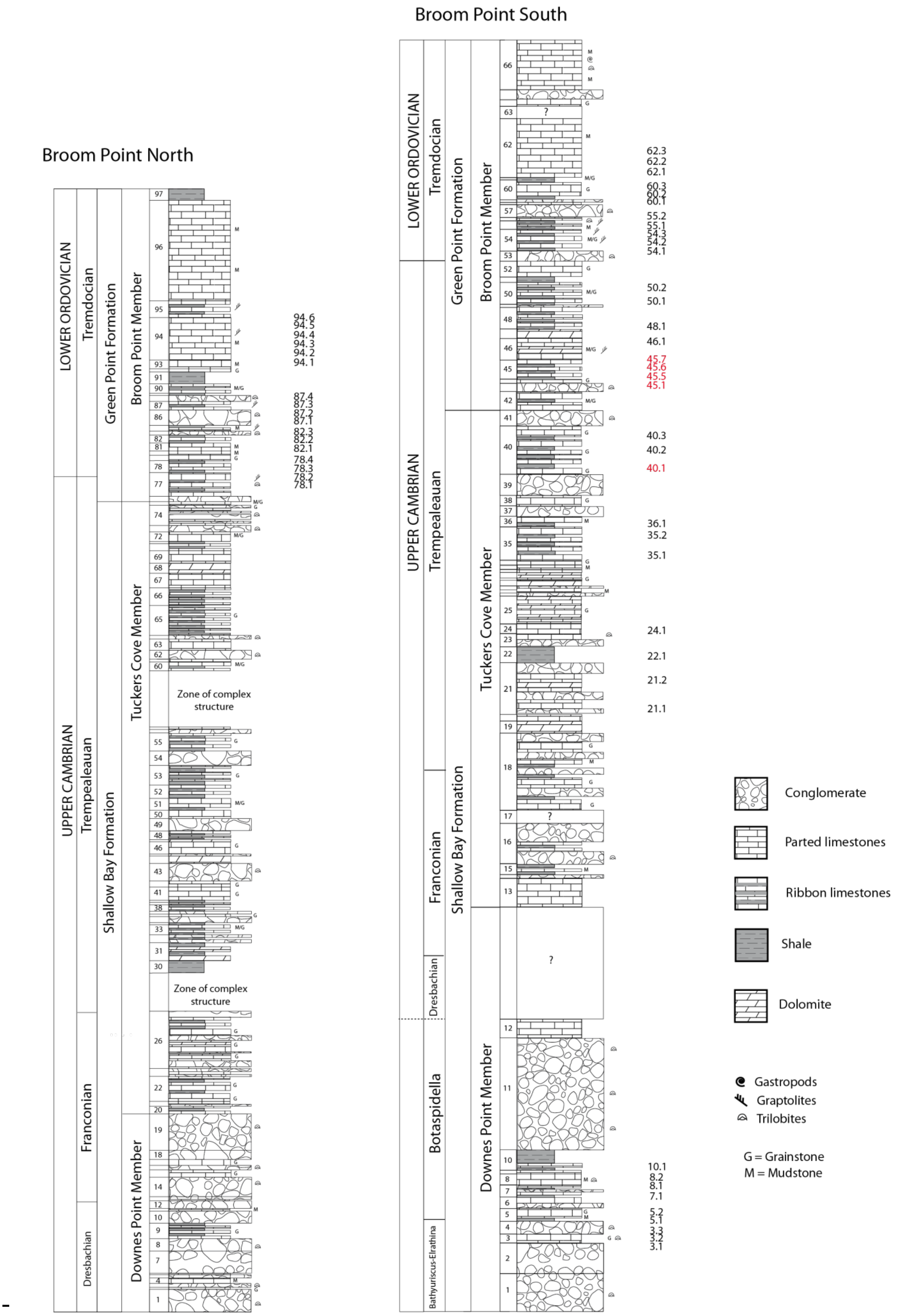


Figure 6 : Colonnes lithostratigraphiques des coupes de Broom Point North et de Broom Point South avec localisation des échantillons prélevés lors des deux missions de terrain.

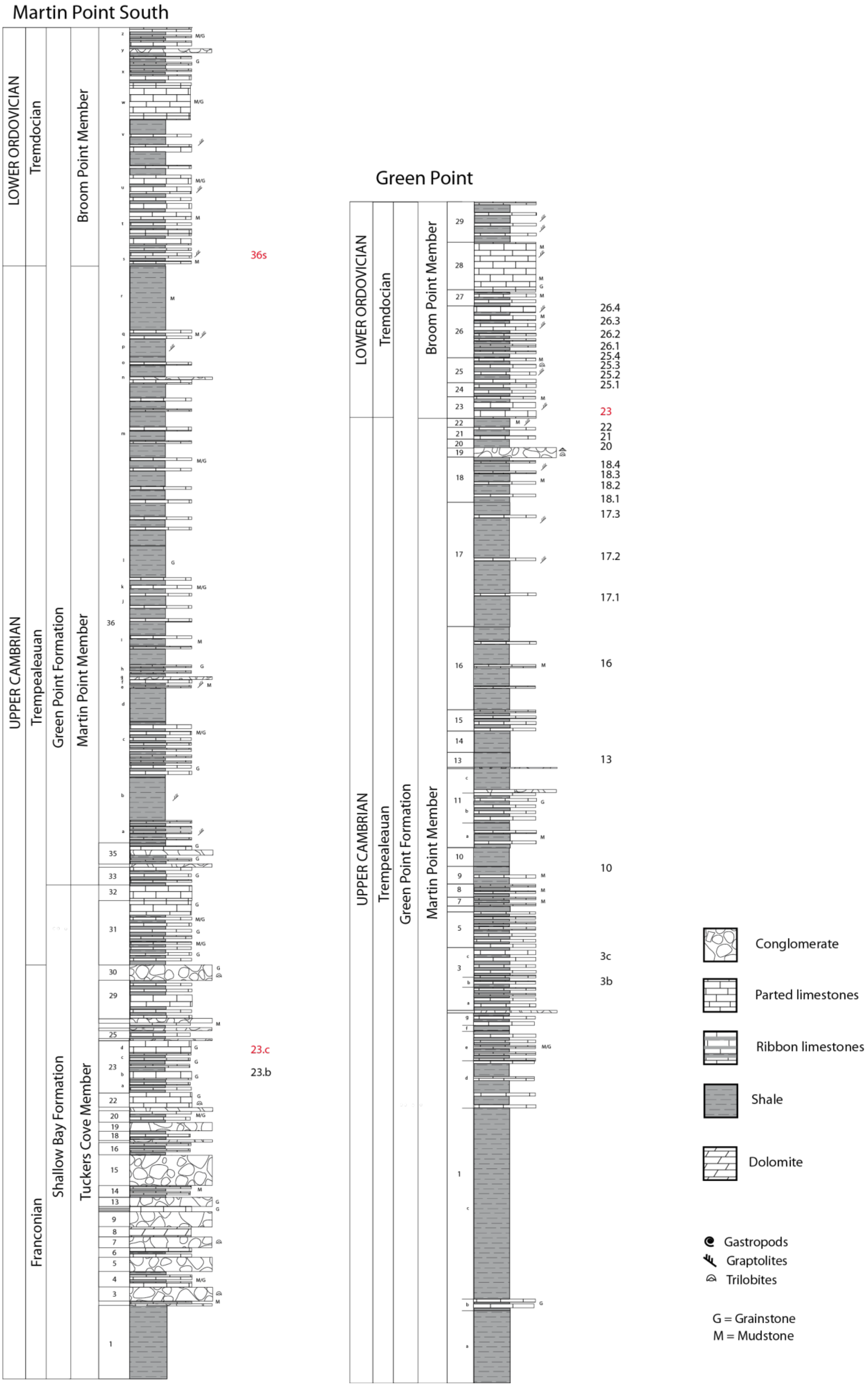


Figure 7 : Colonnes lithostratigraphiques des coupes de Green Point et de Martin Point South avec localisation des échantillons prélevés lors des deux missions de terrain.

Planche 1:

SECTION DE GREEN POINT

1) Photographie des affleurements de la section de Green Point regroupant des séries sédimentaires s'étendant du Cambrien supérieur à l'Ordovicien inférieur. La position de la limite Cambrien-Ordovicien est indiquée par un trait rouge (au niveau de l'unité 23)

2) Plaque commémorant la désignation en 2000 de l'affleurement de Green Point comme point stratotypique mondial marquant la base de l'étage Trémadocien et du système Ordovicien par la commission internationale de stratigraphie.

3) Unité 26 située dans le membre de Broom Point de la Formation de Green Point

4) Unité 23 située dans le membre de Broom Point de la Formation de Green Point. Elle représente la base du Trémadocien et la limite entre le Cambrien et l'Ordovicien

5) Echantillon 23 (indiqué par une flèche) prélevé sur un banc au sommet de l'unité 23, à 2 mètres au-dessus de la base de l'Ordovicien.

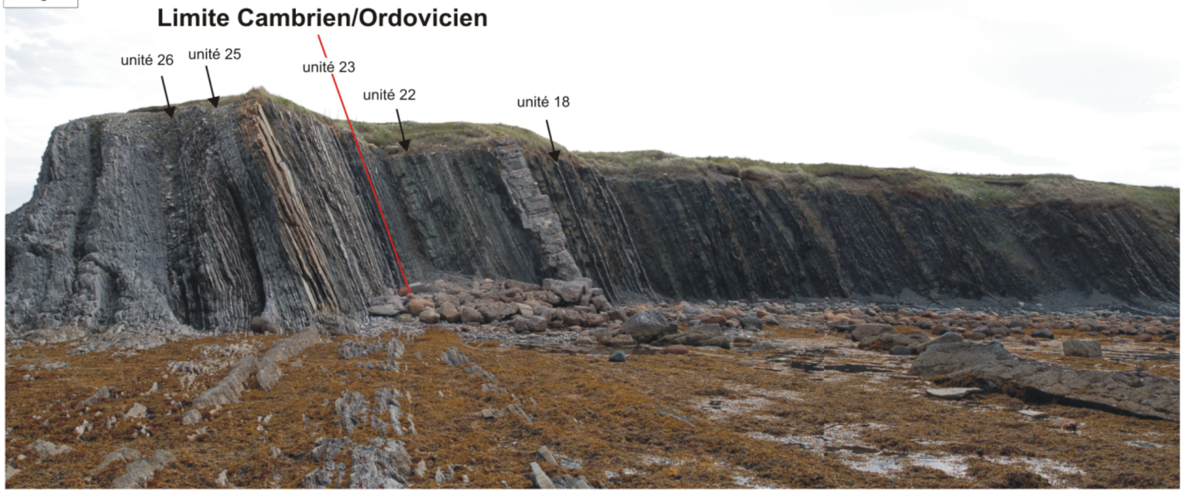
6) Echantillon 25.1, prélevé à la base de l'unité 25, environ 55cm au dessus du conglomérat marquant la base de l'unité.

7) Echantillon 18.1, prélevé sur le premier banc calcaire à partir du sommet de l'unité 18

8) Echantillon 22, prélevé sur le premier banc calcaire à partir de la base de l'unité 22, à environ 12 cm de la base

9) Base de l'unité 25 situé dans le membre de Broom Point de la Formation de Green Point dans laquelle apparaissent les premiers graptolites planctoniques

1)

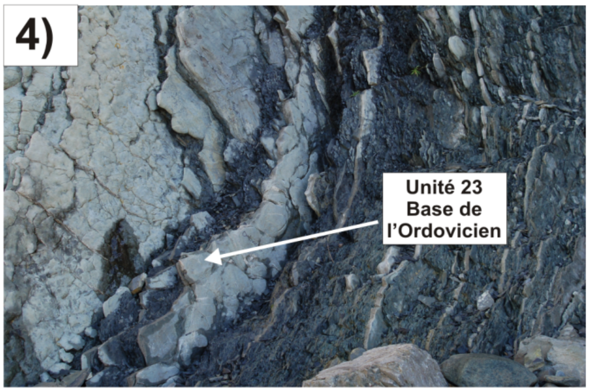

Limite Cambrien/Ordovicien
unité 26
unité 25
unité 23
unité 22
unité 18

2)

3)


Unité 26

4)


Unité 23
Base de
l'Ordovicien

5)


Unité 23

6)


Unité 25

7)


Unité 18

8)


Unité 22

9)


Unité 25

Planche 2:

SECTION DE MARTIN POINT SOUTH

1) Photographie des affleurements de la section de Martin Point situés à la base de l'Ordovicien.

2) On peut observer très nettement la présence d'une faille et de plissures (indiqués par des flèches) au sein de l'unité 36s, représentant la base du membre de Boorm Point et la base de l'Ordovicien sur la coupe de Martin Point South

3) Photographie de l'unité 22 située dans le membre de Tuckers Cove de la Formation de Shallow Bay, datées du franconien.

4) La flèche indique l'emplacement de l'unité 23 située dans le membre de Tuckers Cove de la Formation de Shallow Bay, datées du franconien.

5) Photographie de l'unité 21 située dans le membre de Tuckers Cove de la Formation de Shallow Bay, datées du franconien.

6) Zone faillée montrant la présence d'un graben au niveau de l'unité 20

7) Echantillon 36.s, prélevé environ 2 mètres au dessus de la base de l'unité 36s.

8) Echantillon 23b (=23.1), prélevé à 1 mètre 35 du sommet de l'unité 23

9) Echantillon 23c (=23.2), prélevé à 16 cm sommet de l'unité 23

1)

2)


Unité 36s

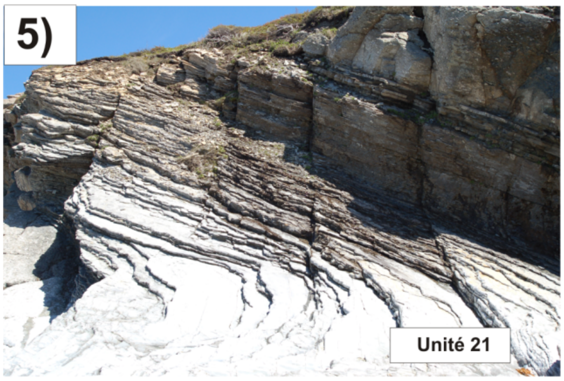
3)


Unités 22

4)


Unité 23

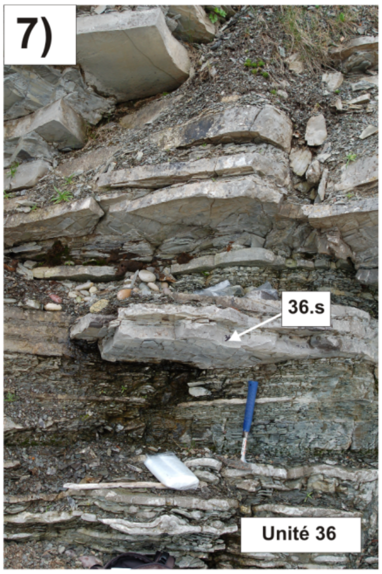
5)


Unité 21

6)


Unité 20

7)


36.s
Unité 36

8)


MP 23.1
23.1
Unité 23b

9)


MP 23.2
Unité 23c

Planche 3:

SECTION DE BROOM POINT SOUTH ET DE BROOM POINT NORTH

1) et 2) Vue du parc national de Gros Morne, site classé au patrimoine mondiale de l'humanité par l'UNESCO, situé à coté des affleurements du Groupe de Cow Head. Photographie prise de l'unité 62 de Broom Point South.

3) Photographie des affleurements du Cambrien supérieur de la section de Broom Point South

4) Photographie de l'unité 45 de la section de Broom Point South, située dans le membre de Broom Point de la Formation de Green Point, datées du Cambrien supérieur.

5) La flèche indique l'emplacement de l'échantillon 45.1, prélevé à la 1 m 30 de la base de l'unité 45.

6) La flèche indique l'emplacement de l'échantillon 45.5, prélevé à la 2 m 10 de la base de l'unité 45

7) Photographie de l'affleurement contenant les unités 55 à 60 de la section de Broom Point South

8) Photographie des affleurements de l'Ordovicien inférieur de la section de Broom Point North (Jörg Maletz donne l'échelle)

9) Photographie de l'unité 87 de la section de Broom Point North, située dans le membre de Broom Point de la Formation de Green Point, datées de l'Ordovicien inférieur.

10) Photographie de l'unité 82 de la section de Broom Point North, située dans le membre de Broom Point de la Formation de Green Point, datées de l'Ordovicien inférieur.

11) Photographies de l'unité 94 de la section de Broom Point North, située dans le membre de Broom Point de la Formation de Green Point, datées de l'Ordovicien inférieur.

12) et 13) Faune typique du parc national de Gros Morne, souvent présente sur les affleurements du Groupe de Cow Head.

1)

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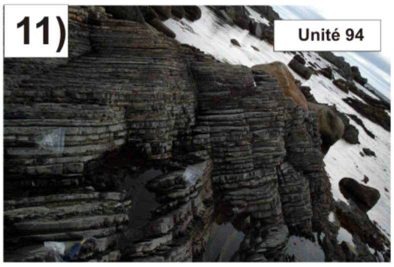
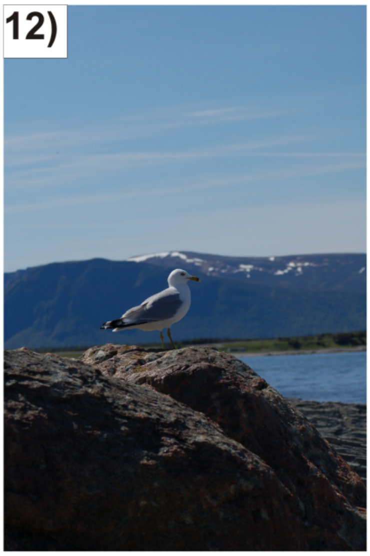


12)



13)

IV. Méthodes

Les divers échantillons calcaires de Terre-Neuve ont été préparés selon le protocole suivant : L'échantillon a été d'abord lavé et brossé puis rincé à l'eau distillée et séché avec un pistolet à air. Pour chaque échantillon, environ 150 à 200 grammes de roche ont été ensuite concassés au marteau en petits fragments de 1-5 cm afin de faciliter les attaques acides et homogénéiser l'échantillon. L'échantillon a été attaqué avec de l'acide acétique concentré à 10% pendant 12 à 24 heures, puis rincé plusieurs fois à l'eau distillée ; le résidu a été récupéré par un tamis de maille 50µm. L'opération a été répétée plusieurs fois jusqu'à destruction totale de la roche (le processus peut durer environ 1 à 2 semaines). Le rinçage a toujours été fait à l'aide d'un léger courant d'eau afin de ne pas détruire le squelette du radiolaire par une trop forte pression. Pour les échantillons très argileux, les résidus ont été filtrés une seconde fois dans une colonne de filtration munie d'un filtre en tissu de maille 50 µm afin d'éliminer les particules fines qui pourraient s'agréger sur le radiolaire au cours du séchage. Le résidu a été alors passé à l'étude à une température de 30 °c pour une durée de 24h. Une fois sec, le résidu a été récupéré dans un petit flacon en verre pour ensuite trier les radiolaires et les monter sur plots pour les étudier au MEB.

V. Résultats et discussion

L'étude de notre matériel nous a permis de mettre en évidence trois assemblages à radiolaires (*Subechidnina*, *Ramuspiculum* et *Protoentactinia kozuriana*) existant entre le Jiangshanian et le Trémadocien inférieur (Voir Article 2, partie 4. « Results » et partie 5.1 « Discussion- *Comparison with previously established radiolarian fauna from Western Newfoundland* »). L'étude des changements de diversité au sein des faunes à radiolaire menée sur notre matériel de Terre-Neuve nous a également permis de mettre en lumière l'existence de deux épisodes de changements fauniques intervenus localement au passage Cambrien-Ordovicien (Voir Article 2, partie 5.2 « Discussion- *Pattern of changes in diversity*»). Le premier épisode de changements fauniques intervient donc entre la base de la zone à conodontes *P. tenuiserratus* et la zone à conodontes *E. notchpeakensis* à la transition entre le Jiangshanian et l'Etage 10 du

Cambrien. Il comprend différentes réponses biotiques de la faune à radiolaire telles que des événements d'extinction au niveau spécifique et une chute importante de la diversité au sein de certains genres. Le second épisode intervient entre la base de la zone à conodontes *C. proavus* et la base de la zone à conodontes *C. linstromi* à la transition entre l'Etage 10 du Cambrien et la base du Trémadocien inférieur. Il montre des réponses biotiques aussi variées que des extinctions sélectives au niveau des genres mais aussi des renouvellements fauniques ainsi que des hausses importantes de diversité au niveau des espèces. L'origine de ces deux épisodes consécutifs de changements fauniques est encore très énigmatique et une étude comparée avec les changements fauniques intervenants dans les autres groupes planctoniques au Cambrien supérieur en Terre Neuve serait d'un intérêt non négligeable.

Nous savons que les différents évènements isotopiques enregistrés dans les isotopes stables du carbone (δ^{13} C_{carb}) témoignent de changements profonds dans le cycle du carbone et marquent donc des périodes de perturbations environnementales importantes pouvant être à l'origine d'importants changements biotiques. De nombreuses études ont déjà révélées que l'excursion isotopique du SPICE δ^{13} C_{carb} intervenant au Paibien (Steptoéen, à la base du Cambrien supérieur) marque le début d'importants changements fauniques chez d'autres groupes bien étudiés tels que les trilobites et ou le groupe planctonique des acritarches. En effet, le début de l'excursion isotopique du SPICE δ^{13} C_{carb} coïncide avec un événement d'extinction globale survenu au sein du groupe des trilobites (horizon d'extinction à *Pterocephaliid–Ptychaspid*) à la base de la zone à *Glyptagnostus reticulatus*, suivit d'un événement de diversification faunique corrélé avec le pic de cette même excursion isotopique (Palmer, 1965, 1984 ; Rowell et Brady, 1976 ; Peng *et al.*, 2004 ; Saltzman, 1999 ; Saltzman *et al.*, 2000). L'excursion isotopique du SPICE δ^{13} C_{carb} marque également une période importante de changements fauniques chez le groupe des acritarches avec l'apparition de nombreuses nouvelles morphologies notamment avec les premiers taxons diacromorphes et les acritarches 'galeates' (Servais *et al.*, 2008) ainsi que le début d'une importante augmentation de diversité.

Il est à noter que deux excursions isotopiques négatives très prononcées, nommées excursions de HERB et de TOCE, sont également présentes à l'échelle globale au Cambrien supérieur (Landing *et al.*, 2011 ; Fig. 8). Ces excursions négatives de la courbe isotopiques du δ^{13} C_{carb} sont en général associées à une diminution de la productivité et des évènements d'extinction (Servais *et al.*, 2008) .

L'excursion isotopique négative HERB $\delta^{13} C_{carb}$ dont l'enregistrement a pu être retrouvé en Terre-Neuve notamment dans la coupe de Green Point débute dans l'unité 5, à la base de la zone à conodontes *E. notchpeakensis* (= base de l'étage 10 du Cambrien) et atteint sa valeur négative maximale à la transition entre les unités 9 et 10, dans la partie inférieure de la zone à *E. notchpeakensis* (Ripperdan *et al*., 1992, 1993 ; Ripperdan et Miller, 1995 ; Cooper *et al*., 2001 ; Miller *et al*., 2011 ; Fig. 9).

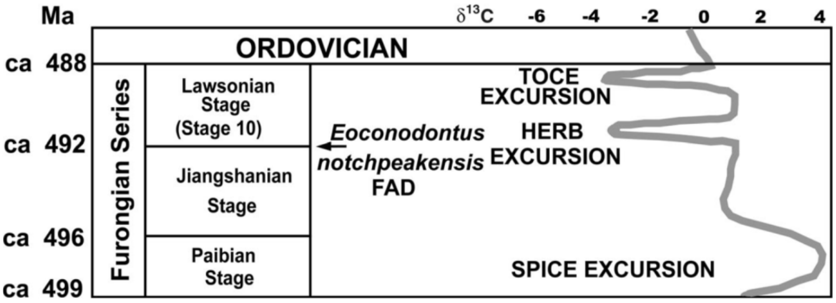


Figure 8 : Evolution de la courbe isotopique du $\delta^{13} C_{carb}$ au cours du Furongien, avec localisation des excursions isotopiques positives et négatives (d'après Landing *et al*., 2011).

Or, le premier épisode de changements fauniques enregistré dans notre matériel de Terre-Neuve intervient quelque part dans l'intervalle de temps séparant la base de la zone à conodontes *P. tenuiserratus* et la partie inférieure de la zone à conodontes *E. notchpeakensis* (dont la base n'a pas pu être identifiée précisément dans notre étude). Cet épisode de changements fauniques s'est donc mis en place à une période antérieure ou concomittante à l'excursion isotopique du HERB $\delta^{13} C_{carb.}$

L'excursion isotopique négative TOCE $\delta^{13} C_{carb}$ intervient quand à elle dans la partie supérieure de l'étage 10 du Cambrien supérieur, à la base de la zone à conodontes *C. proavus* (Zhu *et al*., 2007) et se termine à la base du Trémadocien (= base de la zone à conodontes *C. linstromi* ; Zhu *et al*., 2007). Il est intéressant de constater que le deuxième épisode de changements fauniques enregistré dans notre matériel de Terre-Neuve intervient quelque part dans l'intervalle de temps entre la base de la zone à conodontes *C. proavus* et la base de la zone à conodontes *C. linstromi*, marquant la transition entre l'Etage 10 du Cambrien et la base du Trémadocien inférieur. L'excursion isotopique négative TOCE $\delta^{13} C_{carb}$ est donc concomitante avec notre deuxième épisode de changements fauniques qui est notamment marquée par une extinction sélective au niveau des genres (Fig. 10). On peut donc penser que potentiellement, ces changements fauniques intervenus localement auraient pu être contemporains d'une période de perturbations environnementales ayant entrainé une diminution de la productivité comme le suggèrent la présence d'excursions négatives de la courbe isotopique du δ^{13} $C_{carb.}$

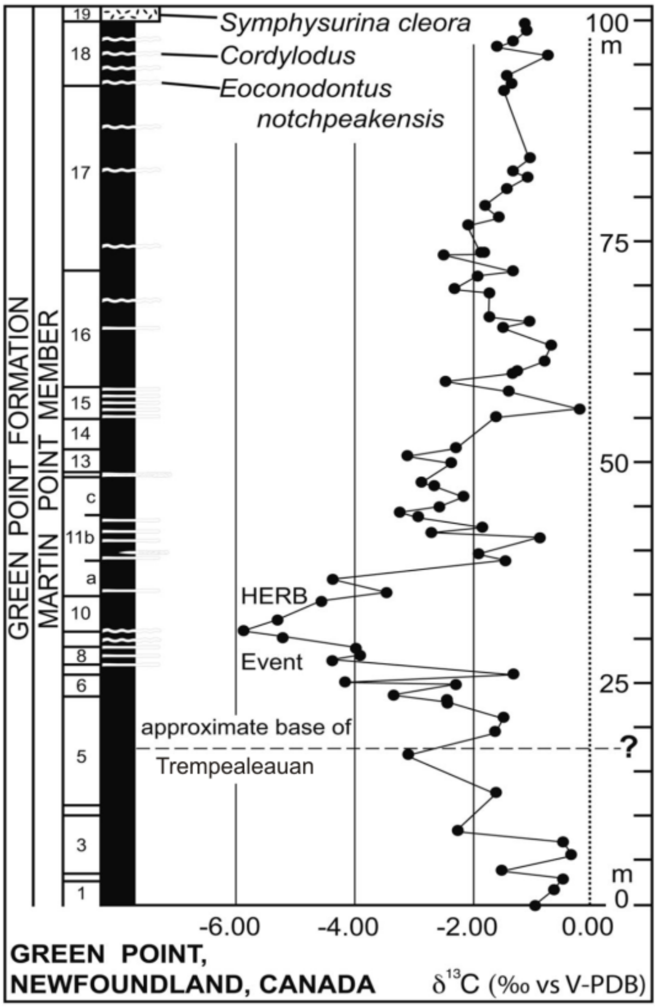


Figure 9 : Profil de la courbe isotopique du δ^{13} C_{carb} enregistrée sur la coupe de Green Point en Terre-Neuve occidentale avec localisation de l'excursion isotopique de HERB (modifiée d'après Miller *et al.*, 2011).

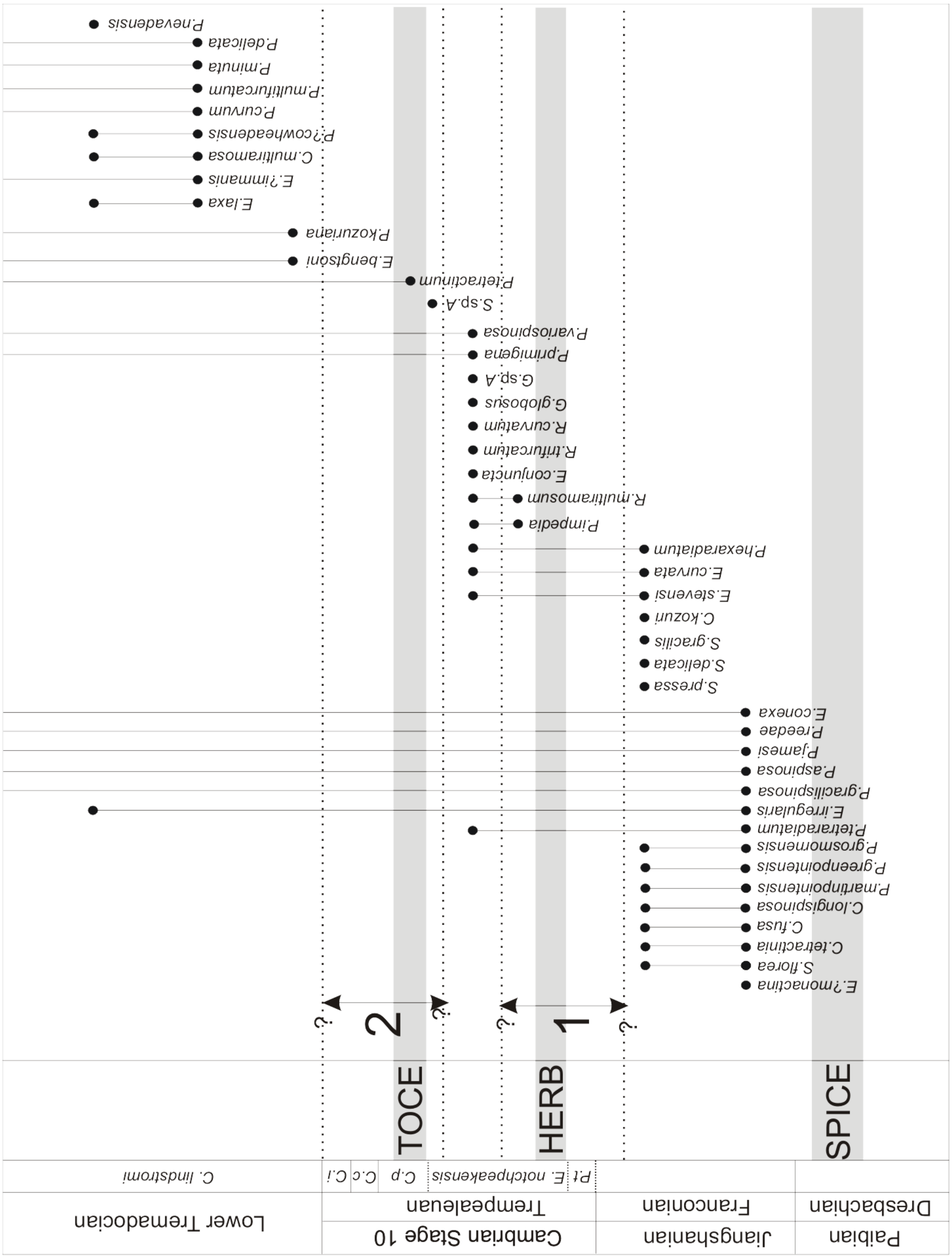


Figure 10 : Tableau de répartition stratigraphique des radiolaires de Terre-Neuve à la transition Cambrien supérieur-Ordovicien. Les zones grisées marquent les excursions isotopiques du δ^{13} C_{carb} (SPICE, HERB, TOCE) intervenues au cours de cet intervalle. Les intervalles temporels 1 et 2 caractérisent les 2 zones d'incertitude temporelle au cours desquelles se seraient déroulés les 2 épisodes de changements fauniques au niveau local : 1. Intervalle d'incertitude au sein duquel se produit le premier épisode de changements fauniques, 2. Intervalle d'incertitude au sein duquel se produit le deuxième épisode de changements fauniques.

Article 2:

The pattern of radiolarian diversity changes during the Late Cambrian-Early Ordovician transition as recorded in the Cow Head Group of Newfoundland (Canada)

Pouille, L., Danelian, T. & Maletz, J.

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Radiolarian diversity changes during the Late Cambrian-Early Ordovician transition as recorded in the Cow Head Group of Newfoundland (Canada)

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Abstract

Upper Cambrian to Lower Ordovician pelagic carbonate rocks of the Cow Head Group in western Newfoundland (Canada) were sampled for the study of their radiolarian fauna. Well-preserved and diverse faunal assemblages were obtained from a number of levels of the Shallow Bay and Green Point formations. Three different assemblages, including a total of five families, eight genera and 20 species, are recognized in three different sections situated on a palaeobathymetric profile. The various recognized assemblages are compared with previous studies conducted on the Cow Head Group; they improve considerably our understanding of the pattern of changes in radiolarian diversity during the Cambrian-Ordovician transition. The Radiolarian biotic record of western Newfoundland unveils a two step faunal change across the Cambrian-Ordovician transitional interval: one situated at the base of the uppermost Cambrian Stage 10 and the second at a poorly constrained interval situated towards the top of the same Stage 10. These biotic changes consist of genus-level selective extinctions, as well as within-clade species faunal-turnover (i.e. *Echidnina*, *Paleospiculum*), decrease of species abundance, species extinction and within-clade episodes of species diversification (i.e. *Protoentactinia*, *Parechidnina*).

Key-words Radiolaria, Cambrian, Ordovician, Newfoundland, Cow Head Group

1. Introduction

The continuous increase of marine biodiversity during the Ediacarian to Late Ordovician interval was fuelled by diversification bursts during the 'Cambrian Explosion' (Bottjer et al., 2000, 2001; Butterfield, 2001; Zhuravlev and Riding, 2001) and the 'Great Ordovician Biodiversification Event' (GOBE) (Miller, 2004; Webby et al., 2004; Harper, 2006; Servais et al., 2008, 2009). The latter resulted in the tripling of marine biodiversity and was accompanied by profound changes in the marine trophic chains (Harper, 2006).

Although animal life may have probably started to colonize hyperbenthic environments (situated above but close to the sea bottom) since the lower Cambrian (Vannier et al., 2007, 2009), colonization of the whole pelagic realm took place in the Ordovician (Vannier et al., 2003), a macroevolutionary event known as the 'Ordovician plankton revolution' (Servais et al., 2008).

However, our understanding of the pelagic trophic chains during this event is still very fragmentary. This is especially true for polycystine Radiolaria, a heterotrophic plankton lineage of Rhizaria, with fossil representatives known since the Early Cambrian (Botomian, Pouille et al., 2011), and present in the oceanic realm since at least the Late Cambrian (Tolmacheva et al., 2001). Indeed, more paleontological data are needed on this key biotic component of the Paleozoic plankton, especially during the Upper Cambrian-Lower Ordovician transitional interval.

The Cow Head Group crops out in Western Newfoundland (Canada, Fig. 1); it is a promising sedimentary sequence for integrated studies of several planktonic groups (i.e. radiolarians, graptolites, conodonts) present at the Cambrian-Ordovician transition interval. Moreover, the Global Stratotype Section and Point for the base of the Ordovician System is defined here (Green Point section; Cooper et al., 2001).

The relatively recent detailed studies conducted by Won and Iams (2002) and Won et al. (2005) established the presence of polycystine Radiolaria in both Upper Cambrian and Lower Ordovician (Tremadocian) sequences of the Cow Head Group. Since 2010, we undertook new field and laboratory studies with the intention to answer to the following questions:

What is the pattern of changes in radiolarian diversity across the Late Cambrian-earliest Ordovician?

What is the radiolarian biotic response across this critical interval and more particularly during the dawn of the "plankton revolution"?

2. Stratigraphic setting

The radiolarian faunas discussed in this paper were recovered from three sections of the Cow Head Group, located in the Great Northern Peninsula of Western Newfoundland, Canada (Fig. 1) displaying an upper Middle Cambrian to lower Middle Ordovician succession. The Cow Head Group is disposed as a series of allochthonous stack of thrust sheets at the northern end of the Humber Arm Allochthon (James and Stevens, 1986; Cooper et al., 2001). It displays a 300 to 500 m-thick sequence of deep-water deposits, which accumulated at the foot of a low-latitude Lower Paleozoic continental margin (James and Stevens, 1986; Cooper et al., 2001). The Cow Head Group is composed of a series of limestones, limestone conglomerates, shales

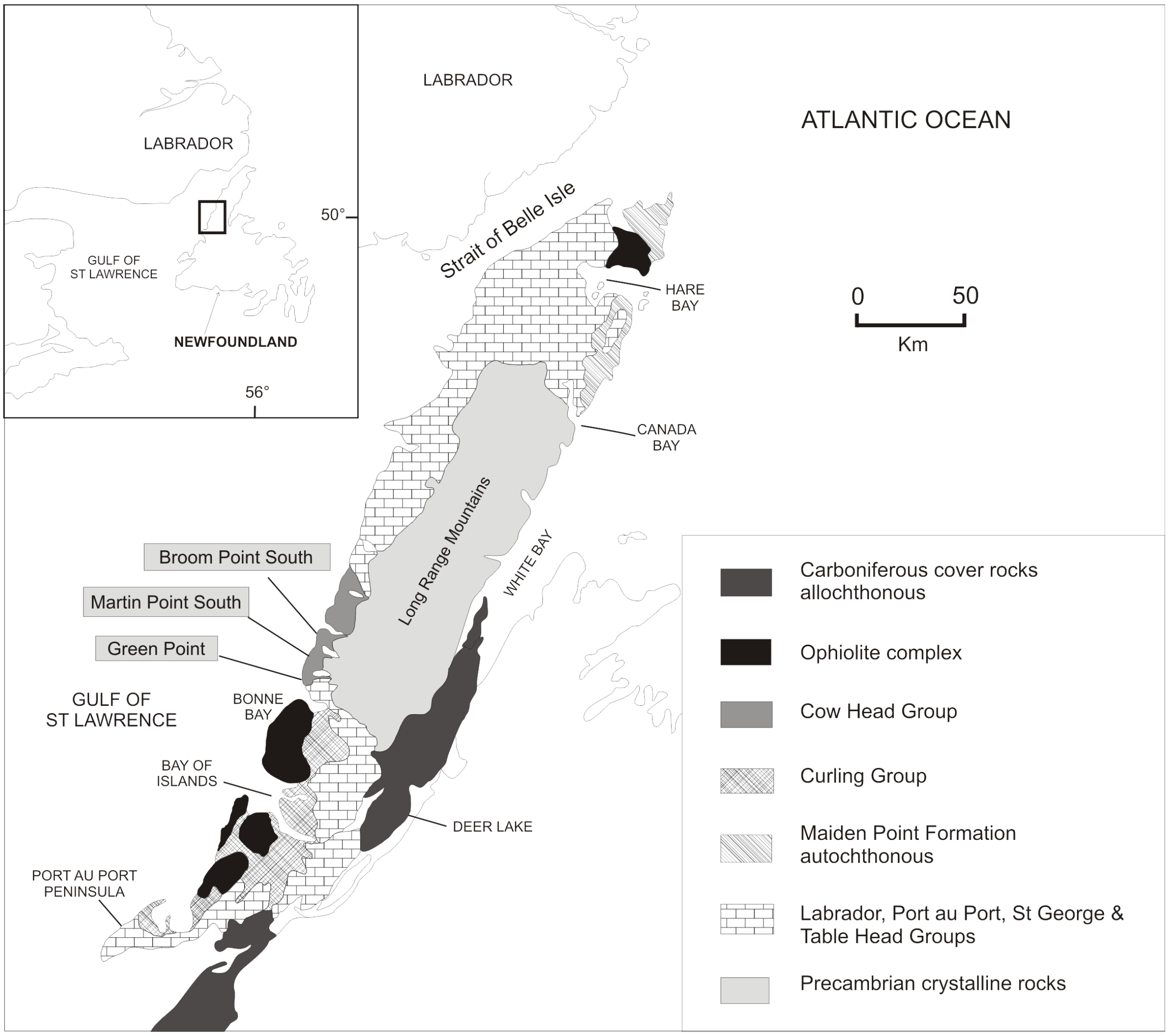

Fig. 1: Geological map of Western Newfoundland, including the allochthonous Cow Head Group and localization of the three radiolarian-bearing sections (modified from James and Stevens, 1986 and Cooper et al., 2001)

and rare sandstone beds, which contain an important fossil record of many Lower Paleozoic marine fossil groups (James and Stevens, 1986).

The general lithostratigraphic framework of the studied sequences is given below. For a more detailed stratigraphic description, including the biostratigraphic framework, the reader is refered to James and Stevens (1986) and especially to Williams and Stevens (1988, 1991).

In the Cow Head Group can be recognized five depositional intervals, which reflect changes of the shallow water platform sedimentation (James and Stevens, 1986).

It is divided into two nearly coeval formations and seven members (Fig. 2), four of which are part of the Shallow Bay Formation, while the other three compose the Green Point Formation. There is a clear NW-SE polarity, with the northwest sequence of the Shallow Bay Formation representing proximal sedimentary environments as opposed to the more distal facies of the southeast Green Point Formation, which represents the fine grained equivalent of the Shallow Bay Formation (*ibidem*).

The Shallow Bay Formation is a 100 to 300 m-thick sequence composed of a coarse-grained, conglomeratic facies and is subdivided into four members (Fig. 2):

- The Downes Point Member, a ca. 100 m-thick series of conglomerates with some intercalations of ribbon limestone/calcarenite (upper Middle to lower Upper Cambrian).
- The Tuckers Cove Member, a 60 m-thick series of quartzose calcarenites and conglomerates with minor intercalations of limestones, sandstones, siltstones and shales (Middle to Upper Cambrian, based on trilobites).
- The Stearing Island Member, a 80 m-thick series of megaconglomerates with rare intercalations of limestones, quartzose calcarenites and shales (uppermost Cambrian to Tremadocian, based on graptolites and conodonts).
- The Factory Cove Member, a 100 m-thick unit, composed essentially of limestones and minor intercalations of shales, punctuated by some beds of megaconglomerates (Middle Ordovician - Dapingian to Darriwilian, based on graptolites).

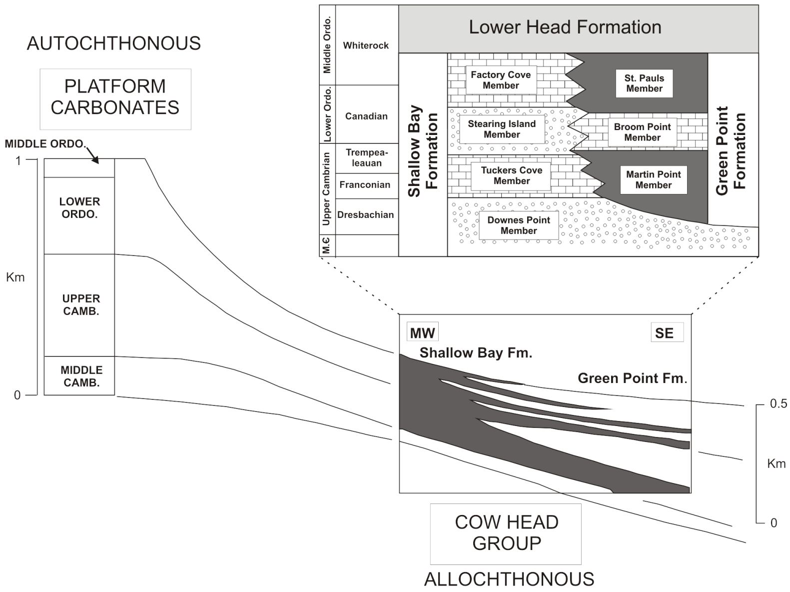

Fig. 2: Simplified sketch illustrating the different formations and members composing the Cow Head Group and their approximate position on the carbonate platform slope at the time of deposition, showing the NW-proximal (Shallow Bay Formation) to SE-distal (Green Point Formation) polarity (modified from James and Stevens, 1986).

The Green Point Formation is contemporaneous to the Shallow Bay Formation. It is a 400 to 500 m-thick sequence of fine grain rocks, subdivided in three members (Fig. 2):

- The Martin Point Member, a 100 to 150 m-thick sequence composed mainly of black shales, with intercalations of limestones, siltstones, calcareous sandstones and a few thin beds of conglomerates (Late Cambrian).
- The Broom Point Member, a 80 m-thick sequence composed predominantly of limestones with rare intercalations of siltstones, sandstones and conglomerates (uppermost Cambrian to Lower Tremadocian based on graptolites and conodonts; Cooper et al., 2001).
- The St. Pauls Member, a 130 to 150 m-thick unit of varicoloured shales intercalated by ribbon limestones and few beds of thin limestone conglomerates, siltstones and dolomites (middle/upper Tremadocian to lower Darriwilian, largely dated by well preserved graptolite faunas; Williams and Stevens, 1988).

The Green Point Formation overlies the lower parts of the Shallow Bay Formation at some transitional localities (e.g. Broom Point South section, Martin Point South section). The distal Martin Point Member is mostly contemporaneous with the proximal Tuckers Cove Member of the Shallow Bay Formation. The two members were both deposited under euxinic conditions (James and Stevens, 1986). The Broom Point Member is a distal equivalent to the proximal Stearing Island Member. They record a period of extensive deep-water carbonate sedimentation associated with the establishment of well-oxygenated deep-water conditions on the seafloor (*ibidem*).

3. Material and Methods

3.1. Material

Three sections, extending from the Middle Cambrian to Lower Ordovician, have been sampled in the Cow Head Group; these are the Martin Point South, Broom Point South and Green Point sections. Broom Point South represents the most proximal and Green Point the most distal section (Fig. 3). A total of 65 samples were collected as detailed below (Fig. 4), with the mentioned unit numbers following the designation of James and Stevens (1986):

- 24 samples were collected from Green Point section (GP); they come from units 3, 10, 13, 16, 17, 18, 20, 21 and 22 of the Martin Point Member (Green Point Formation) and from units 23, 25 and 26 of the Broom Point Member (Green Point Formation).

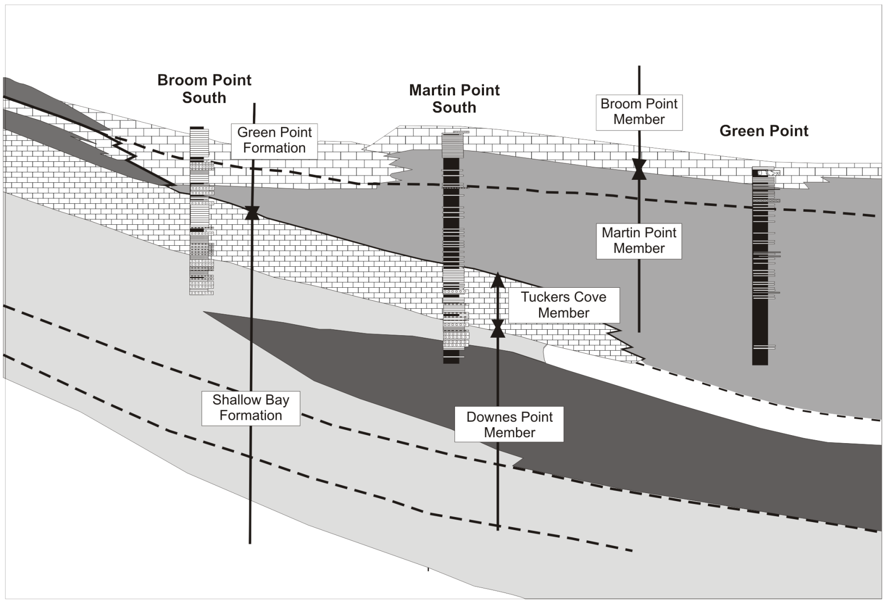

Fig. 3: Simplified sketch illustrating the position of Green Point, Martin Point South and Broom Point South sections on an interpretive, restored cross-section of the Cambrian to Lower Ordovician Cow Head Group strata (modified from James and Stevens, 1986).

- 38 samples were collected from Broom Point South section (BPS); they come from units 3, 5, 7, 8 and 10 of the Downes Point Member (Shallow Bay Formation), from units 21, 22, 24, 35, 36 and 40 of the Tuckers Cove Member (Shallow Bay Formation) and from units 45, 46, 48, 50, 54, 55, 60 and 62 of the Broom Point Member (Green Point Formation).
- 3 samples from Martin Point South section (MP); they were collected from unit 23 of the Tuckers Cove Member (Shallow Bay Formation), and from unit 36s of the Broom Point Member (Green Point Formation).

Productive samples, containing well-preserved radiolarians, sponge spicules and rare conodonts, were recovered from six different units (Figs. 4 and 5). In the Martin Point South section, radiolarian-bearing samples were recovered from the limestones of unit 23 (Tuckers Cove Member, Shallow Bay Formation) and from lime mudstones of unit 36s (Broom Point Member, Green Point Formation). Unit 23 is considered to be Franconian in age based on trilobites found in boulders overlying unit 30 and the absence of any index species of the lowermost Trempealeauan *Proconodontus tenuiserratus* conodont Zone (Won and Iams, 2002). Since *P. tenuiserratus* is found in unit 31, the boundary between the Franconian and the Trempealeauan is placed between units 30 and 31, both situated stratigraphically above unit 23 (*ibidem*). Unit 36s is dated as early Tremadocian in age based on the radiolarian

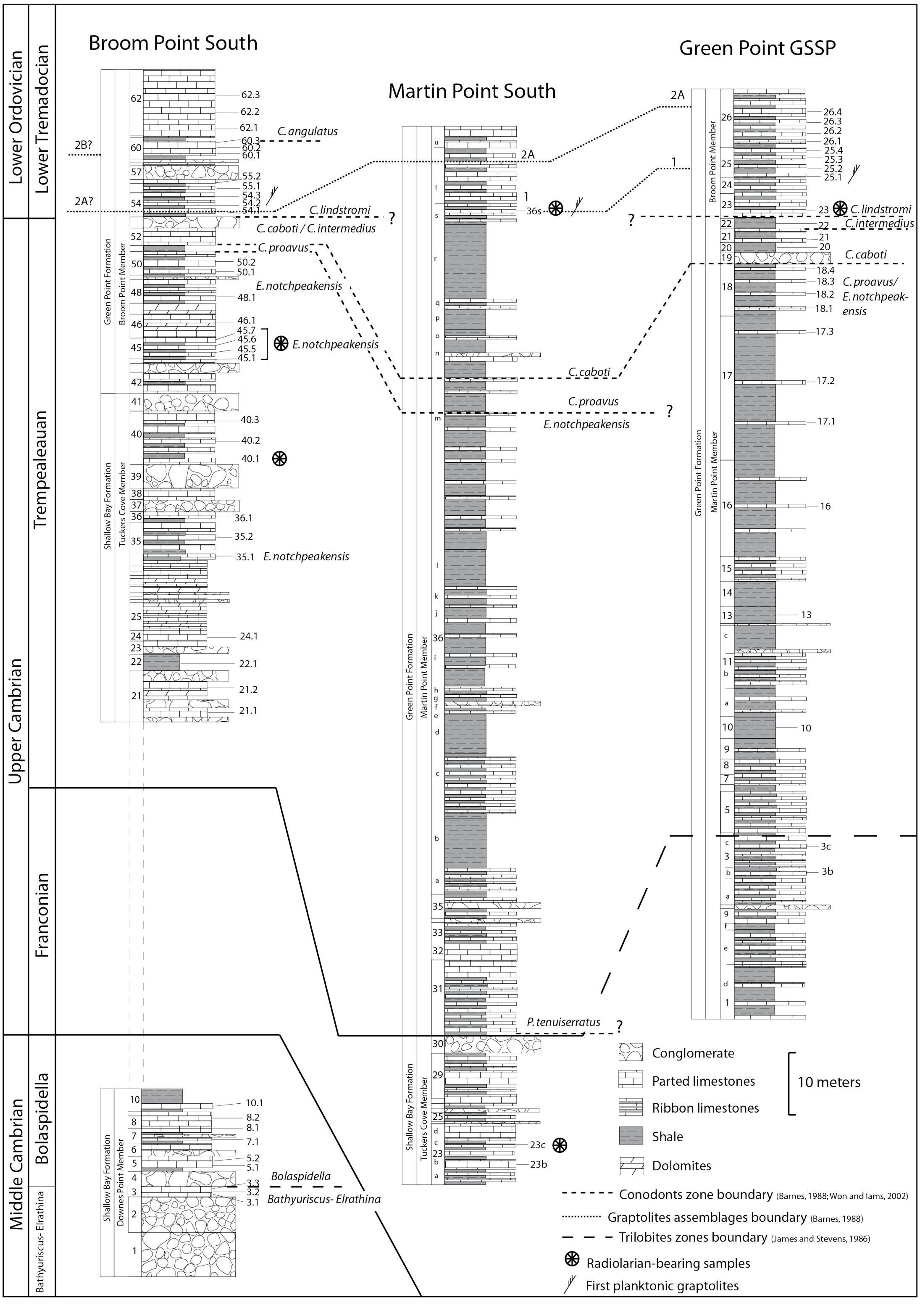

Fig. 4: Stratigraphic columns of the three studied sections from Cow Head Group which display the lithologic changes, the position of studied samples and the Cambrian-Ordovician boundary. It also shows the biostratigraphic correlations based on conodonts, trilobites, graptolites (after Cooper, 1979, Cooper et al. 1998) and first planktonic graptolites (based on the data of Barnes, 1988; James and Stevens, 1986; Won and Iams, 2002). Lithostratigraphic assignment of the studied sections follows James and Stevens (1986).

assemblage found by Won and Iams (2002) which, biostratigraphically, corresponds to the radiolarian assemblages found within the conodont *Cordylodus lindstromi* Zone (Lower Tremadocian age) in the Green Point section (Barnes, 1988; Won and Iams, 2002). This correlation is also supported by the presence of the graptolite *Rhabdinopora flabelliformis* and *Staurograptus dichotomus* (found 1m above the base of unit 36s) and *R*. cf. *praeparabola*, *R*. cf. *parabola* and *Aletograptus* (found in unit 36s) indicative of the graptolite Assemblage 1 of Cooper (1979) and Cooper et al. (1998), which can be correlated with the *C. lindstromi* Zone (Barnes, 1988; James and Stevens, 1986).

In the Broom Point South section productive samples were recovered from parted to ribbon limestones of unit 40 (Tuckers Cove Member, Shallow Bay Formation) and from ribbon lime grainstones of unit 45 (Broom Point Member, Green Point Formation). These units are dated as Trempealeauan in age based on conodonts characteristic of the *Eoconodontus notchpeakensis* Zone found in units 35 and 45 (Barnes, 1988; Fortey et al., 1982; Won and Iams, 2002).

In the Green Point section a productive sample was recovered from ribbon limestones situated at the upper part of unit 23 (Broom Point Member, Green Point Formation). These strata are dated as lowermost Tremadocian in age as they are situated within the *C. lindstromi* Zone and just above the Cambrian-Ordovician boundary defined by the FAD of the conodont *Iapetognathus fluctivagus* situated in the middle of unit 23 (Cooper et al., 2001). The Cambrian-Ordovician boundary is defined precisely here, as Green Point represents the Global Stratotype Section and Point for the base of the Ordovician System.

3.2. Methods

More than 2600 specimens were extracted from the radiolarian-bearing samples (Fig. 3) after standard treatment with diluted acetic acid. For each sample, about 150 to 200g of rock were crushed each time into small fragments of 1-5cm size in diameter; they were soaked into 10% diluted acetic acid for a maximum of 24 hours. After washing out the acid, the sample residues were sieved through a 50µm sieve and radiolarian specimens were mounted on SEM stubs. The entire radiolarian fauna found during this study is housed in the public palaeontological collections of the Earth Sciences Department (SN5) of the University of Lille-1 (France). USTL numbers correspond to the number of the SEM stub in Lille collection/specimen n° on the stub. Unless mentioned differently in chapter 4b, taxonomic concepts used during this study follow those of Won and Iams (2002) and Won et al. (2005).

4. Results

4.1. Identified Radiolarian assemblages

Five families, eight genera and 20 species were identified in our material (their occurrence and number of specimens are given in Table 1). Three different radiolarian assemblages were recognized from the Franconian to Lowermost Tremadocian interval (Fig. 6) as follows:

- *Subechidnina* assemblage: This fauna was extracted from unit 23 of the Martin Point South section and is Franconian in age. It is characterized by species *Subechidnina florae* Won and Iams, 2002*, Echidnina stevensi* Won and Iams, 2002*, Echidnina irregularis* Won and Iams, 2002*, Echidnina curvata* Won and Iams, 2002 and *Pararcheoentactinia reedae* gr. Won and Iams, 2002 (Plate 1). It is dominated at 97% by representatives of the family Echidninidae (i.e. *Echidnina* and *Subechidnina*; Fig. 6), with nearly half of the assemblage being composed of species *Echidnina irregularis* (45%).

- *Ramuspiculum* assemblage: This fauna was extracted from units 40 and 45 of the Broom Point South section and is Trempealeauan in age. It displays a very diverse fauna, characterized by the presence of species *Echidnina curvata* Won and Iams, 2002*, Parechidnina variospinosa* Won et al, 2005, *Protoentactinia primigena s.s.* Won et al, 2005 and of genera *Grosmorneus* and *Ramuspiculum* (Plates 2 and 3). Two-thirds of this fauna are equally dominated by representatives of the Archeoentactiniidae (i.e. *Pararcheoentactinia reedae* gr.) and Echidninidae (i.e. *Echidnina*; Fig. 6). The rest of the fauna is composed of Aspiculidae (i.e. *Parechidnina* 26%), Palaeospiculidae (i.e. *Ramuspiculum* 10%) and Protoentactiniidae (i.e. *Protoentactinia* 5%).

- *Protoentactinia kozuriana* assemblage: This fauna was recovered from unit 36s of the Martin Point South section and unit 23 of the Green Point section; it is earliest Tremadocian in age and characterized by species *Protoentactinia kozuriana s.s.* Won et al, 2005 and *Echidnina bengtsoni* Kozur et al, 1996, in addition to abundant *Echidnina conexa* Won et al, 2005 (Plates 4 and 5). The fauna is largely dominated by representatives of the families Echidninidae (i.e. *Echidnina conexa*; Fig. 6) and Protoentactinidae (i.e. *Protoentactinia kozuriana s.s.* and *P. gracilispinosa* Kozur et al, 1996).

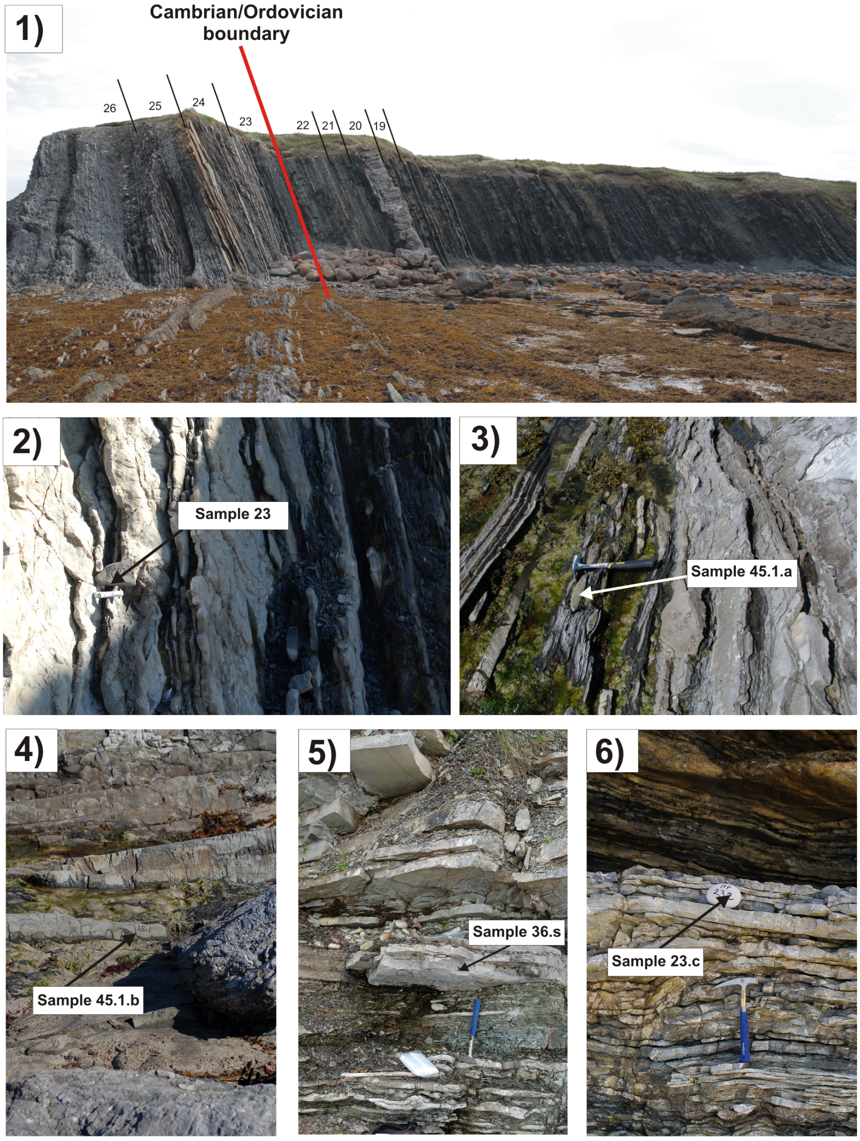

Fig. 5: 1) Outcrop photograph of Upper Cambrian to Lower Ordovician sedimentary sequences exposed in Green Point section (GSSP for the base of the Ordovician). The different units around the critical interval of the Cambrian-Ordovician transition are also delimited (units 19-26). 2) The arrow indicates the position of the radiolarian-bearing sample 23, coming from a Lowermost Tremadocian limestone bed situated at the top of unit 23 of Green Point section. 3) and 4) Pictures of the Upper Cambrian (Trempealeauan) sequence at the base of unit 45 of the Broom Point south section. Arrows point to the radiolarian-bearing samples 45.1a and 45.1b. 3) Sample 45.1a was collected from a limestone nodule intercalated in shales situated at ca. 60 cm from the base of unit 45 and 4) Sample 45.1b was collected from a thin limestone bed situated at ca. 1.30 m above the base of unit 45. 5) Picture of the Lowermost Ordovician (base of Tremadocian) sequence of sub-unit 36.s located at the top of unit 36 of Martin Point south section. The arrow points to radiolarian-bearing sample 36.s, coming from a limestone bed situated about 2 m above the base of the sub-unit 36.s. 6) Picture of the lower Upper Cambrian (Franconian) sequence of sub-unit 23.c located in the middle of unit 23, from Martin Point south section. The arrow indicates the position of the radiolarian-bearing sample 23.c, collected from a limestone bed situated at 16 cm below the top of unit 23.

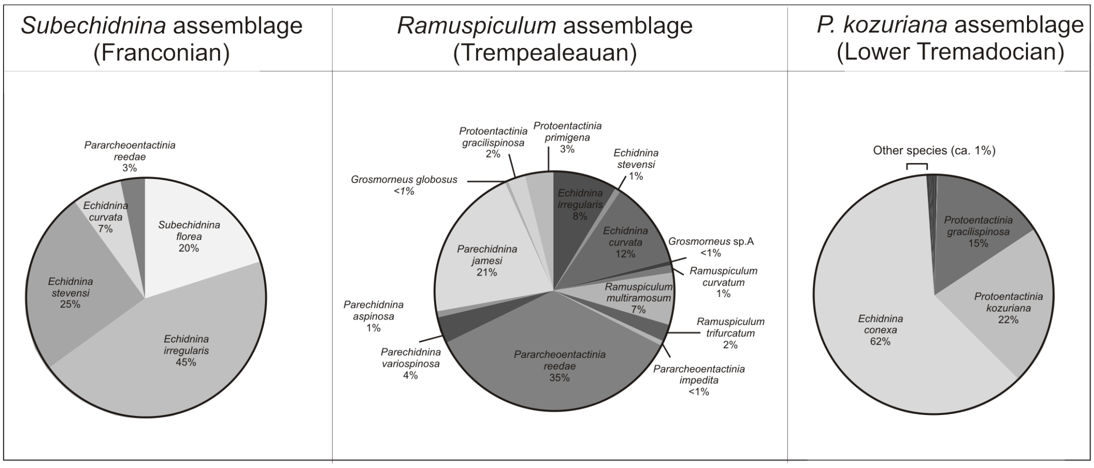

Fig. 6: Pie-diagrams displaying the % relative abundance of radiolarian taxa in each one of the three radiolarian assemblages present in our material.

		Upper Cambrian						Lower Ordovician	
Regional stages	Franconian	Trempealeauan						Lowermost Tremadocian	
Locality	*Martin Point South*	*Broom Point South*						*Green Point*	*Martin Point South*
Sample number	23c	40.1	45.1 a	45.1 b	45.5	45.6	45.7	23	36s
Radiolarian assemblage	*Subechidnina*	*Ramuspiculum*						*Protoentactinia kozuriana*	
Subechidnina florea Won and Iams, 2002	14								
Echidnina irregularis Won and Iams, 2002	27	3	5	11	1				
Echidnina curvata Won and Iams, 2002	4	9	5	21			1		
Echidnina stevensi Won and Iams, 2002	15	1		1	1				
Grosmorneus globosus Won and Iams, 2002				1					
Grosmorneus sp. A *in* Won and Iams, 2002				1		1			
Ramuspiculum curvatum Won and Iams, 2002				2	1		1		
Ramuspiculum multiramosum Won and Iams, 2002		2	7	16	1				
Ramuspiculum trifurcatum Won and Iams, 2002			5	8	1				
Pararcheoentactinia ? impedita Won and Iams, 2002				2					
Pararcheoentactinia reedae gr. Won and Iams, 2002	2	3	62	112		30			1
Parechidnina variospinosa Won *et al.*, 2005			3	4		6			3
Parechidnina aspinosa s.l. Won *in* Won and Below, 1999			1	2		1			2
Parechidnina jamesi Won and Iams, 2002		1	17	55	1	13		7	1
Paleospiculum multifurcatum Won *et al.*, 2005								1	
Protoentactinia gracilispinosa Kozur *et al.*, 1996, *sensu* Won et al., 2005			6	4				312	2
Protoentactinia primigena s.s. Won *et al.*, 2005			4	12					6
Protoentactinia kozuriana s.s. Won *et al.*, 2005								444	
Echidnina conexa Won *et al.*, 2005; emend.								1256	
Echidnina bengtsoni Kozur *et al.*, 1996								9	

Table 1: Occurrence and abundance table of Late Cambrian to Early Ordovician radiolarian taxa extracted from the radiolarian-bearing samples recovered from Green Point unit 23, Martin Point South units 23c and 36s and Broom Point South units 40 and 45.

4.2. Systematic paleontology

Class: RADIOLARIA Müller, 1858
Order: POLYCYSTINA Ehrenberg, 1838; emend. Riedel 1967
Suborder: ARCHAEOENTACTINARIA Dumitrica et al., 2000
Family: Echidninidae Kozur, Mostler and Repetski, 1996

Genus: *Echidnina* Bengtson, 1986, emend. Won and Iams, 2002
Type species: *Echidnina runnegari* Bengtson, 1986, p. 202.

Echidnina conexa Won et al., 2005
Plate 5, figs 1-29

2002 *Echidnina* sp.*;* Won and Iams, p.26, Figs 12.15-12.16
2005 *Echidnina conexa* n.sp.; Won et al.,; p.447, Figs 3.14-3.16a-b
2005 *Echidnina semiconexa* n.sp.; Won et al.,; p.447, Figs 3.7-3.12
2005 *Echidnina severedeformis* n.sp.; Won et al.,; p.449, Figs 4.7-4.8a-b

Material: 1256 specimens from sample 23 of the Green Point section.
Emended diagnosis: A compact spherical skeleton consisting of spicules whose rays are fused to form a latticed meshwork. The rays of the spicule may range from slightly fused at their meeting point to strongly modified, due to a significant intergrowth of neighbouring fused rays. The inner surface of the shell is more or less smooth. No rays intrude into the inner space of the shell as they are tangentially arranged to the inner surface of the shell meshwork.
Description: The skeleton consists of numerous six-rayed point-centred spicules, packed densely together in such a way to form a hollow shell meshwork. All specimens are made of more or less fused spicules forming a latticed meshwork. The specimens vary from slightly fused at their ray meeting points to strongly modified by intergrowth of fused rays. The rays pass tangentially to the inner surface and when fused, display a smooth inner structure. The free ends of the rays, directed outwardly, can be more or less short. The spicules can be spiny on some specimens, certainly due to preservation (Plate 5, fig. 1b).
Discussion: Although Won et al. (2005) considered a possible affinity between *E. conexa* and *E. semiconexa*, they distinguished the former by its smoother inner surface, shorter protruding

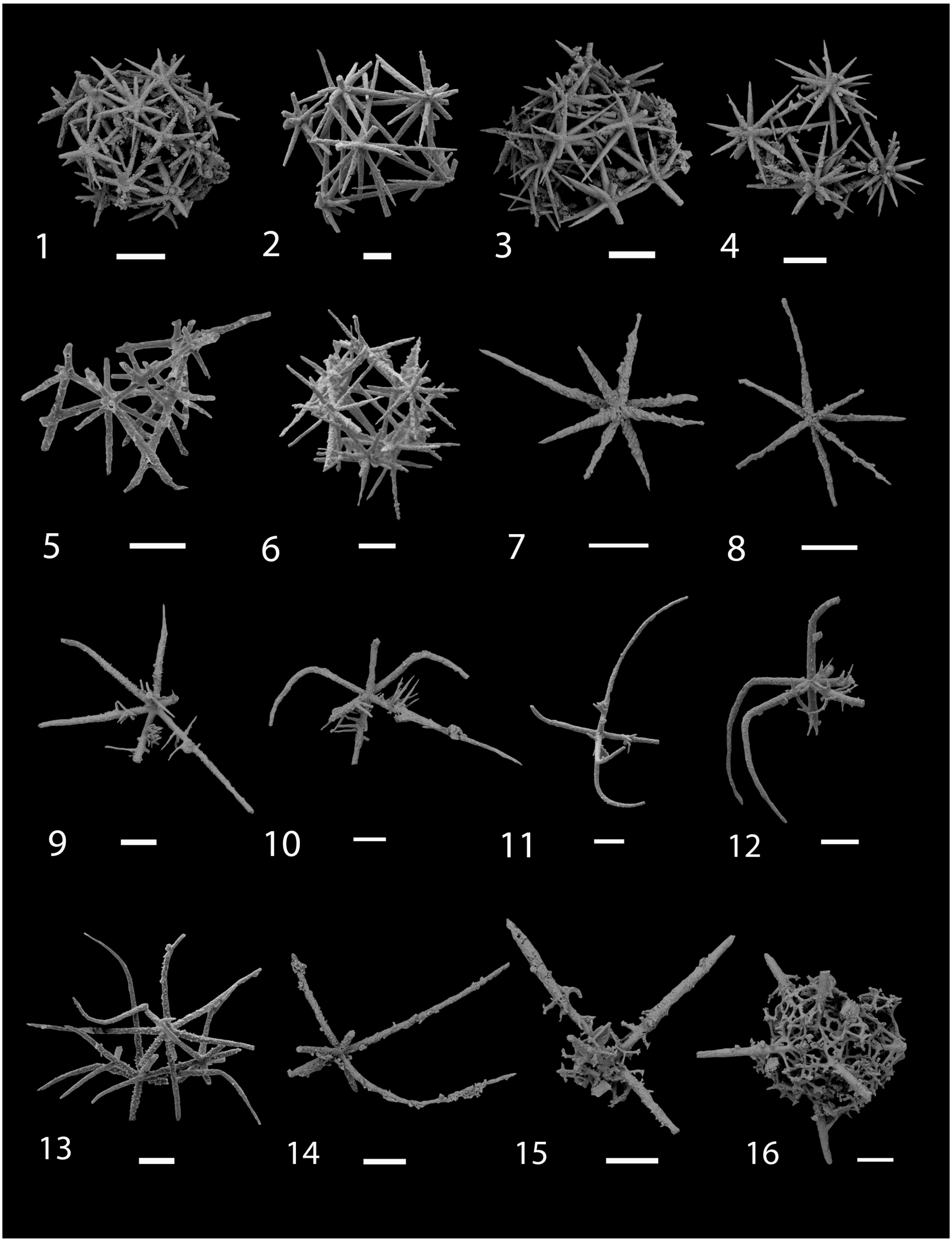

Plate 1: Scanning Electron Micrographs of radiolarian species characteristic of the Franconian *Subechidnina* assemblage. All specimens were recovered from sample 23c of Martin Point South section. Scale bar corresponds to 50 µm on all figures. 1-4, *Subechidnina florea*; 5-8, *Echidnina irregularis*; 9-12, *Echidnina stevensi*; 13-14, *Echidnina curvata*; 15, *Pararcheoentactinia reedae*.

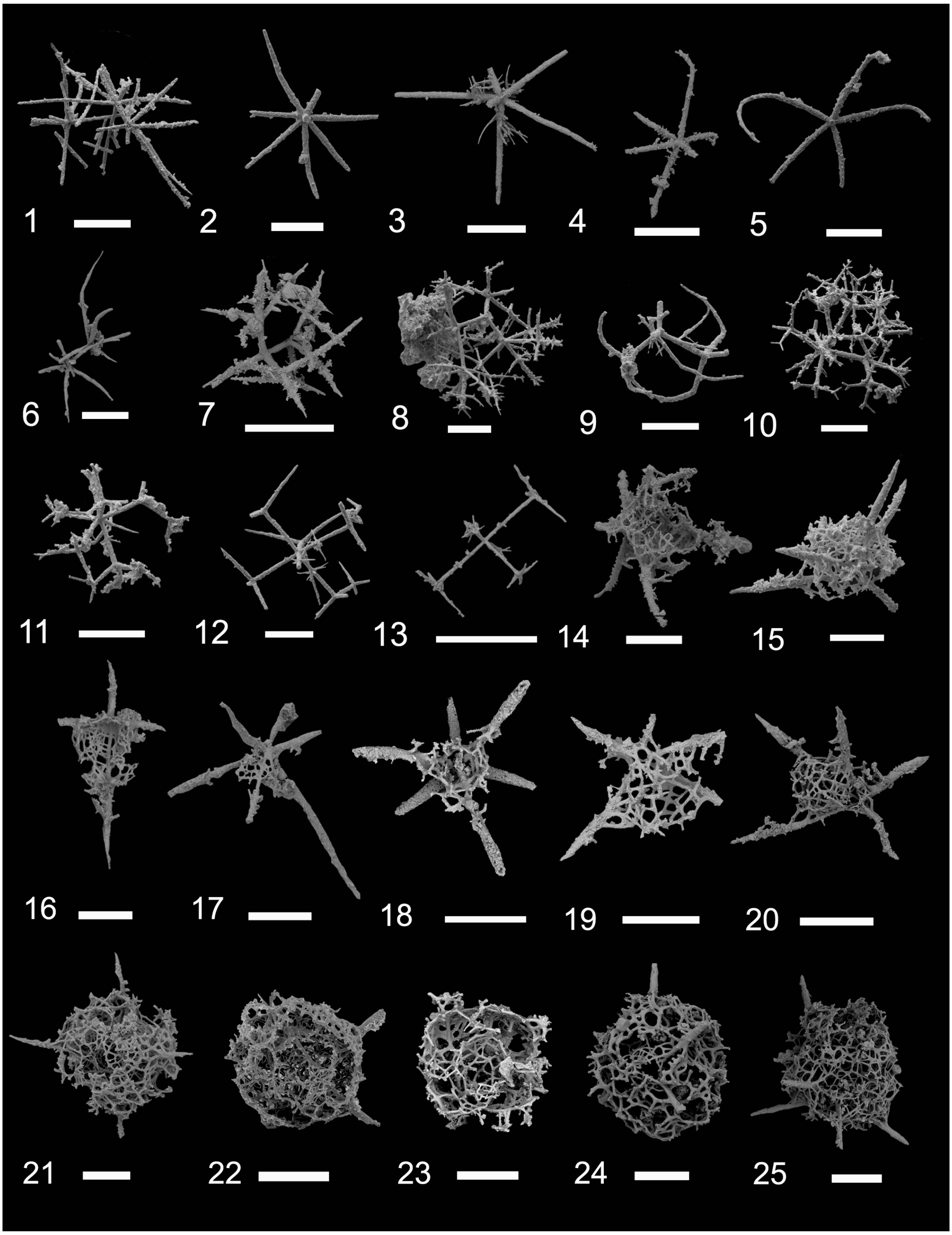

Plate 2: Scanning Electron Micrographs of radiolarian specimens yielded from the Trempealeauan *Ramuspiculum* assemblage. All illustrated specimens come from sample BP45.1 (Broom Point South section), with the exception of fig. 4-5 that come from sample BP40.1, fig. 9 from sample BP45.5, fig. 7, 19 and 22 from sample BP45.6. Scale bar corresponds to 100 µm on all figures. 1-2, *Echidnina irregularis*; 3-4, *Echidnina stevensi*; 5-6, *Echidnina curvata*; 7, *Grosmorneus* sp. A; 8, *Grosmorneus globosus*; 9, *Ramuspiculum curvatum*; 10-11, *Ramuspiculum multiramosum*; 12-13, *Ramuspiculum trifurcatum*; 14-15, *Pararcheoentactinia impedita*; 16-25, *Pararcheoentactinia reedae*; 16-20 Juvenile specimens; 21-25, Mature specimens.

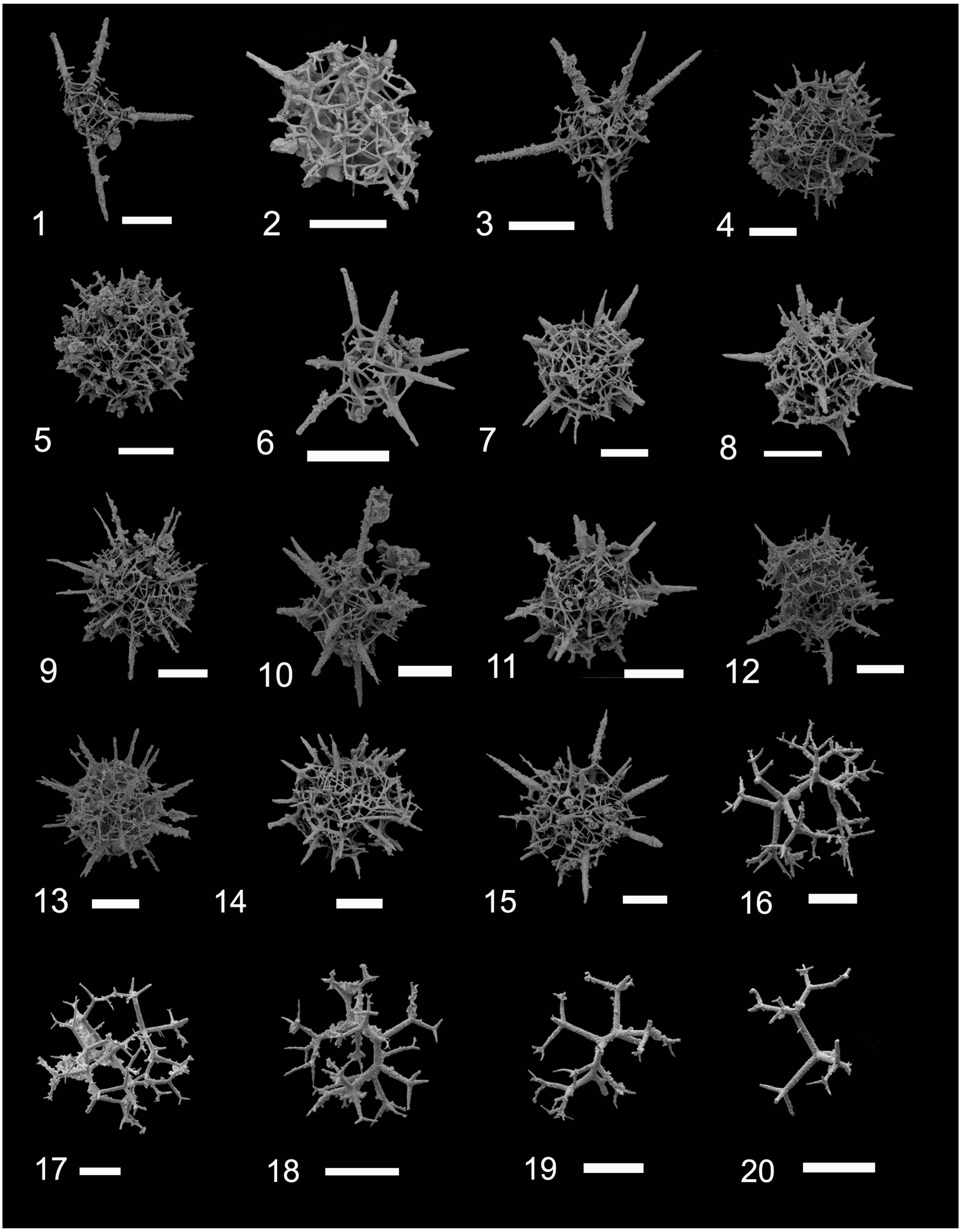

Plate 3: Scanning Electron Micrographs of radiolarian species yielded from the Trempealeauan *Ramuspiculum* assemblage. All illustrated specimens come from sample BP45.1 (Broom Point South section), with the exception of fig. 4, 1-3 and 18 that come from sample BP45.6. Scale bar corresponds to 100 µm on all figures. USTL numbers correspond to n° of the SEM stub in Lille collection/specimen n° on the stub. 1-3, *Parechidnina variospinosa;* 1,3, juvenile specimens ; 2, Mature specimen ; 4-5, *Parechidnina aspinosa*; 6-15, *Parechidnina jamesi;* 6, Juvenile specimen ; 7-15, Mature specimens ; 16-18, *Protoentactinia gracilispinosa*; 19-20, *Protoentactinia primigena* .

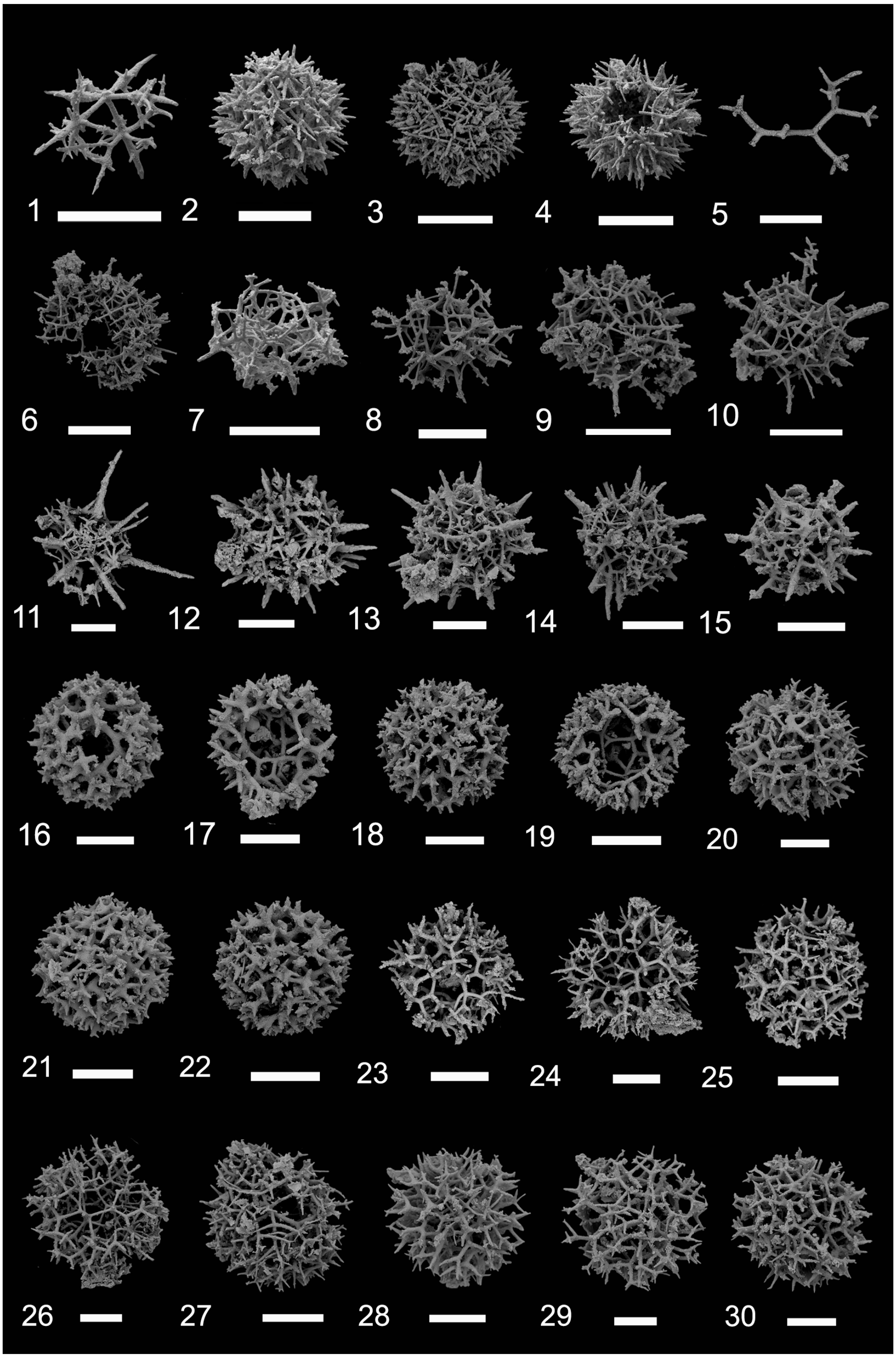

Plate 4: Scanning Electron Micrographs of radiolarian species yielded from the lowermost Tremadocian *Protoentactinia kozuriana* assemblage. All illustrated specimens come from sample GP23 (Green Point section) with the exception of fig. 5-6 and 8-10 that come from sample MP36s (Martin Point South section). Scale bar corresponds to 100 µm on all figures. 1, *Paleospiculum multifurcatum*; 2-4, *Echidnina bengtsoni*; 5, *Protoentactinia primigena*; 6-8, *Parechidnina aspinosa*; 9-10, *Parechidnina variospinosa*; 11-15, *Parechidnina jamesi*; 16-22, *Protoentactinia kozuriana*; 23-30, *Protoentactinia gracilispinosa*.

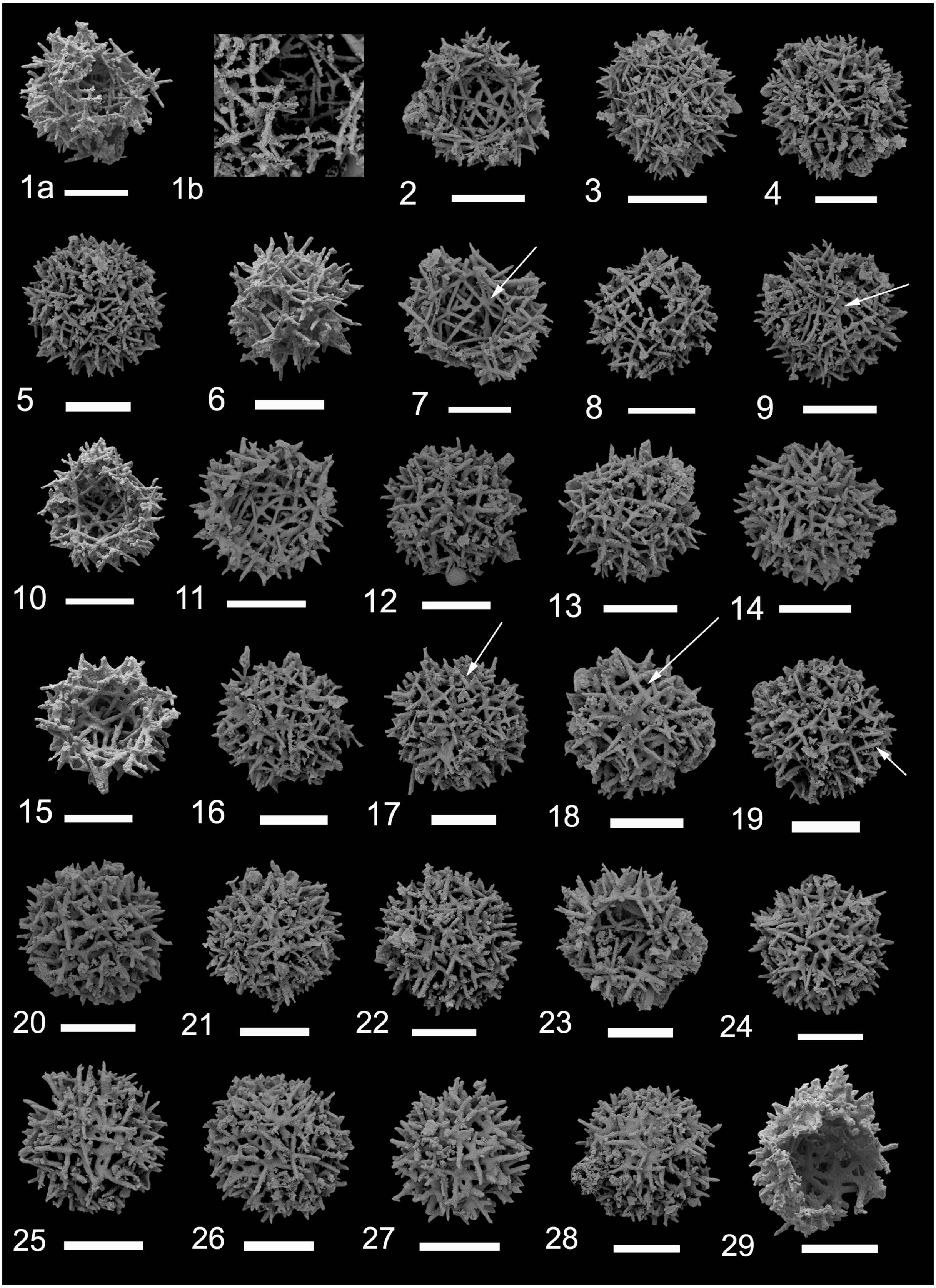
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Plate 5: Scanning Electron Micrographs of *Echidnina conexa* yielded from the lowermost Tremadocian *Protoentactinia kozuriana* assemblage. All specimens were recovered from sample 23 of the Green Point section. Scale bar corresponds to 100 µm on all figures. USTL numbers correspond to n° of the SEM stub in Lille collection/specimen n° on the stub. 1-29, *Echidnina conexa*; 1a, 2, 3,4, morphotypes which display rays fused only at their contact points as in *Echidnina semiconexa*; 1b, magnified view of figure 1a, showing spiny spicules (1-USTL2203/01; 2- USTL2207/02; 3-USTL2207/03; 4- USTL2208/04); 5-19, intermediate morphotypes between simply fused rays showing at some places rare modified spicules numerous modified rays and rare rays only fused at their contact points; arrows on fig. 7 and 9 point to modified spicules, while those on fig. 17, 18 and 19 point to rare rays that are only fused at their contact points while the majority of rays are intergrown. (5-USTL2206/05; 6- USTL2203/06; 7-USTL2204/07; 8- USTL2206/08; 09-USTL2204/09; 10-USTL2203/10; 11- USTL2204/11; 12-USTL2204/12; 13-USTL2204/13; 14- USTL2207/14; 15-USTL2204/15; 16- USTL2203/16; 17-USTL2206/17; 18-USTL2205/18; 19-USTL2207/19); 20-24, morphotypes which display strongly modified spicules with intergrowth of silica as in *Echidnina conexa* (20-USTL2206/20 ; 21-USTL2203/21; 22- USTL2206/22; 23-USTL2206/23; 24- USTL2207/24); 25-29, morphotypes which display an importantly developed intergrowth of silica as in *Echidnina severedeformis* (25-USTL2206/25; 26-USTL2206/26; 27- USTL2206/27; 28-USTL2205/28; 29-USTL2206/29).

rays and modified spicules. However, they also stressed that some specimens of *E. semiconexa* appear to consist of modified spicules due to numerous fused contact points and they may display short rays. Won et al. (2005) distinguished *E. severedeformis* by the extensive intergrowth of its fused rays leading to a compact shell structure.

Our material displays intermediate morphotypes between these three species, all of them present in the same sample (GP23). Some specimens display rays fused only at their contact points (Plate 5, fig.1-4), as in typical *E. semiconexa sensu* Won et al. (2005); others display strongly modified spicules with intergrowth of silica (Plate 5, fig. 21-25), as in *E. conexa sensu* Won et al. (2005). Numerous intermediate morphotypes are also found in our material, ranging from specimens with simply fused rays showing at some places rare modified spicules due to intensive fusion (Plate 5, fig. 7, 9) to specimens of numerous modified rays which possess rare rays only fused at their contact points (Plate 5, fig. 17-19). Morphotypes corresponding to *E. severedeformis sensu* Won et al. (2005) may also be regarded as a highly modified form of *E. conexa* (Plate 5, fig. 25-29) possessing an extensively developed intergrowth of silica. Finally, all of the three morphotypes considered by Won et al. (2005) as distinct species are found together in the same assemblage, which is an additional argument to consider them as a single species.

5. Discussion

5.1. Comparison with previous data from W. Newfoundland

Won and Iams (2002) and Won et al. (2005) recognized nine different radiolarian assemblages from the Franconian to lower Tremadocian strata of the Cow Head Group. Three of them are described from the Franconian; assemblages RA 1 and RA 2 were extracted from units 1e and 3a (respectively) of the Green Point section, while RA 3 was recovered from both unit 3c of the Green Point section and unit 23c of the Martin Point South section. Our Franconian *Subechidnina* assemblage is chronostratigraphically coeval to assemblage RA3 of Won and Iams (2002). In our material, assemblage RA 3 is dominated by echidninids (77% of the entire fauna) and it is characterized by the presence of abundant *Subechidnina* and *Echidnina*. All species present in our *Subechidnina* assemblage were also recovered from assemblage RA 3 of Won and Iams (2002). However, the latter provides a more complete insight to the levels of Radiolarian diversity during the Franconian, since it also records the presence of sixteen additional species (Fig. 7); this includes abundant *Pararcheoentactinia reedae*, *Subechidnina pressa*, *S. delicata* and *S. gracilis*, which compose a large part of assemblage RA 3. We here consider assemblages RA 1, RA 2 and RA 3 of Won and Iams (2002) as part of the same assemblage; indeed, out of the 16 species present in their assemblage RA 1, thirteen are also present in RA 3. Their assemblage RA 2 consists of only 5 rare species, all present in both of their assemblages RA 1 and RA 2. Therefore, we have chosen to assign all three Franconian assemblages of Won and Iams (2002) and ours to one single assemblage characterized by the occurrence of genus *Subechidnina* and *Curvechidnina* (Fig. 7). Species *Subechidnina florea* is very abundant; it is consistently present in all radiolarian-bearing strata recovered from the Franconian and it may be revealed in the future to be a useful marker species for the Franconian. *Echidnina irregularis* and *Echidnina stevensi*, although present in younger strata, are particularly abundant to the Franconian levels of the Cow Head Group. Various species of genus *Paleospiculum* appear also to be restricted in the Franconian (Fig. 7).

Regarding the Trempealeauan, three different assemblages (RA 4, RA 5 and RA 6) were described by Won and Iams (2002). Our Trempealeauan *Ramuspiculum* assemblage is coeval with their assemblages RA 5 and RA 6, since they are all extracted from units 40 and 45 of the Broom Point South section. Assemblages RA 4 and RA 5 of Won and Iams (2002) are composed of only two and seven rare species (respectively), all of which are abundantly present in assemblage RA 6. Therefore, we consider that both assemblages RA 4 and RA 5 represent a depauperate fauna of RA 6. The latter shares a fairly similar number of species with our *Ramuspiculum* assemblage; they are both dominated by representatives of the families Echidninidae and Archeoentactiniidae, although to a lesser extent than in the Franconian. Indeed, the 2 families account for 62% of the total fauna in our assemblage and for 76% of the RA 6 assemblage of Won and Iams (2002). The diversity recorded in the two latter assemblages is complementary, since assemblage RA 6 of Won and Iams (2002) includes rare specimens of the species *Echidnina conjuncta*, *E. conexa*, *Paleospiculum hexaradiatum* and *P. tetraradiatum*, while our *Ramuspiculum* assemblage contains also the species *Echidnina stevensi*. It is worth noting that the genus *Pararcheoentactinia* represents nearly one third of the fauna in both our *Ramuspiculum* assemblage and RA 6 of Won and Iams (2002). Therefore, we consider that all four assemblages recorded in the Trempealeauan *Eoconodontus notchpeakensis* Zone belong to one single assemblage (*Ramuspiculum* assemblage, Fig. 7), characterized by the presence of genera *Ramuspiculum* and *Grosmorneus*. We can also notice the extreme rarity of genus *Subechidnina*, which although dominant in the Franconian assemblage, it is hardly detectable in the *Ramuspiculum* Assemblage. Won et al. (2005) also reported a single specimen of *Subechidnina* sp. from the Upper Cambrian unit 18 of the Green Point section.

Finally, Won et al. (2005) distinguished three different radiolarian assemblages (TRA 1, TRA 2 and TRA 3) from the Lower Tremadocian strata of the Cow Head Group. Our *Protoentactinia kozuriana* assemblage is comparable to their assemblage TRA 1 extracted from unit 25 at Green Point and unit 78 at Broom Point North. Assemblage TRDA 3 is largely dominated by *Echidnina* (representing 62% of the fauna), followed by *Protoentactinia* (representing 37% of the assemblage), whereas TRA 1 is dominated by *Protoentactinia* (63%), followed by *Echidnina* (36%); it is composed at about 98% of one single species: *Echidnina conexa*. By comparison with TRA 1 assemblage, our fauna lacks five species (*Protoentactinia minuta*, *Curvechidnina multiramosa*, *Echidnina irregularis*, *E. laxa* and *E.*? *immanis*), which are however quite rare in assemblage TRA 1, representing in total less than 5% of the fauna. We consider that the assemblages TRA 1 and TRA 2 of Won et al. (2005) represent one single assemblage, since they have similar faunal composition and are both largely dominated by the species *Protoentactinia gracilispinosa* and *Echidnina conexa*. Their assemblage TRA 3 contains a very similar fauna (except for two species the faunal composition is similar) to the one recorded in their assemblages TRA 1, TRA 2, and our *Protoentactinia kozuriana* assemblage. However, it also differs by being largely dominated by representatives of *Parechidnina* (38% of the assemblage) and *Pararcheoentactinia* (36%), and especially by *Pararcheoentactinia reedae*; whereas the assemblage TRA 3 of Won et al. (2005) is characterized by the abundant presence of *Parechidnina nevadensis*. For this reason we regard the assemblage TRA 3 as being distinct from the *P. kozuriana* assemblage (Fig. 7).

5.2. Pattern of changes in diversity

Based on our data and on those published by Won and Iams (2002) and Won et al. (2005), Figure 7 synthesizes the age range of all known radiolarian species in Newfoundland during the upper Cambrian – lowermost Tremadocian interval, in a biochronostratigraphic framework provided by associated conodonts and graptolites. Diversity analysis at genus level reveals the step-by-step extinction of three out of nine Late Cambrian genera recorded before the Cambrian-Ordovician boundary. More specifically, the genera *Ramuspiculum*, *Grosmorneus* and *Subechidnina* recorded in the *E. notchpeakensis* Zone (Late Trempealeauan) are all absent from the basal Tremadocian *C. lindstromi* Zone strata. It is worth noting that no new genera appear in the Early Ordovician. Regarding the genus *Ramuspiculum*, only one specimen, (identified as *R.* sp. A), is known from the Lower Tremadocian (Won et al., 2005). However, since this specimen displays bifurcated rays (*Ramuspiculum* bears trifurcated rays), it is here considered as an unidentified Paleospiculidae (rather than a specimen assigned to genus *Ramuspiculum*).

At species level, one can notice an important faunal turnover at the local scale during the Cambrian-Ordovician transition interval. Out of the 22 species recorded from the Franconian and 21 species from the Trempealeauan, only nine are still present in the Lower Ordovician. This faunal turnover is highlighted by two successive steps of changes in diversity as detailed below.

(1) A first episode of faunal turnover is recorded in the lowermost Trempealeauan of Newfoundland, between the base of the *P. tenuiserratus* and the base of the *E. notchpeakensis* conodont Zones, with the extinction of 12 out of the 22 species known from the Franconian. This first step of changes in diversity is marked by a number of important within-clade extinctions. More particularly, the genus *Subechidnina*, which

passed from four very common species in the Franconian to only one single specimen of *Subechidnina* (identified as *S.* sp.A) that is found in the Late Trempealeauan *E. notchpeakensis*/*C. proavus* Zone. It also records a severe diversity decrease of the genus *Paleospiculum*, with the extinction of three out of its five Franconian species and a wipeout of the Franconian species of genus *Curvechidnina*. A significant decrease in the abundance of the species *Echidnina irregularis* and *Echidnina stevensi* is also worth noting.

(2) After this first step of faunal changes, two genera (*Ramuspiculum* and *Grosmorneus*) and nine species occur for the first time in the *E. notchpeakensis* Zone. A second faunal turnover is recorded during the late Trempealeauan-earliest Tremadocian of Newfoundland (during the interval situated between the base of the *C. proavus* and the base of the *C. lindstromi* Zones). This is first highlighted by the extinction of 12 species (out of a total of 19 present previously) and the selective extinction of three genera (*Ramuspiculum*, *Subechidnina* and *Grosmorneus*) at the top of the *E. notchpeakensis* Zone and/or the base of the *C. proavus* conodont Zones. It is also well illustrated by the within-clade diversity pattern of the species of *Echidnina*, an important taxonomic component of Franconian to Tremadocian radiolarian assemblages. More specifically, out of the five *Echidnina* species present in the Trempelauean *E. notchpeakensis* Zone, three went extinct and two survived into the Lower Tremadocian *C. lindstromi* Zone, where they co-occur with three newly appeared *Echidnina* species. A complete species turnover is also recorded within the genus *Paleospiculum*; more specifically, two of its species, still present in the *E. notchpeakensis* Zone, appear to go extinct and followed by the appearance of three new species. The genus *Curvechidnina*, although completely absent from the *E. notchpeakensis* Zone, reappears in the Lower Tremadocian *C. lindstromi* Zone with one new species.

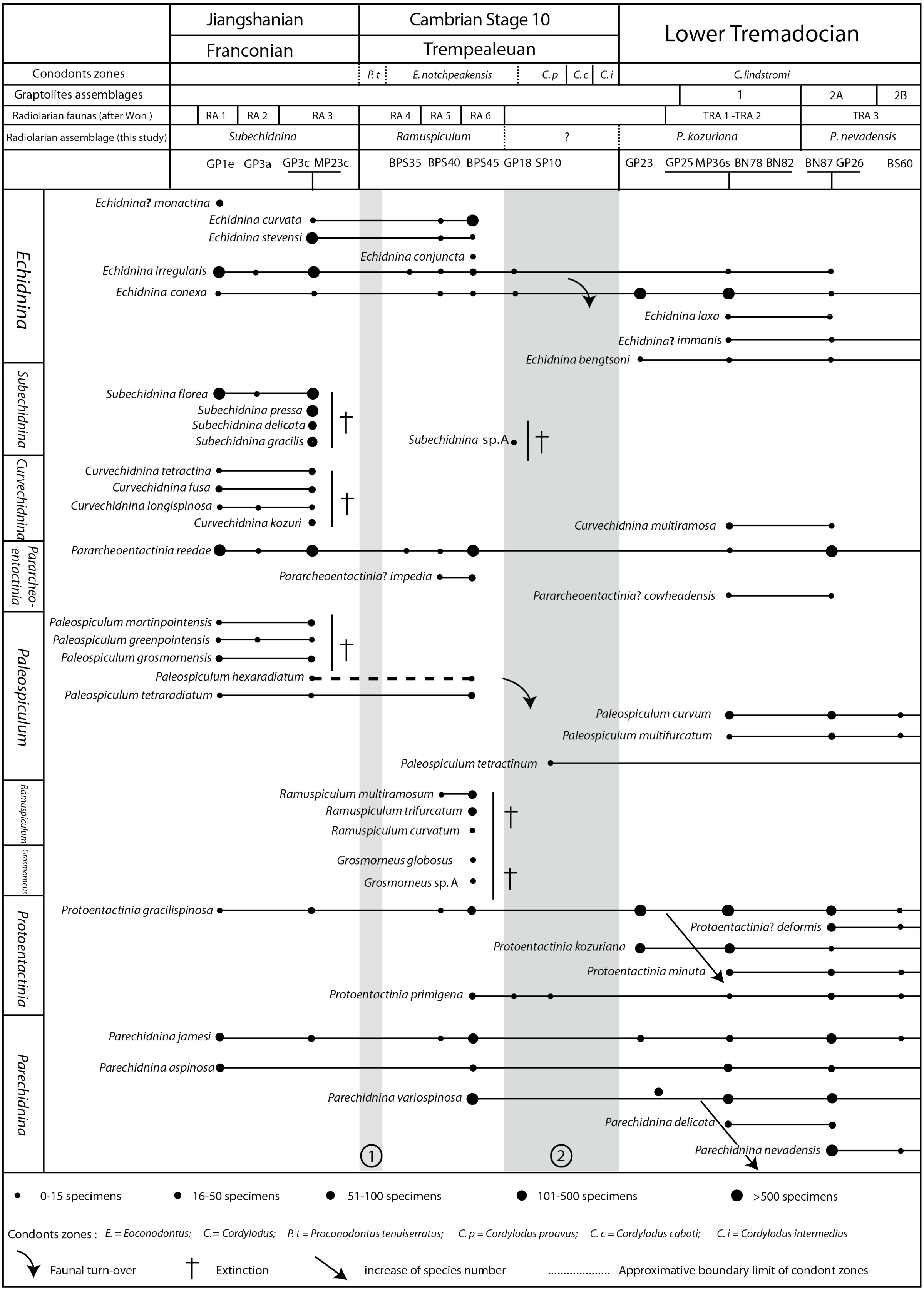
Two genera (*Protoentactinia* and *Parechidnina*) stand out by their completely different biotic response during these two steps of faunal changes. Not only they did not suffer any species extinction, but on the contrary, both of them witnessed a progressive increase of the number of their species. Species diversity within the genus *Protoentactinia* increased from one single species during the Franconian to two species in the Trempealeuan *E. notchpeakensis* Zone and finally to five species in the lowermost Tremadocian *C. lindstromi* Zone. The same trend is also observed for the genus *Parechidnina*, increasing from two species in the Franconian

(*P. jamesi* and *P. aspinosa*) to three species in the Trempealeuan *E. notchpeakensis* Zone and finally to five species in the lowermost Tremadocian *C. lindstromi* Zone. Moreover, the various representatives of the genus *Protoentactinia* became increasingly more abundant. More specifically, while they represented less than 1% of the total fauna in the Franconian and 5-6% during the Trempealeuan, their abundance exploded during the Lower Ordovician, since they represent 63% of the fauna; we here take into consideration the results of Won et al. (2005), as their Lower Ordovician study is based on a more abundant material than ours.

Fig. 7: Pattern of diversity changes and biotic response of various radiolarian taxa recorded in the Upper Cambrian to Lowermost Ordovician of Western Newfoundland. Species age ranges are compiled based on data from both this study and those of Won and Iams (2002) and Won et al. (2005). GP=Green Point, MP=Martin Point and BPS= Broom Point South. The grey intervals represent zones of uncertainty during which the two episodes of biotic changes took place.

(1) = First episode of extinction recorded in the interval situated between the base of the *P. tenuiserratus* Zone and the base of the *E. notchpeakensis* Zone (Trempealeauan); it is characterized by the extinction of 12 out of the 22 species known from the Franconian.

(2) = Second episode of extinction and faunal turn-over between the base of the *C. proavus* and the base of the *C. lindstromi* Zones (late Trempealeauan-early Tremadocian transition); it is characterized by the extinction of 12 out of the 19 species present in the Trempealeauan, including the complete extinction of genera *Ramuspiculum*, *Subechidnina*, and *Grosmorneus*.


Jiangshanian
Cambrian Stage 10
Lower Tremadocian
Franconian
Trempealeuan
Conodonts zones
P. t
E. notchpeakensis
C. p
C. c
C. i
C. lindstromi
Graptolites assemblages
1
2A
2B
Radiolarian faunas (after Won)
RA 1
RA 2
RA 3
RA 4
RA 5
RA 6
TRA 1 -TRA 2
TRA 3
Radiolarian assemblage (this study)
Subechidnina
Ramuspiculum
?
P. kozuriana
P. nevadensis
GP1e
GP3a
GP3c
MP23c
BPS35
BPS40
BPS45
GP18
SP10
GP23
GP25
MP36s
BN78
BN82
BN87
GP26
BS60
Echidnina
Echidnina? monactina
Echidnina curvata
Echidnina stevensi
Echidnina conjuncta
Echidnina irregularis
Echidnina conexa
Echidnina laxa
Echidnina? immanis
Echidnina bengtsoni
Subechidnina
Subechidnina florea
Subechidnina pressa
Subechidnina delicata
Subechidnina gracilis
†
Subechidnina sp.A
†
Curvechidnina
Curvechidnina tetractina
Curvechidnina fusa
Curvechidnina longispinosa
Curvechidnina kozuri
†
Curvechidnina multiramosa
Pararcheo-entactinia
Pararcheoentactinia reedae
Pararcheoentactinia? impedia
Pararcheoentactinia? cowheadensis
Paleospiculum
Paleospiculum martinpointensis
Paleospiculum greenpointensis
Paleospiculum grosmornensis
†
Paleospiculum hexaradiatum
Paleospiculum tetraradiatum
Paleospiculum curvum
Paleospiculum multifurcatum
Paleospiculum tetractinum
Ramuspiculum
Ramuspiculum multiramosum
Ramuspiculum trifurcatum
Ramuspiculum curvatum
†
Grosmorneus
Grosmorneus globosus
Grosmorneus sp. A
†
Protoentactinia
Protoentactinia gracilispinosa
Protoentactinia? deformis
Protoentactinia kozuriana
Protoentactinia minuta
Protoentactinia primigena
Parechidnina
Parechidnina jamesi
Parechidnina aspinosa
Parechidnina variospinosa
Parechidnina delicata
Parechidnina nevadensis
①
②
● 0-15 specimens
● 16-50 specimens
● 51-100 specimens
● 101-500 specimens
● >500 specimens
Condonts zones : E. = Eoconodontus; C. = Cordylodus; P. t = Proconodontus tenuiserratus; C. p = Cordylodus proavus; C. c = Cordylodus caboti; C. i = Cordylodus intermedius
Faunal turn-over
† Extinction
increase of species number
.... Approximative boundary limit of condont zones

5.3. Correlation of biotic changes with Carbon isotope excursions

Isotopic events recorded in the stable carbon isotopes (δ^{13} Ccarb) testify of profound changes in the carbon cycle and mark periods of environmental disruption, often associated with important biotic changes. Various studies have shown that the SPICE δ^{13} Ccarb positive excursion that took place in the Paibian (Steptoean, basal Upper Cambrian) coincides with important changes in the trilobite and acritarch fossil record. Indeed, the onset of the SPICE δ^{13} Ccarb positive excursion, which started at the base of *Glyptagnostus reticulatus* zone, is coeval with the *Pterocephaliid–Ptychaspid* extinction horizon of Trilobites and it is followed by an episode of faunal diversification coeval with the peak of this isotopic excursion (Palmer, 1965, 1984; Rowell and Brady, 1976; Peng *et al*., 2004; Saltzman, 1999; Saltzman *et al*., 2000). This SPICE δ^{13} Ccarb positive excursion also marks a period of important faunal changes within the acritarchs, with the introduction of new morphologies and the beginning of an important increase of acritarch diversity (Servais *et al.*, 2008).

We here notice that two pronounced δ^{13} Ccarb negative excursions (HERB and TOCE) occurred during the Late Cambrian (Landing *et al*., 2011). The HERB δ^{13} Ccarb negative excursion which has been recorded in the Green Point section starts at the base of the *E. notchpeakensis* zone and reaches its maximal negative value in its lower part (Ripperdan *et al*., 1992, 1993; Ripperdan and Miller, 1995; Cooper *et al*., 2001; Miller *et al*., 2011). Yet, the first episode of faunal change recorded in our radiolarian material from Newfoundland took place somewhere in the interval between the base of the *P. tenuiserratus* zone and the lower part of the *E. notchpeakensis* zone. The first episode of faunal changes is therefore either coeval or slightly anterior to the HERB δ^{13} Ccarb isotopic excursion.

The onset of the TOCE δ^{13} Ccarb negative isotopic excursion is situated at the base of the *C. proavus* zone (Upper Cambrian stage 10) and it ends at the base of the *C. lindstromi* zone (basal Tremadocian) (Zhu *et al*., 2007). It is interesting to notice that the second episode of faunal changes recorded in our Newfoundland material took place in the interval between the base of *C. proavus* and *C. lindstromi* zones. The TOCE δ^{13} Ccarb negative isotopic excursion is therefore coeval with the second episode of faunal changes (Fig. 8). It is likely that these two episodes of faunal changes took place during a period of environmental disruption which has lead to a decrease of productivity and extinction events, the latter being often associated with negative excursions of the δ^{13} Ccarb isotopic curve (Servais *et al.*, 2008).

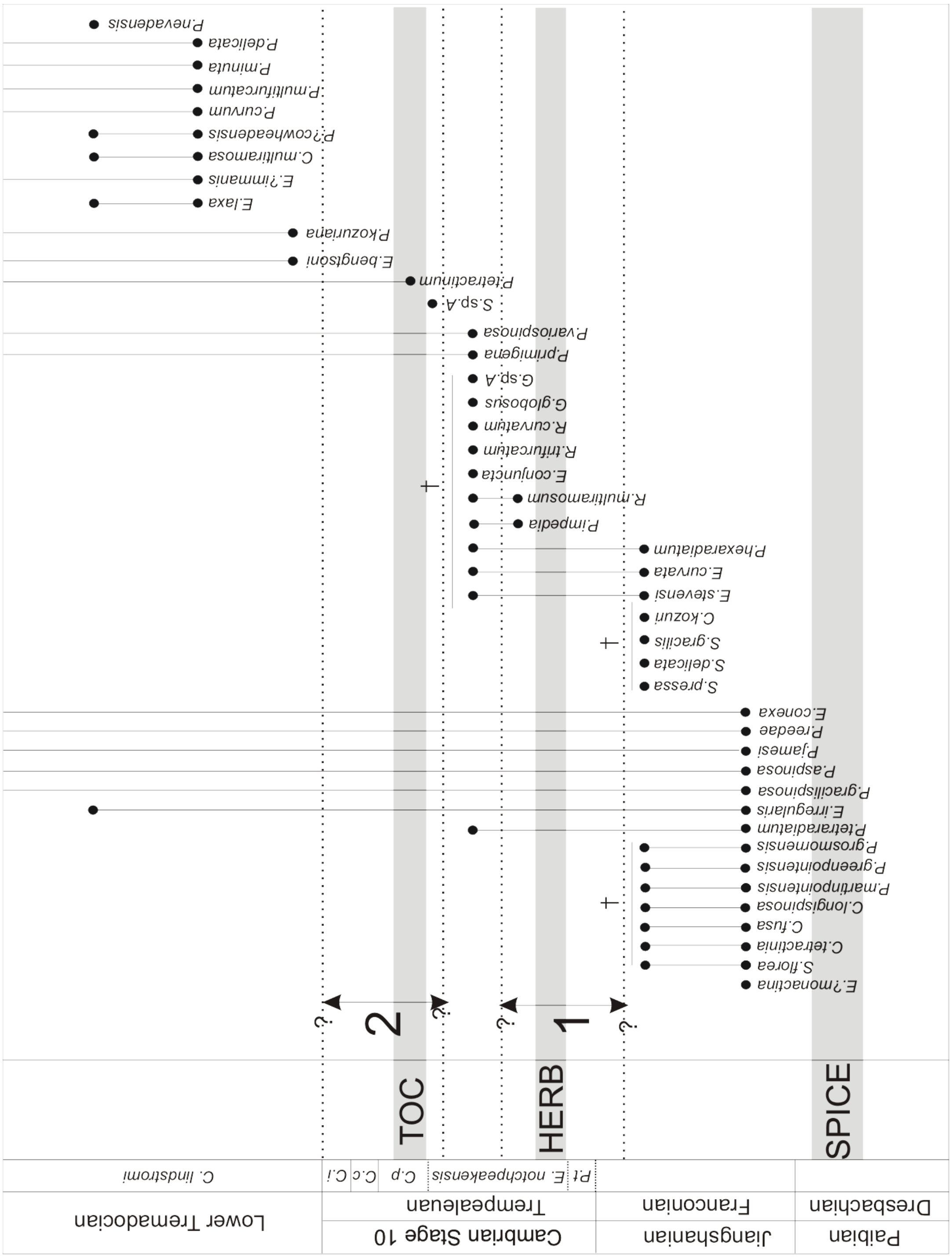


Fig. 8: Stratigraphical distribution of Newfoundland radiolarians species identified by Won and Iams, 2002, Won et al, 2005 and our study at the Cambrian-Ordovician transition. The grey zones mark the δ^{13} Ccarb isotopic positive (SPICE) and negative (HERB, TOCE) excursions that took place during this critical interval. The arrow delimiting the intervals 1 and 2 represent zones of uncertainty during which the two episodes of biotic changes took place. The crosses represent extinctions events at the species-level.

6. Conclusion

The pattern of changes in radiolarian diversity during the Upper Cambrian to Lower Ordovician transition in Newfoundland reveals two episodes of local faunal changes. The first is situated between the base of the *P. tenuiserratus* and the base of the *E. notchpeakensis* conodont Zones (basal Trempealeauan). It records a severe diversity decrease, which corresponds to within-clade extinctions of a number of important Franconian genera (i.e. *Paleospiculum*, *Curvechidnina*, *Subechidnina*). The second episode of faunal changes, situated between the base of the *C. proavus* and the base of the *C. lindstromi* conodont Zones, displays various biotic responses, including a selective extinction of three out of the nine Cambrian genera (*Subechidnin*a, *Ramuspiculum* and *Grosmorneus*) below the basal Ordovician, but also a within-clade species turnover (*Echidnina*, *Paleospiculum*) and diversity increase (*Protoentactinia* and *Parechidnina*). The family Echidninidae is very dominant in the Franconian and it represents a major component of the radiolarian faunas during the Cambrian-Ordovician transition. The Trempealeauan is characterized by assemblages dominated by both Archeoentactiniidae and Echidninidae, which include also a large amount of Aspiculidae while the Lower Ordovician is is characterized by assemblages dominated mostly by representatives of the Protoentactiniidae, followed by the Echidninidae.

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Partie 2

Etude d'un assemblage à radiolaires d'Australie du Jingshanien (Cambrien supérieur) et comparaison avec le matériel de Terre-Neuve

I. Contexte géologique et stratigraphique

L'assemblage à radiolaires décrit dans cette étude provient des calcaires de Chastworth, une série sédimentaire déposée dans le bassin intra-cratonique peu profond de Georgina couvrant les territoires du Nord et du Queensland occidentale, sur environ 325,000 km², à l'est de l'Australie (Fig. 1A). La localité fossilifère se situe dans les environs de Chastworth Homestead, à 80 km au sud de la ville de Duchess, dans la région de Duchess Embayment, sur la marge sud-ouest du bassin de Georgina (Shergold, 1975, 1980 ; Fig. 1B).

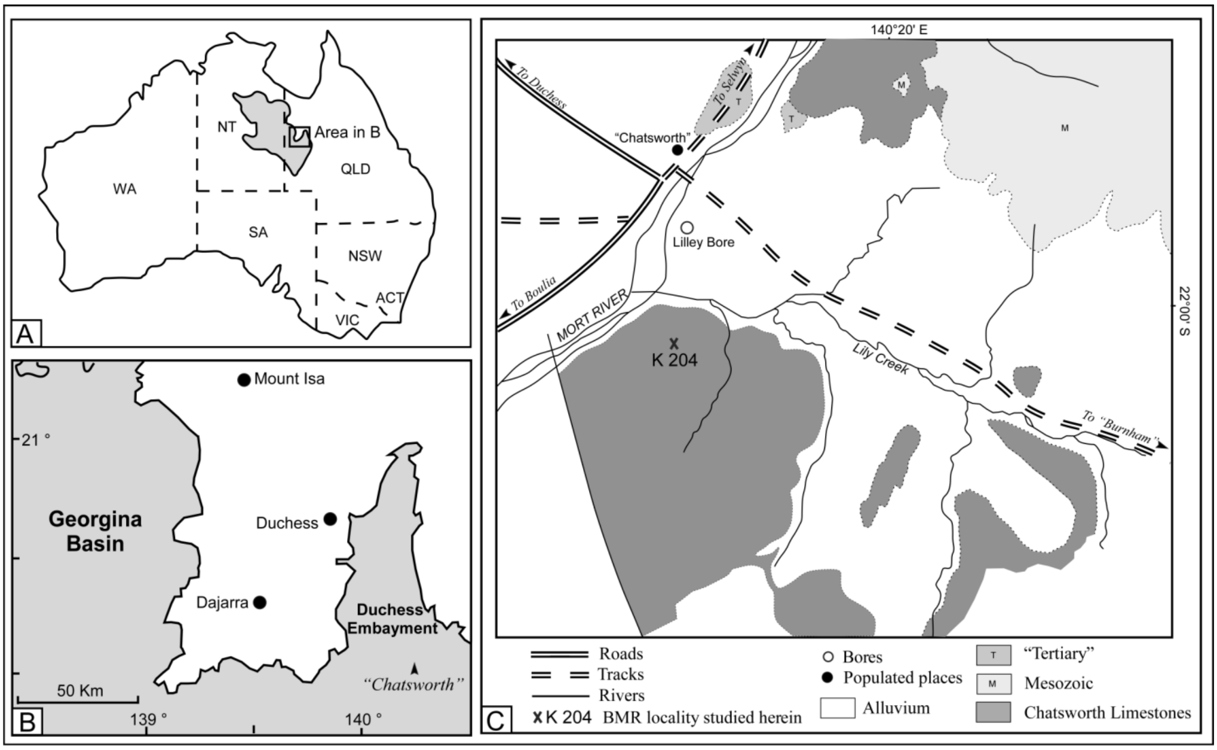


Figure 1: Localisation de la région de « Chatsworth » dans la baie de Duchess du bassin de Georgina situé au nord-ouest du Queensland et dans le centre-est des territoires du Nord. (A–B; d'après Porter, 2004) et emplacement géographique de la localité K 204, au sud de Lily Creek et de « Chatsworth » (C; d'après Shergold, 1980)

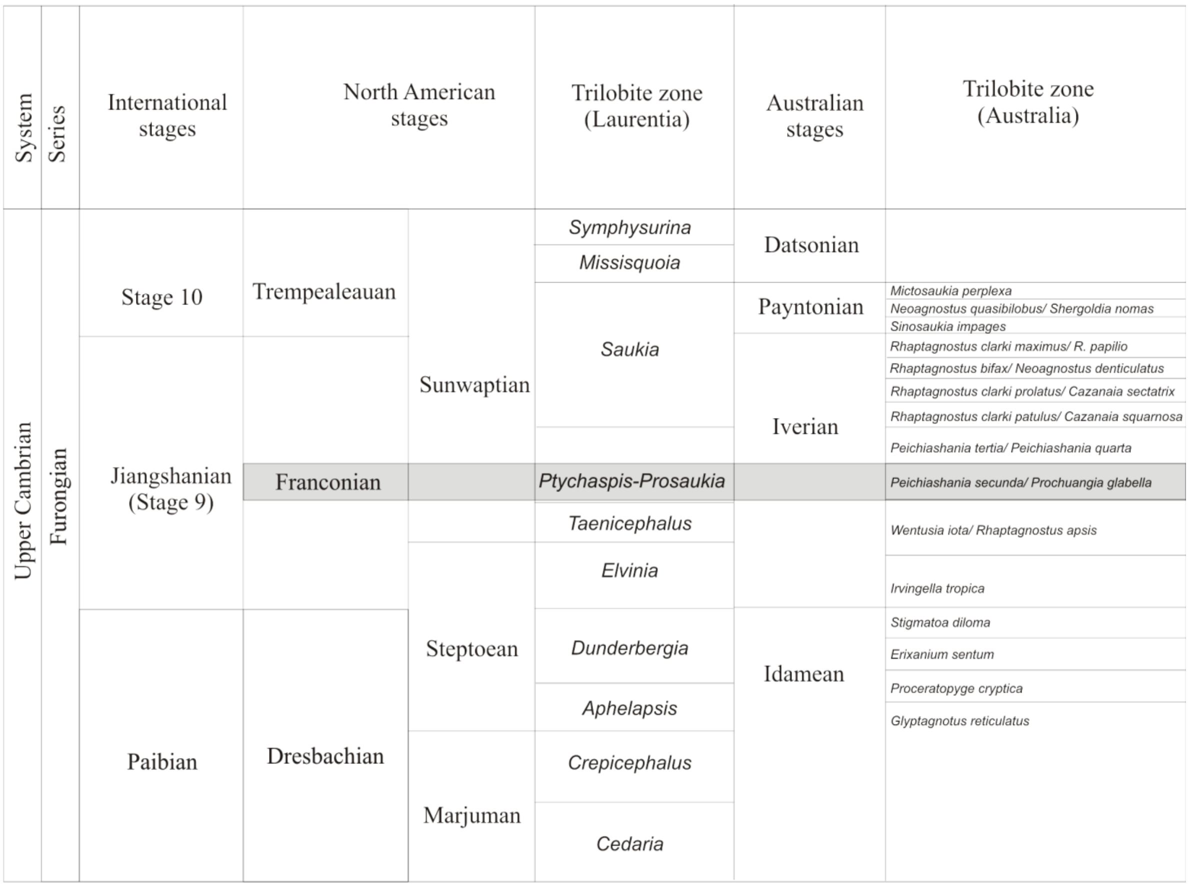
L'échantillon étudié m'a été confié par Sébastien Clausen (UMR8217 Géosystèmes) ; il provient de la localité K204, listée par le bureau des ressources minérales (Shergold, 1980). Ici, la série sédimentaire affleure sur 4 mètres d'épaisseur ; elle est formée principalement de grainstones à péloides, contenant des fragments de *Girvanella*, des calcisphères et des bioclastes silicifiés. Cette série carbonatée comprend également des trilobites du Cambrien supérieur de la zone d'assemblage à *Peichiashania secunda-Prochuangia glabella* (Shergold, 1980, p. 97; Furongien, Etage 9 d'après Kruse *et al*., 2009), des brachiopodes, des monoplacophores et des échinodermes (Jell *et al*., 1985; Smith and Jell, 1990).

II. Résultats

L'échantillon étudié a révélé la présence d'un assemblage à radiolaires assez abondant (415 spécimens) et bien préservé. La faune des trilobites trouvée dans la série permet sa corrélation avec la base du Sunwaptien en Laurentia (Franconien moyen ; Fig. 2). Deux familles (Echidninidae et Archeoentactiniidae), trois genres (*Subechidnina, Echidnina* et *Pararcheoentactinia*) et cinq espèces (*Subechidnina florea, Echidnina stevensi, Echidnina irregularis, Echidnina curvata* et *Pararcheoentactinia reedae*, voir Planche 1) ont été identifié dans cet assemblage. Le Tableau 1 ci-dessous précise leur occurrence et le nombre de spécimens retrouvés pour chaque espèce. On peut constater que cette faune est dominée par la famille des Echidninidae composée en large majorité des genres *Echidnina* et *Subechidnina*, représentant à eux seuls environ 99% de notre assemblage (Fig. 3). Ces genres sont constitués essentiellement de deux espèces prédominantes : *Subechidnina florea* (56% de notre assemblage) et *Echidnina irregularis* (43% de notre assemblage). Le reste de l'assemblage (environ 1%) est composé de rares *Echidnina stevensi*, *Echidnina curvata* et *Pararcheoentactinia reedae*.

III. Discussion

Jusqu'à présent, l'unique assemblage connu au Jiangshanien (Etage 9 du Cambrien) provenait des terrains du groupe de Cow Head en Terre-Neuve (Canada, cf. Chap.2 Partie 1, I. Etat de l'art) ; il avait été décrit par Won et Iams (2002) et identifié par la suite comme l'assemblage à *Subechidnina* par Pouille *et al*. (2012a, soumis). Ce nouvel assemblage d'Australie constitue donc la deuxième faune désormais connue du Jiangshanian (cf. Chap.2 Partie 1, I. Etat de l'art). Or, la composition de cette faune est très similaire à celle trouvée dans l'assemblage à *Subechidnina*, extrait de l'unité 23 de la section de Martin Point South en Terre-Neuve, lequel est bien datés du Jiangshanien.



System	Series	International stages	North American stages		Trilobite zone (Laurentia)	Australian stages	Trilobite zone (Australia)
Upper Cambrian	Furongian	Stage 10	Trempealeauan	Sunwaptian	*Symphysurina*	Datsonian	
					Missisquoia		
					Saukia	Payntonian	*Mictosaukia perplexa*
							Neoagnostus quasibilobus/ Shergoldia nomas
							Sinosaukia impages
		Jiangshanian (Stage 9)				Iverian	*Rhaptagnostus clarki maximus/ R. papilio*
							Rhaptagnostus bifax/ Neoagnostus denticulatus
							Rhaptagnostus clarki prolatus/ Cazanaia sectatrix
							Rhaptagnostus clarki patulus/ Cazanaia squarnosa
							Peichiashania tertia/ Peichiashania quarta
			Franconian		*Ptychaspis-Prosaukia*		*Peichiashania secunda/ Prochuangia glabella*
					Taenicephalus		*Wentusia iota/ Rhaptagnostus apsis*
				Steptoean	*Elvinia*		*Irvingella tropica*
		Paibian	Dresbachian		*Dunderbergia*	Idamean	*Stigmatoa diloma*
							Erixanium sentum
					Aphelapsis		*Proceratopyge cryptica*
							Glyptagnotus reticulatus
				Marjuman	*Crepicephalus*		
					Cedaria		

Figure 2 : Charte stratigraphique du Cambrien supérieur présentant une tentative de corrélation entre les zones à trilobites de la Laurentia (incluant les terrains de Terre-Neuve) et de l'Australie (construite d'après la charte stratigraphique internationale de 2012 et les travaux de Gayer *et al.*, 2000).

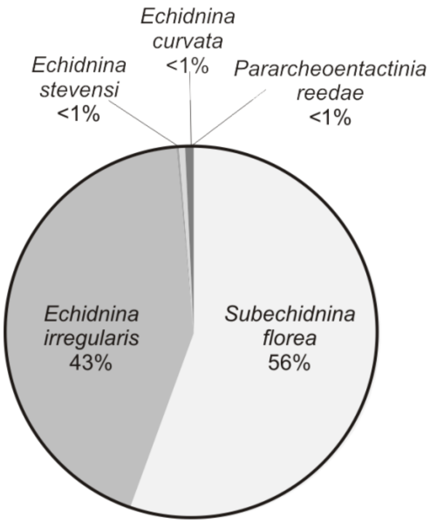


Fig. 3: Diagramme indiquant le pourcentage d'abondance relative des espèces extraites de notre assemblage à radiolaire d'Australie.

En effet, d'après Pouille *et al*. (2012a, soumis) l'assemblage à *Subechidnina* est caractérisé par la présence de *Subechidnina florea, Echidnina stevensi, Echidnina irregularis, Echidnina curvata* and *Pararcheoentactinia reedae* gr., qui se sont révélés être les cinq espèces composant également notre matériel (Fig. 4, Planche 1). Ces deux faunes montrent une prédominance des représentants de la famille des Echidninidae (i.e. *Echidnina*, *Subechidnina*; Fig. 4), représentant au moins 97% de ces deux assemblages, et ne diffèrent que par l'abondance relative des espèces composant leurs assemblages. Ainsi, la faune australienne est composée à 99% des espèces *Subechidnina florae* (56%) et *Echidnina irregularis* (43%) tandis que la faune terreneuvienne décrite par Pouille *et al*. (2012) montre la même proportion d'*Echidnina irregularis* (45%) mais une quantité relative moins importante de *Subechidnina florae* (20%) et plus importante d'*Echidnina stevensi* (25%) et d'*Echidnina curvata* (7%). *Pararcheoentactinia reedae* gr. reste une espèce rare dans les deux assemblages. Ainsi nous pouvons attribuer l'assemblage retrouvé dans notre matériel d'Australie à l'assemblage à *Subechidnina*. Cet assemblage à *Subechidnina* a également été étudié de manière plus exhaustive par le travail de Won et Iams (2002) mené sur des échantillons extraits de l'unité 23 de la section de Martin Point South en Terre-Neuve mais également des unités 1 e, 3a et 3c de la section de Green Point. Won et Iams (2002) retrouvent ainsi la présence de 3 genres et 18 espèces supplémentaires dans l'assemblage à *Subechidnina* (voir Tableau 1). Or nous pouvons constater qu'à l'exception de *Subechidnina pressa*, les espèces retrouvées dans notre matériel et le matériel de Pouille *et al*. (2012a, soumis) constituent toute les espèces décrites comme étant les plus abondantes dans matériel de Won et Iams (< 500 spécimens ; Tableau 1). Ces deux assemblages peuvent donc être considérés comme des faunes appauvries de l'assemblage à *Subechidnina* dont seules les espèces les plus abondantes ont pu être observées.

	Upper Cambrian				
International stage	Jingshanian				
Regional stages	Franconian				Iverian
Locality	Newfoundland				Australia
	(Won and Iams, 2002)			(Pouille *et al.*, 2012)	(This study)
Radiolarian assemblage	*Subechidnina* assemblage				
Samples	RA 1	RA 2	RA 3	MP 23c	K204
Subechidnina florea	>500	1-5	>500	14	231
Echidnina irregularis	>500	1-5	>500	27	179
Echidnina curvata			1-5	4	2
Echidnina stevensi			>500	15	1
Pararcheoentactinia reedae	>500	6-15	>500	2	2
Subechidnina pressa			>500		
Subechidnina gracilis			50-99		
Subechidnina delicata			50-99		
Solechidnina isolata	16-49				
Echidnina? monactina	16-49				
Palaeospiculum martinpointensis	6-15		6-15		
Palaeospiculum greenpointensis	6-15	1-5	6-15		
Curvechidnina tetractina	1-5		6-15		
Curvechidnina fusa	16-49		6-15		
Curvechidnina longispinosa	6-15	1-5	6-15		
Palaeospiculum grosmornensis	16-49		6-15		
Curvechidnina kozuri			6-15		
Palaeospiculum hexaradiatum			1-5		
Palaeospiculum tetraradiatum	1-5		1-5		
Protoentactinia gracilispinosa	1-5		6-15		
Parechidnina aspinosa	50-99				
Parechidnina jamesi	50-99				
Echidnina conexa	1-5		1-5		

Tableau 1 : Comparaison des espèces identifiées au Cambrien supérieur dans le matériel de Terre-Neuve (Won et Iams, 2002 ; Pouille *et al.*, 2012 (soumis)) et d'Australie. Le nombre de spécimens trouvés pour chaque espèce est précisé.

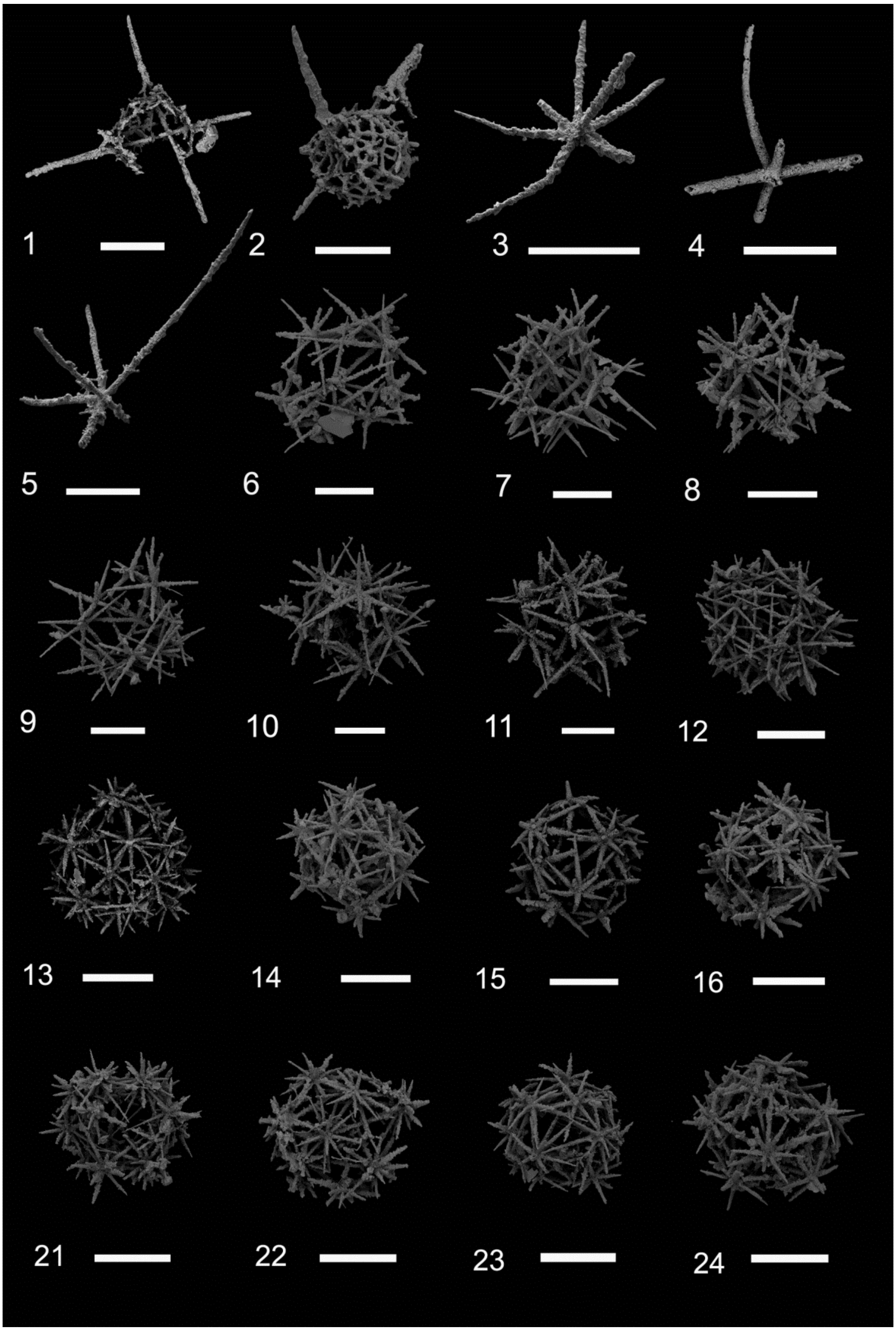


Planche 1 : 1-2, *Paracheoentactinia reedae* ; 3-4, *Echidnina curvata*; 5, *Echidnina stevensi*; 6-12, *Echidnina irregularis*; 13-24, *Subechidnina florea*

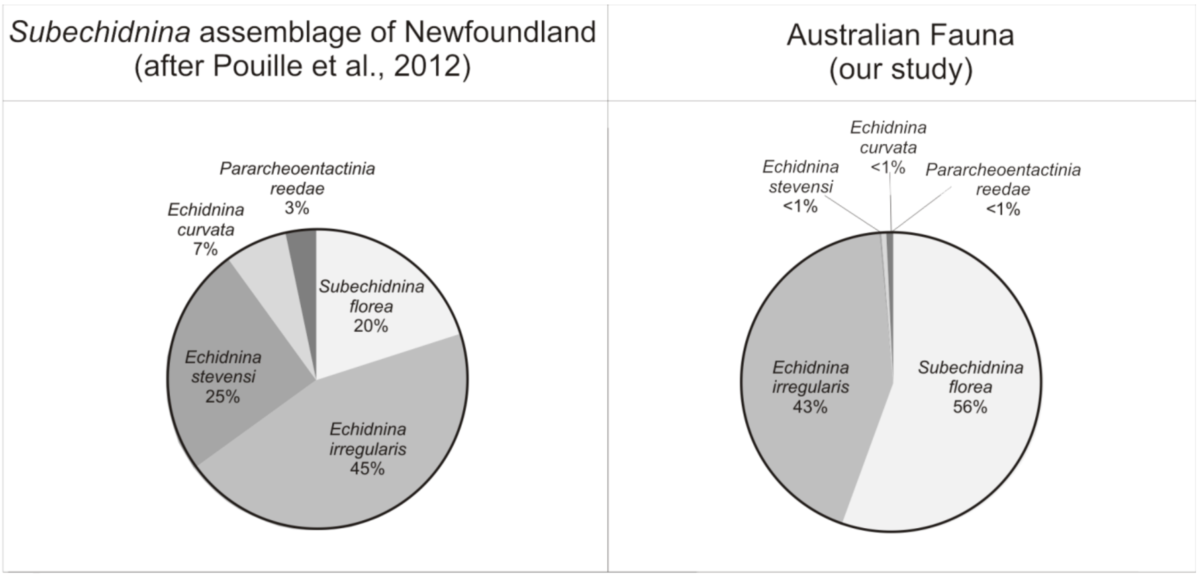


Figure 4: Diagramme indiquant le pourcentage d'abondance relative des espèces extraites de l'assemblage à *Subechidnina,* décrit par Pouille *et al*. (2012a, soumis) et de notre assemblage à radiolaire d'Australie.

On peut remarquer que les espèces *Subechidnina florea* et *Echidnina irregularis* restent toutefois très abondantes même dans les assemblages appauvris du Jiangshanien, que ce soit en Laurentia (Terre-Neuve) ou en Australie (Tableau 1). Ces deux espèces peuvent donc être envisagées comme de très bons marqueurs stratigraphiques pour la détermination de l'âge Jiangshanien en Terre-Neuve et en Australie. Ceci se révèle d'autant plus utile que nous avons pu remarquer que sur certaines coupes de Terre-Neuve (ex : Green Point, Martin Point) les strates d'âge Franconien étaient dépourvues de fossiles susceptibles d'apporter une indication biostratigraphique (conodontes, graptolites). Les études que nous avons menées sur les radiolaires du Cambrien supérieur de Terre-Neuve et d'Australie nous permettent donc de définir ici une zone à *Subechidnina florea- Echidnina irregularis* caractérisant l'âge Jiangshanien dans les terrains de Laurentia (Terre-neuve) et de l'Est Gondwana (Australie). De plus, d'après les reconstitutions paléogéographiques récentes (Álvaro *et al*., 2007), les terrains de Terre-Neuve et d'Australie semblent très éloignés géographiquement au Cambrien supérieur (fig.5). La répartition de cet assemblage à *Subechidnina*, découvert dans deux endroits si éloignés géographiquement, est conforme avec un mode de vie planctonique des radiolaires du Cambrien supérieur.

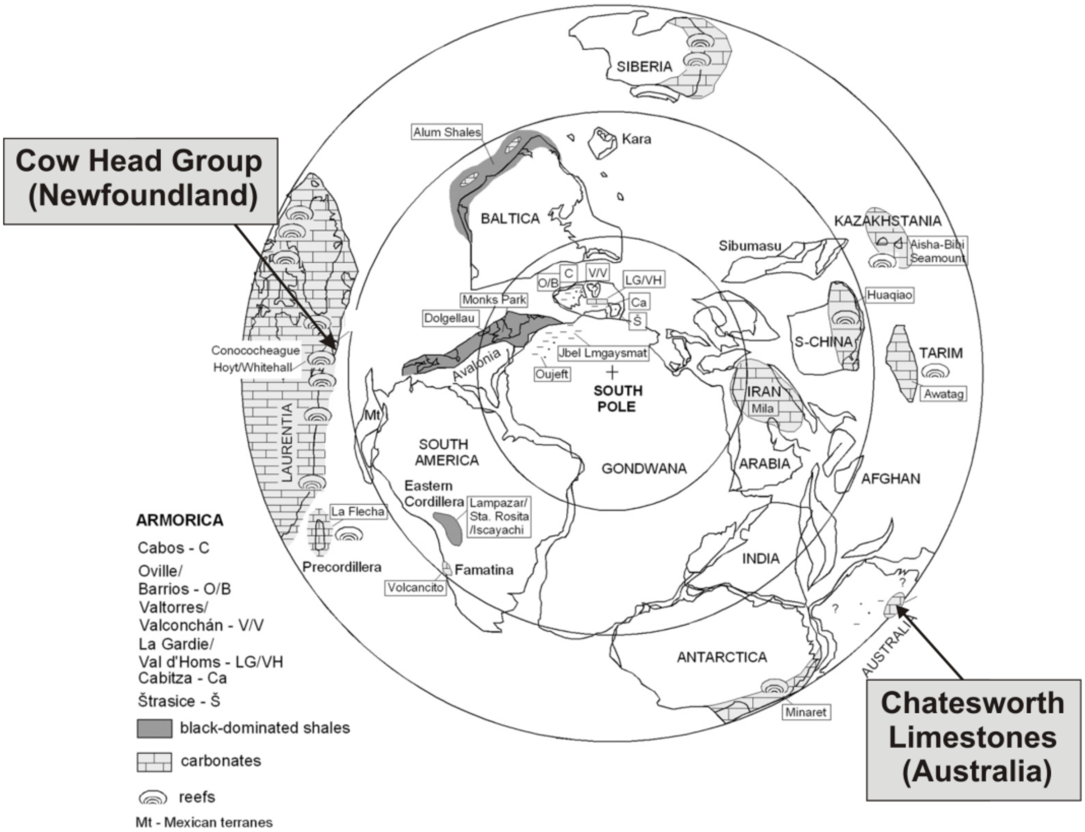


Figure 5: Reconstitution paléogéographique globale du Furongien (Cambrien supérieur) indiquant la position du groupe de Cow Head (Terre-Neuve) et la position des calcaires de Chatesworth (Australie) (modifiée d'après Álvaro *et al*., 2007).

Chapitre 3

Etude d'un nouvel assemblage à radiolaires du Kazkhstan d'intérêt majeur pour la compréhension de la diversité des radiolaires au Darriwilien supérieur (Ordovicien moyen)

I. Etat de l'art

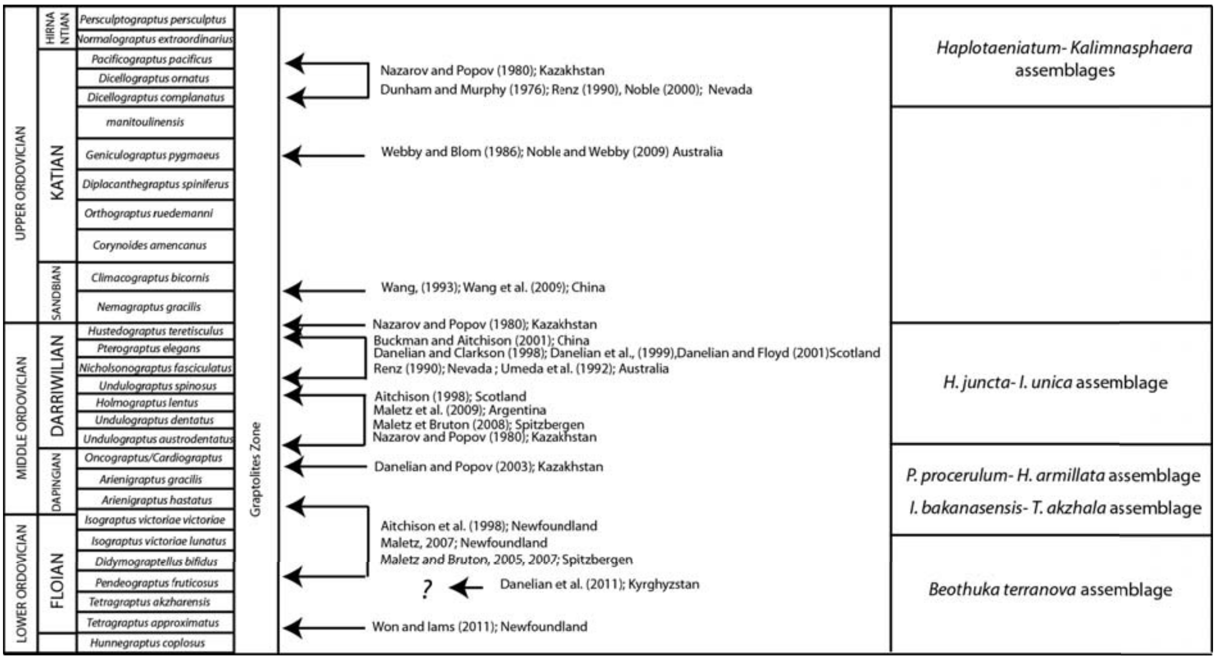


Figure 1 : Schéma récapitulatif des enregistrements à radiolaires les plus significatifs de l'Ordovicien inférieur (Floien) à l'Ordovicien supérieur (Hirnantien) ainsi que leur provenance géographique et les assemblages qu'ils constituent.

L'état de l'art des assemblages à radiolaire du Trémadocien ayant été traité précédement dans le chapitre II, partie, 1, I) nous abordons ici l'étude des assemblages à radiolaires de l'Ordovicien à partir du Floien.

La plus ancienne faune à radiolaire connue au Floien a été découverte très récemment par Won et Iams (2011) dans des strates du groupe de Cow Head en Terre-Neuve, datées de la base du Floien (zone à *Tetragraptus approximatus*). Cet assemblage très diversifié voit l'apparition des genres *Svalbardospiculum*, *Beothuka*, *Neoaspiculum*, *Proventocitum* et des premiers spumellaires avec les genres *Inanigutta* et *Antygopora* dont la structure interne est formée par une microsphère. Cet assemblage est ici considéré comme appartenant à l'assemblage à *Beothuka terranova* connu jusqu'à présent uniquement au Floien supérieur. L'assemblage à *Beothuka terranova* a été découvert par Aitchison *et al*. (1998) dans des cherts provenant de la région de Little Port Complex en Terre-Neuve, datés à l'époque du Trémadocien basal. Il a ensuit été réattribué au Floien supérieur grâce à la découverte d'autres assemblages à *Beothuka terranova* dans des terrains bien datés (zone à *Didymograptellus bifidus* - *Isograptus vicotriae lunatus*) du groupe de Cow Head en Terre-Neuve (Maletz, 2007a) et de la Formation de Valhallfonna au Spitzbergen (Maltez et Bruton, 2005, 2007). Ces faunes retrouvées au Floien supérieur sont également très diversifiées et contiennent de nombreux genres dont les premiers représentant des genres *Nyfrieslandia*, *Sphaeroentactinia*, *Labyrinthia*, *Haplentactinia* ou encore *Haplotaeniatum*. La présence de rares radiolaires dans la zone à *Pendeograptus fruticosus* (Floien moyen) a également été mentionnée par Maletz (2007a) mais l'étude de ces spécimens n'a pas encore été approfondie. Quelques larges Inaniguttidae provenant des formations de Oldzhobai et de East Sarydzhaz au Kirghizstan ont également été décrits récemment par Danelian *et al*. (2011). Certains de ces Inaniguttidae sont datés par les conodontes d'un âge Floien moyen-supérieur. Pour les autres, l'absence de conodontes rend la datation plus imprécise (Trémadocien supérieur à Dapingien)

La présence au Spitzbergen de radiolaires dans des strates datées du Dapingien inférieur a été mentionnée par Maletz et Bruton, 2007. Cette faune contient des genres caractéristiques des faunes du Floien supérieur (*Labyrinthia*, *Antygopora*, *Nyfrieslandia*) mais également deux espèces caractéristiques de l'assemblage à *Proventocitum procerulum*-*Haplentactinia armillata* (Darriwilien) remettant en doute l'âge attribué à cette faune. Wang *et al*. décrit en 2008 un assemblage à radiolaire provenant de Chine daté du Dapingien supérieur (Zone à *Exigraptus clavus*). Cependant, les spécimens composant cet assemblage se sont révélés être trop abimés pour permettre leur attribution avec certitude au groupe des radiolaires (Maletz, 2011). En 2003, Danelian et Popov décrivent un nouvel assemblage oligospecifique représenté par quatre espèces : *Inanihella bakanasensis*, *Inanihella* (?) *akzhala*, *Triplococcus acanthicus* et *Proventocitum* sp.cf. *P. procerulum* provenant de la Formation Akzhal au Kazakhstan. Cet assemblage est d'abord considéré d' âge Floien par Danelian et Popov (2003) a été par la suite attribué au Dapingien supérieur –Darriwilien par Maletz en 2007. Cette attribution se voit confortée par la découverte d'un assemblage similaire en Argentine par Maletz *et al*. (2009) très précisément daté par la présence de conodontes appartenant à la zone à *Lenodus variabilis* (Darriwilien inférieur). La présence de radiolaires au Darriwilien a également été mentionnée dans le groupe de Table Head en Terre-Neuve par certains auteurs (Bergström, 1979 ; Zhang et Pratt, 2000 ; Maletz et Bruton, 2007) et dans la région de Marathon, à l'ouest du Texas par Bergström (1979). Ces radiolaires n'ont cependant jamais été décrits.

L'assemblage à *Proventocitum procerulum*-*Haplentactinia armillata* constitue l'assemblage de référence du Darriwilien moyen. Il a été considéré au départ comme étant étendu du Floien inférieur jusqu'au Darriwilien inférieur (Nazarov et Popov, 1980; Danelian et Popov, 2003) mais il a été par la suite restreint à un âge strictement Darriwilien (Maletz et Bruton, 2007, 2008; Maletz, 2011). Il a été découvert pour la première fois dans des terrains du Spitzbergen par Fortey et Holdsworth en 1971, puis réétudié par Holdsworth (1977) et Maletz et Bruton (2008) qui lui attribuèrent un âge Darriwilien inférieur. Cet assemblage a également été retrouvé au Kazakhstan par Nazarov et Popov (1980) et en Ecosse par Aitchison (1998). De nombreuses faunes composées de représentant de la famille des Inaniguttidae ainsi que du genre *Protoceratoikiscum* ont été retrouvées dans du matériel provenant de Chine (Buckman et Aitchison, 2001), d'Ecosse (Danelian et Clarkson, 1988 ; Danelian, 1999 ; Danelian et Floyd, 2001), d'Amérique du Nord (Renz, 1990a) et d'Australie (Umeda *et al.*, 1992) daté du Darriwilien supérieur au Sandbien inférieur. Ces assemblages peuvent être corrélés avec l'assemblage à *Haplentactinia juncta- Inanigutta unica* (Danelian et Clarkson, 1988 ; Danelian, 1999). L'assemblage à *Haplentactinia juncta- Inanigutta unica* a été décrit par Nazarov et Popov (1980) sur du matériel provenant de la Formation de Bestomak au Kazakhstan et daté du Darriwilien terminal (juste en dessous de la zone à *Nemagraptus gracilis*). De nombreux autre assemblages étudiés au Kazakhstan par Nazarov et datés du Darriwilien supérieur au Sandbien inférieur peuvent être assimilé à cet assemblage à *Haplentactinia juncta- Inanigutta unica* (Nazarov, 1975, 1977 ; Nazarov *et al.*, 1977 ; Nazarov et Ormiston, 1986, 1993 ; Nazarov et Popov, 1976)

Trois autres assemblages possédant des faunes similaires à celle de l'assemblage à *Haplentactinia juncta- Inanigutta unica* ont été retrouvés au Sandbien (zone à *Nemagraptus gracilis- Climacograptus bicornis*) dans des cherts de l'état de New York (Ruedemann et Wilson, 1936), dans calcaires de la Formation de Pingliang en Chine (Wang, 1993 ; Wang *et al.*, 2009) et dans des calcaires de la Formation de Zhaolaoyu du Nord de la Chine (Cui *et al.*, 2000). De nombreuses faunes à radiolaires d'un âge incertain (du Katien à l'Hirnantien) ont été découvertes en Australie (Goto et Ishiga, 1991 ; Goto *et al.*, 1992), en Chine (Cui *et al.*, 1995), en Scandinavie (Górka, 1994) ; en Sibérie (Ivanov et al., 2007) et au Kazakhstan (Nazarov et Ormiston, 1993). Trois assemblages du Katien ont tout de même pu être datés avec précision. Le premier, décrit par Webby et Blom (1986) et Noble et Webby (2009), provenant d'Australie a été corrélé avec la zone à conodontes *O.velicuspis* (Katien moyen). Les deux autres assemblages retrouvés par Dunham et Murphy (1976), Renz (1990b) et Noble (2000) en Amérique du Nord (Nevada), datés du Katien supérieur, montrent une faune à radiolaire dominée par les spumellaires avec l'assemblage à *Haplotaeniatum spinatum*, corrélé avec la zone à *O. quadramucronatus* et l'assemblage à *Kalimnasphera*, corrélé avec la zone à *Pacificograptus pacificus*. La présence de quelques radiolaires d'âge Katien supérieur (*Pacificograptus pacificus*) provenant du Kazakhstan a également été mentionnée par Nazarov, 1975 et Nazarov et Popov (1980).

II. Contexte géologique et stratigraphique

Les terrains datant du Paléozoique inférieur au Kazakhstan représentent pour la plupart une mosaïque de plusieurs microcontinents et d'arcs insulaires intra-océaniques qui étaient situés à l'Ordovicien au sein de l'océan paléo-asiatique, à l'est des continents Baltica - Siberia (Apollonov, 2000 ; Holmer *et al*., 2001). L'évolution paléogéographique du Kazakhstan au cours du Paléozoïque inférieur est encore très énigmatique. De nombreux modèles paléotectoniques de l'évolution de ces terrains ont été proposés mais leurs interprétations sont souvent contradictoires et la rareté des données paléomagnétiques ne permet pas à ce jour une reconstruction plus précise de l'histoire paléogéographique du Kazakhstan (Didenko *et al*, 1994 ; Sengör et Natal'in, 1996 ; Fig. 2).

La région d'Atasu-Zhamshy est située au nord-ouest du lac Balkash, entre la rivière Atasu à l'ouest et la rivière Zhamshy à l'est (Fig. 3). Les terrains de cette région sont majoritairement composés de calcaires ou dolomies allant du Précambrien supérieur au Paléozoique inférieur. Ils représenteraient une ancienne plateforme carbonatée et des dépôts de pente datant de la fin du Précambrien jusqu'à l'Ordovicien moyen situés sur le microcontinent de Dzhungaro-Balkhash (Sengör *et al*., 1993; Apollonov, 2000).

Les affleurements carbonatés datés de l'Ordovicien moyen à l'Ordovicien supérieur de la région d'Atasu-Zhamshy sont représentés par deux formations : La Formation de Kurchilik (Dapigien supérieur-Darriwilien) et la Formation de Shundy (Darriwilien supérieur-Sandbien), représentant un large spectre de faciès allant d'un milieu peu profond jusqu'à un environnement de base de pente.

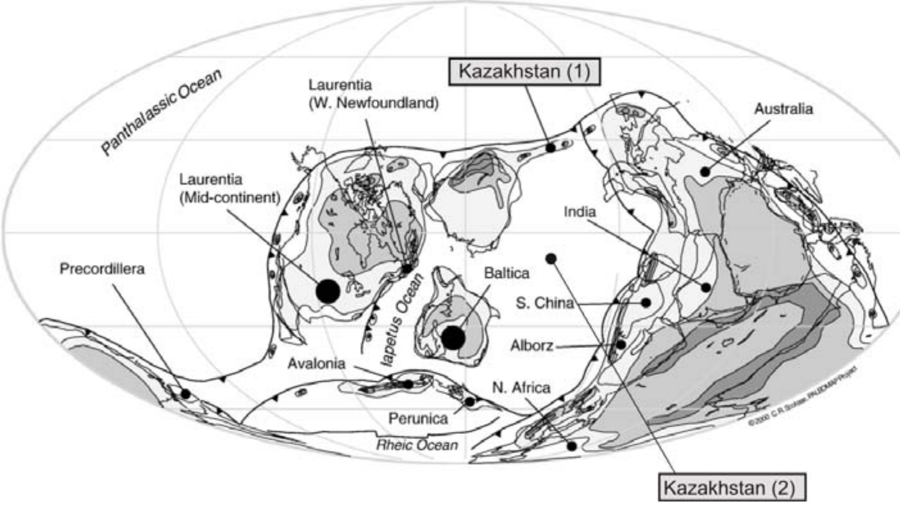


Figure 2 : Reconstitution paléogéographique de l'Ordovicien (modifiée d'après Hints et Eriksson, 2007, d'après le projet PALEOMAP de Scotese, cf. http://www.scotese.com). Kazakhstan (1) marque la position des terrains du Kazakhstan à l'Ordovicien selon l'interprétation de Didenko *et al*, 1994 ; Kazakhstan (2) marque la position des terrains du Kazakhstan à l'Ordovicien selon l'interprétation de Sengör et Natal'in, 1996.

La Formation de Kurchilik est majoritairement composée de calacaires argileux, de calcarenites et de roches carbonatées à lithologie variable (Apollonov *et al*, 1990). La formation de Shundy qui va du Darriwilien supérieur au Sandbien, peut-être divisée en 4 unités informelles représentant la pente d'une plate-forme carbonatée (Apollonov *et al*, 1990 ; Fig. 4) :

- L'unité 1 est composée de calcaires brèchés, dépôts caractéristiques d'une base de pente.
- L'unité 2 est caractérisé par des dépôts turbiditiques carbonatés noirs à gris foncé avec des cycles de Bouma bien défini, pouvant représenter un éventail sous-marin. Un banc de schistes noir à gris épais d'1 à 3 mm situé dans la partie inférieur de l'unité 2 représente une couche pélagique caractéristique du sommet d'une séquence de Bouma
- L'unité 3 est composée pour sa part de calcaires lités fortement bioturbés
- L'unité 4, au sommet de la séquence, est composée de calcarénites caractéristiques d'un environnement marin peu profond.

Il y a une diminution évidente de la paléo-profondeur de l'unité 1 à l'unité 4, cette dernière, au sommet de la séquence, représentant un environnement marin peu profond.

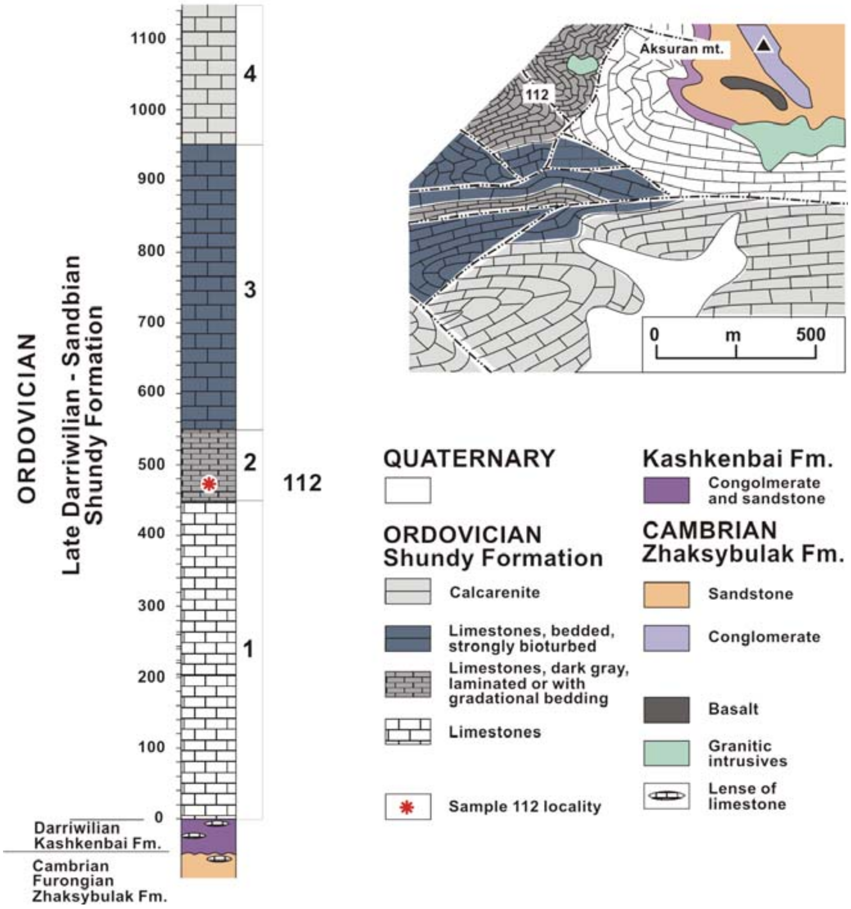


Figure 3: Carte géologique schématique de la région d'Atsu-Zhamshy avec localisation de l'échantillon (à droite) et colonne stratigraphique simplifiée de la Formation de Shundy (Cambrien moyen à supérieur) indiquant l'emplacement de l'échantillon 112 (à gauche)(d'après Pouille *et al*., 2012b).

III. Matériel

L'échantillon 112 étudié ici a été prélevé dans la localité 112 à environ 1100m au sud-ouest de la montagne Aksuran, dans la region d'Atasu-Zhamshy au Nord Ouest du lac Balkash (Fig. 3). Il a été extrait des calcaires noirs à gris foncés situés au milieu de l'unité 2 de la Formation de Shundy (Fig. 4). Un travail d'identification de la faune à triolobite provenant de la localité 112 a été mené par Mansoureh Ghobadipour et Leonid Popov. Cette faune s'est révélée très peu diversifiée avec la présence de seulement trois taxons : *Endymionia semielliptica*, *Porterfieldia* sp. aff. *P. delicata* et *Nambeetella* ? sp. Cette faune représente un biofaciès à Olenidae, caractéristique d'un environnement distal, dysaérobique qu'on pourrait positionner au niveau de l'offshore inférieur, en dessous de la limite d'action des vagues de tempête. Les trilobites *Endymionia semielliptica* et *Porterfieldia* sp. aff. *P. delicata* suggèrent un âge

Darriwilien supérieur, en accord avec l'âge donné par les graptolites découverts dans l'unité 2 dans les années 80.

Figure 4: Carte schématique du Kazakhstan central indiquant l'emplacement des montagnes d'Aksuran et de l'échantillon 112.

IV. Méthodes

L'échantillon a été traité pour l'analyse micropaléontologique selon le protocole décrit dans le Chapitre II, Partie 1, IV. Méthodes.

Nous avons expérimenté deux méthodes de section des radiolaires afin de tester leur intérêt sur l'étude les radiolaires du paléozoïque et sur ce qu'elles pouvaient apporter pour améliorer l'observation de la structure interne des radiolaires. En effet, la connaissance de la systématique et de la biodiversité des radiolaires du Paléozoïque inférieur se heurte à la difficulté de l'accès à la structure interne, notamment chez les formes sphériques dont la partie la plus interne (spicule ou microsphère) est rarement visible et dont l'attribution aux Entactinaires ou aux Spumellaires est souvent incertaine.

La première technique de section des radiolaires mise au point par Paulian Dumitrica est une technique destructive consistant à sectionner physiquement l'individu à l'aide d'une lame de rasoir. Elle présente l'avantage d'être peu couteuse et facilement réalisable. Néanmoins, cette méthode s'est révélée être assez infructueuse due à la mauvaise qualité des images obtenues au microscope optique et aux trop nombreuses pertes dues à la difficulté de ne pas casser le radiolaire au cours du processus.

La deuxième technique utilise l'imagerie 3D par microtomographie de rayons X. Cette technique non destructive permettant la reconstruction en 3 dimensions du radiolaire et son sectionnement artificiel. Néanmoins, elle présente l'inconvénient d'être extrêmement couteuse en temps et en matériel.

IV.1. Technique de sectionnement des radiolaires (d'après De Wever et al., 2001)

Cette étape consiste à poser les spécimens sur un plot métallique préalablement enduit en surface de vernis à ongle. Lorsque le vernis est sec, le plot peut être métallisé et le spécimen photographié au MEB. L'utilisation de vernis n'altère en aucun cas la qualité des photos. Après la prise de photo au MEB, il suffit de placer le plot MEB dans une boite de pétri avec un coton imbibé d'acétone et de fermer la boite quelques instants. Les vapeurs d'acétones permettre de dissoudre suffisamment le vernis pour pouvoir récupérer le radiolaire sans l'abimer à l'aide d'un cil monté sur une tige. Le radiolaire est ensuite déposé dans une goutte de baume du Canada sur une lame mince placée sur une plaque chauffante (l'idéal est d'utiliser de l'Hyrax pour les radiolaires du paléozoïque, souvent recristallisés, mais cette résine est très difficile à trouver). Lorsque le spécimen est totalement englué dans la goutte, la lame mince est retirée de la plaque chauffante et le baume est laissé à refroidir jusqu'à ce qu'il soit complètement durci. La goutte de baume du Canada peut alors être sectionnée très finement par une lame de rasoir tenue verticalement jusqu'à section partielle du radiolaire. On pose ensuite ¼ de lamelle en périphérie de la plaque chauffante puis on retourne la lame avec la résine durci au dessus du ¼ de lamelle et on attend que la résine fonde sur la lamelle. On obtient alors une lame avec un radiolaire sectionné que l'on peut observer et photographier au microscope optique (Fig. 5).

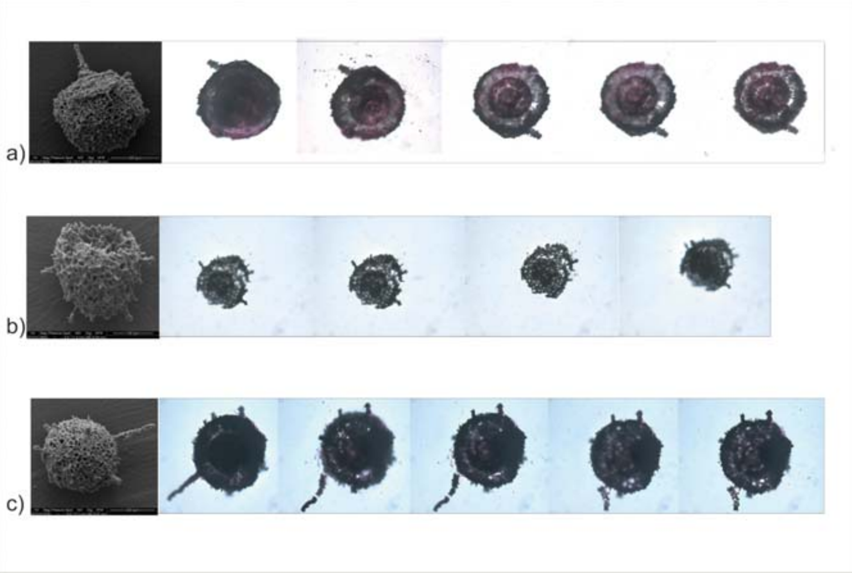


Figure 5 : Exemple de radiolaires sectionnés en plusieurs étapes et photographiés au microscope optique a) *Triplococcus* sp., b) *Triplococcus* sp. cf. *T. akzhala*, c) *Triplococcus aksuranensis*

IV.2. Imagerie 3D par tomographie de rayons X

La technique de l'Imagerie 3D par tomographie SRXTM (Synchrotron radiation X-ray tomographic microscopy) que nous avons utilisée permet de visualiser la structure interne et externe du radiolaire sans avoir à le sectionner. Cette technique consiste à reconstruire une image tri-dimensionnelle complète de haute qualité des structures internes du spécimen étudié par l'enregistrement sous forme de coupes sériées des différentes réactions produites par le passage du rayonnement synchrotron sur les structures. Nous avons appliqué cette méthode du SRXTM dans le but d'obtenir des images 3D complètes à la résolution du submicromètre de quatre radiolaires. Les analyses ont été effectuées par la ligne de faisceaux pour la tomographie à rayon X TOMCAT de la Swiss Light Source (SLS), synchrotron de troisième génération situé à l'institut Paul Scherrer en Suisse. Le nombre de projections réalisées pour les quatre échantillons s'élève à 4348. Ces 4348 coupes ont ensuite été reconstituées au laboratoire « Géosystèmes » de l'Université de Lille 1 à l'aide du logiciel de reconstruction 3D « AVIZO» (Avizo Fire Edition 3.6). Par l'intermédiaire de ce logiciel, les images une fois reconstruites peuvent être orientées et sectionnées sous tous les angles possibles (Fig. 6).

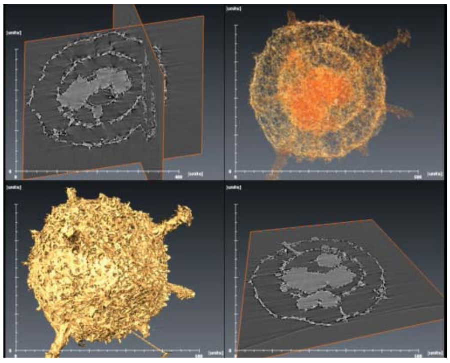


Figure 6 : Exemple de reconstitutions 3D obtenues grâce au logiciel Avizo. Le logiciel permet de contrôler la l'angle de section et la transparence des structures du radiolaire.

Ces reconstitutions ont permis l'observation de la structure interne de deux de ces radiolaires appartenant au genre *Triplococcus*. L'un est attribué à *Triplococcus aksuranensis*, que nous décrivons ici comme une nouvelle espèce (cf. Chapitre 3, Article 3), l'autre est attribué à *Inanihella ? akzhala* que nous attribuons dans ce travail de thèse à *Triplococcus akzhala* (cf. Chapitre 3, Article 3). L'observation de la structure interne de ces deux espèces confirme la présence de trois coques et d'une microsphère (Fig. 7). La structure interne des deux autres radiolaires s'est révélée malheureusement rempli par des grains de quartz, rendant toute observation impossible. Même si les images que nous avons pu reconstituer ne nous ont pas apportés d'informations supplémentaires par rapport aux nombreuses images MEB de spécimens cassés que nous avions déjà obtenues, cette expérience démontre la faisabilité de la méthode du SRXTM pour l'étude de la structure interne des radiolaires. Cette méthode pourrait se montrer d'une grande importance pour l'étude des radiolaires du Cambrien inférieur, qui sont retrouvés en quantité si rare qu'il est essentiel d'utiliser au maximum les méthodes non-destructives pour les analyser.

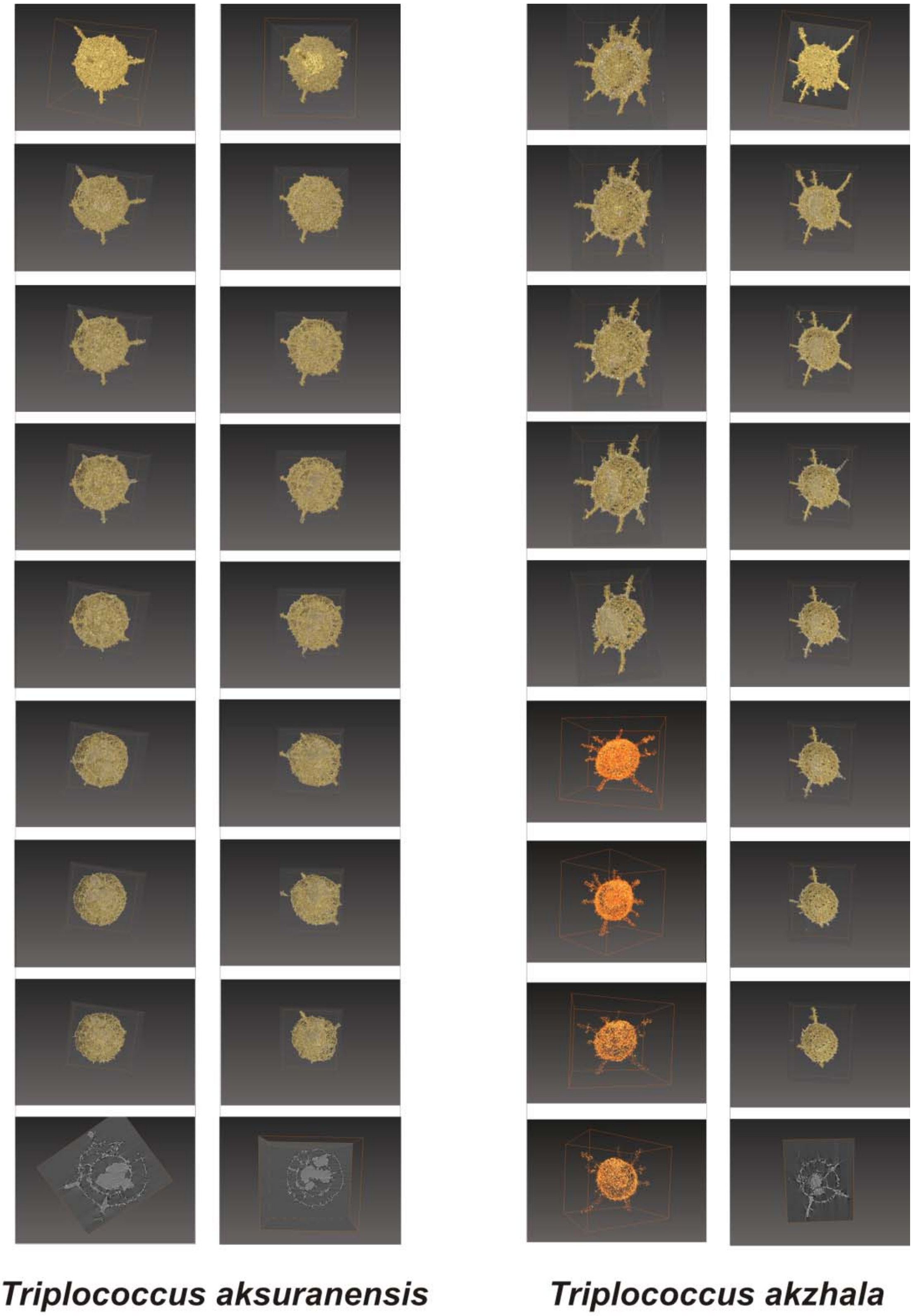


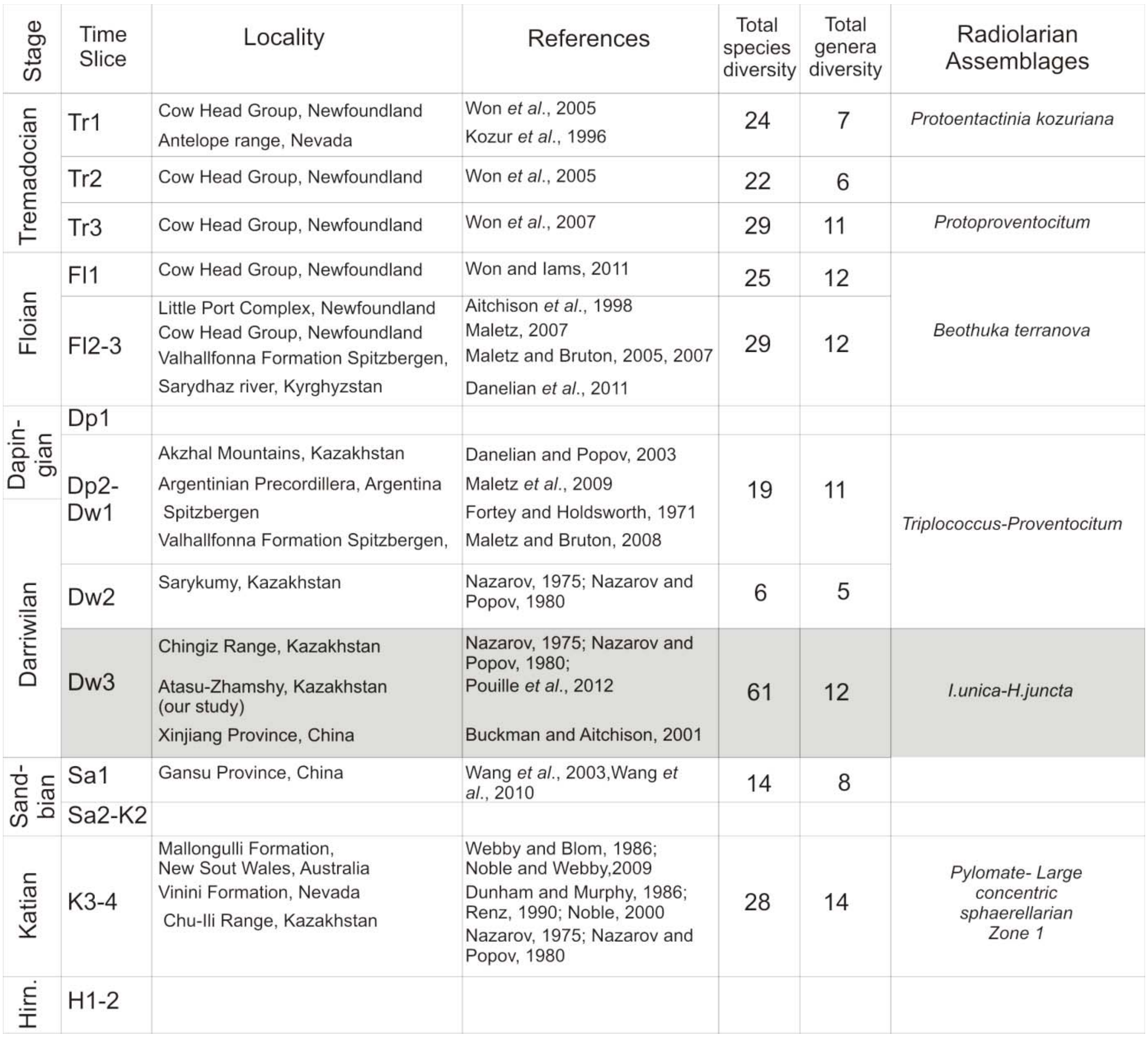
Figure 7 : Exemples de deux série de sections effectuées sur les radiolaires *Triplococcus aksuranensis* et *Triplococcus akzhala* par la logiciel Avizo permettant d'avoir un bon aperçu de la structure interne. Les deux rangées verticales de photos attribuées à chaque espèce correspondent à des séries de section effectuées sous deux angles de vue différents.

V. Résultats et discussion

Notre étude de l'échantillon Kazakhstanien 112 a donc permis de découvrir un assemblage à radiolaire très riche et bien préservé du Darriwilien supérieur (zone à *Hustedograptus teretiusculus*), dominé par les représentant de la famille des Inaniguttidae, constituant 69% de cet assemblage. L'étude taxonomique menée sur cet assemblage nous a permis d'identifier 30 nouveaux morphotypes dont neuf sont décrits ici comme de nouvelles espèces mais également de mieux appréhender la structure interne des Inaniguttidae. (Voir Articles 3 et 4). La biodiversité des radiolaires à l'Ordovicien a été bien étudiée par Noble et Danelian (2004) qui ont pu compiler de nombreuses études menées sur les radiolaires de l'Ordovicien permettant ainsi d'estimer le nombre total d'espèces et de genres présents dans chaque intervalle de temps de l'Ordovicien. Les données acquises lors de notre étude nous permettent ici de compléter cette base de données dans un nouveau tableau (Fig. 8), prenant également en compte les données plus récentes sur les radiolaires de l'Ordovicien. Pour ce faire, nous avons suivi les codes adoptés par Noble et Danelian (2004) à savoir : exclure les assemblages dont l'âge est indéterminé ou insuffisamment précis, prendre en compte les taxons laissés en nomenclature ouverte (ex : *Inanihella* sp.A) si ils sont correctement décrits et considérer les taxons présentant des affinités avec une espèce (ex : *Inanihella* aff. sp. *I. bakanasensis*) comme une espèce à part entière si aucune synonymie n'a été établie. Nous avons également exclu les radiolaires dont la détermination était trop ambigüe ou problématique.

Notre étude a permis d'identifier 30 espèces supplémentaires présentes au Darriwilien supérieur, doublant ainsi le nombre d'espèces connues au cours de cet intervalle. Elle permet donc de mettre en lumière une diversité spécifique beaucoup importante au Darriwilien supérieur que celle connue jusqu'à présent. En effet, nous pouvons constater que dans les intervalles de temps où des assemblages radiolaires ont été retrouvés majoritairement très bien préservés et en abondance (Trémadocien (Tr1-3), Floien (Fl1-3), Katien (K3-4)) le nombre d'espèces identifiées par intervalle de temps varie entre 22 et 29. Or, notre étude à permis de répertorier un total de 61 espèces au Darriwilien supérieur (Dw3). Il ne semble en revanche n'y avoir aucune tendance particulière notable au niveau de la diversité générique. Celle-ci garde un niveau stable avec 6 à 7 genres reconnus au Trémadocien inférieur puis 8 à 14 genres identifiés par intervalle de temps entre le Trémadocien supérieur et le Katien supérieur, à l'exception des intervalles peu ou non documentés (Dp1, Dw2, Sa2-K2, H1-2). La découverte d'un nombre important de nouvelles espèces au sein de l'assemblage à *I.unica-*

H.juncta apporte ici de nouveaux argument en faveur de la présence un pic de diversité au niveau spécifique au Darriwilien supérieur. Or, nous avons vu que les courbes de diversité de nombreux groupes planctoniques tels que les acritarches, les graptolites ou les chitinozoaires montrent toutes un pic de diversité au Darriwilien (Servais *et al*., 2008, 2009). Dans ce cas, la dynamique de diversité spécifique chez le groupe des radiolaires suivrait donc la tendance générale de la diversité des organismes planctonique lors de cette période.



Stage	Time Slice	Locality	References	Total species diversity	Total genera diversity	Radiolarian Assemblages
Tremadocian	Tr1	Cow Head Group, Newfoundland Antelope range, Nevada	Won *et al*., 2005 Kozur *et al*., 1996	24	7	*Protoentactinia kozuriana*
	Tr2	Cow Head Group, Newfoundland	Won *et al*., 2005	22	6	
	Tr3	Cow Head Group, Newfoundland	Won *et al*., 2007	29	11	*Protoproventocitum*
Floian	Fl1	Cow Head Group, Newfoundland	Won and Iams, 2011	25	12	*Beothuka terranova*
	Fl2-3	Little Port Complex, Newfoundland Cow Head Group, Newfoundland Valhallfonna Formation Spitzbergen, Sarydhaz river, Kyrghyzstan	Aitchison *et al*., 1998 Maletz, 2007 Maletz and Bruton, 2005, 2007 Danelian *et al*., 2011	29	12	
Dapingian	Dp1					
	Dp2-Dw1	Akzhal Mountains, Kazakhstan Argentinian Precordillera, Argentina Spitzbergen Valhallfonna Formation Spitzbergen,	Danelian and Popov, 2003 Maletz *et al*., 2009 Fortey and Holdsworth, 1971 Maletz and Bruton, 2008	19	11	*Triplococcus-Proventocitum*
Darriwilan	Dw2	Sarykumy, Kazakhstan	Nazarov, 1975; Nazarov and Popov, 1980	6	5	
	Dw3	Chingiz Range, Kazakhstan Atasu-Zhamshy, Kazakhstan (our study) Xinjiang Province, China	Nazarov, 1975; Nazarov and Popov, 1980; Pouille *et al*., 2012 Buckman and Aitchison, 2001	61	12	*I.unica-H.juncta*
Sandbian	Sa1	Gansu Province, China	Wang *et al*., 2003,Wang *et al*., 2010	14	8	
	Sa2-K2					
Katian	K3-4	Mallongulli Formation, New Sout Wales, Australia Vinini Formation, Nevada Chu-Ili Range, Kazakhstan	Webby and Blom, 1986; Noble and Webby,2009 Dunham and Murphy, 1986; Renz, 1990; Noble, 2000 Nazarov, 1975; Nazarov and Popov, 1980	28	14	*Pylomate- Large concentric sphaerellarian Zone 1*
Hirn.	H1-2					

Figure 8 : Tableau synthétique du nombre total d'espèces et de genres répertoriés par assemblage et par intervalle de temps. La provenance de ces assemblages et leurs références sont également indiquées.

Article 3:

New and revised Inaniguttid Radiolaria and associated trilobites from the upper Darriwilian (Ordovician) Shundy Formation of Kazakhstan

Pouille, L., Danelian, T., Ghobadi Pour, M & Popov, L. E.

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(41 pp.)

NEW AND REVISED INANIGUTTID RADIOLARIA AND ASSOCIATED TRILOBITES FROM THE UPPER DARRIWILIAN (ORDOVICIAN) SHUNDY FORMATION OF KAZAKHSTAN

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ABSTRACT— Representatives of the family Inaniguttidae dominate a diverse and well-preserved radiolarian assemblage from Kazakhstan. The fauna was extracted from the Shundy Formation, a limestone sequence that accumulated on the slope of a carbonate platform and which crops out in the Aksuran Mountains (North Balkhash Region). The family Inaniguttidae dominates the studied assemblage, with the genus *Triplococcus* being particularly abundant. Inaniguttids are represented by five genera and 14 species (including two: *Triplococcus aksuranensis* and *Inanibigutta maletzi*). Based on the presence of species *Haplentactinia juncta*, the fauna can be correlated with the upper Darriwilian *Haplentactinia juncta-Inanigutta unica* assemblage. Identified trilobites (*Endymionia semielliptica* and *Porterfieldia* sp. aff. *P. delicata*) found in the same sample also suggest a late Darriwilian age, which is in agreement with the age suggested by graptolites identified in the 1980s.

INTRODUCTION

KAZAKHSTAN HAS been crucial to our understanding of Ordovician Radiolarian biodiversity. A number of localities around Lake Balkash have yielded relatively well-preserved Radiolaria from Middle-Upper Ordovician carbonate rocks (Nazarov, 1975, 1988; Nazarov et al., 1975, 1977; Nazarov and Popov, 1980; Nazarov and Ormiston, 1993; Danelian and Popov, 2003). Coeval sequences represented by radiolarian cherts (e.g. Scotland;

Danelian and Clarkson, 1998; Danelian and Floyd, 2001; China; Buckman and Aitchison, 2001) reveal some species in common, but the assemblages are less diverse, possibly because they are more affected by taphonomic bias. The family Inaniguttidae Nazarov and Ormiston, 1984 represents one of the major faunal components of Ordovician radiolarian assemblages (Nazarov and Ormiston, 1993; Noble and Danelian, 2004; Maletz, 2011). Its earliest known representatives date from the early Ordovician (late Dapingian (?), Maletz, 2007) and the family diversified substantially during the Middle Ordovician (Noble and Danelian, 2004; Maletz, 2011). Although first described nearly 30 years ago (Nazarov and Ormiston, 1984), the family Inaniguttidae is nevertheless still poorly understood in terms of its inner test construction and diversity (e.g. discussion in De Wever et al., 2001). This preliminary report on the radiolarians yielded from a carbonate sample of the Shundy Formation in Kazakhstan contains a large number of relatively well preserved specimens and in some cases allows observation of the innermost parts of the skeleton. This paper focuses on the taxonomic study of Inaniguttidae including the description of two new species and emendation of the genus *Triplococcus* Danelian and Popov, 2003. It also describes the Trilobites found at the same level, which provide additional biochronological and palaeoenvironmental constraints. The entire Radiolarian assemblage will be presented in a subsequent publication.

GEOLOGICAL SETTING

The Kazakhstan mountain belt represents a complex agglomerate of pre-Cambrian and Lower Paleozoic microplates and intraoceanic island arc terranes (Yakubchuk, 1990; Zonenshain et al., 1990; Sengör et al., 1993; Popov et al., 2009). The Atasu-Zhamshy region (Popov et al., 2009) is located north-west of Lake Balkhash (Fig. 1). The sedimentary rocks in the area are mainly composed of Lower Paleozoic limestones and dolomites exposed in numerous scattered outcrops. These sedimentary sequences accumulated on a carbonate platform, situated on the passive continental margin of a Lower Palaeozoic microplate (Apollonov, 2000). Outlines of the Lower Palaeozoic geology and stratigraphy of the area have been published by Alperovich et al. (1971), Pupyshev (1974) and Apollonov et al. (1990).

The Middle to Upper Ordovician (Darriwilian to Sandbian) Shundy Formation, in which radiolarians occur sporadically in deep-water carbonates, is divided into four informal stratigraphic units (Apollonov et al., 1990) as follows (Fig. 2):

FIGURE 1— Schematic map of central Kazakhstan indicating the location of the Radiolarian and Trilobite bearing strata of this study in the Atasu-Zhamshy region (modified after Danelian and Popov, 2003).

- Unit 1 (≤ 450 m) is composed of limestones, which often contain carbonate debris flows characteristic of the base of a slope;
- Unit 2 (≤ 100 m) is composed of bedded, black or dark grey limestones with thin (1-3 mm thick) dark grey chert intercalations present in the lower part of the Unit; carbonate turbidites with well-defined Bouma cycles are also present in this unit, suggesting accumulation in a possible base-of-slope carbonate apron system.
- Unit 3 (≥ 400 m) is comprised of bedded and strongly bioturbated limestones;
- Unit 4 (≤ 200 m), situated at the top of the sequence, is composed of calcarenites.

Sample 112 was collected from a deep-water limestone sequence situated in the middle part of Unit 2 of the Shundy Formation at a locality of the Atasu-Zhamshy Region (47°32'40.77"C, 73° 2'47.34"E) situated about 1100 m west-southwest of the Aksuran Mountains (north-west of Lake Balkhash).

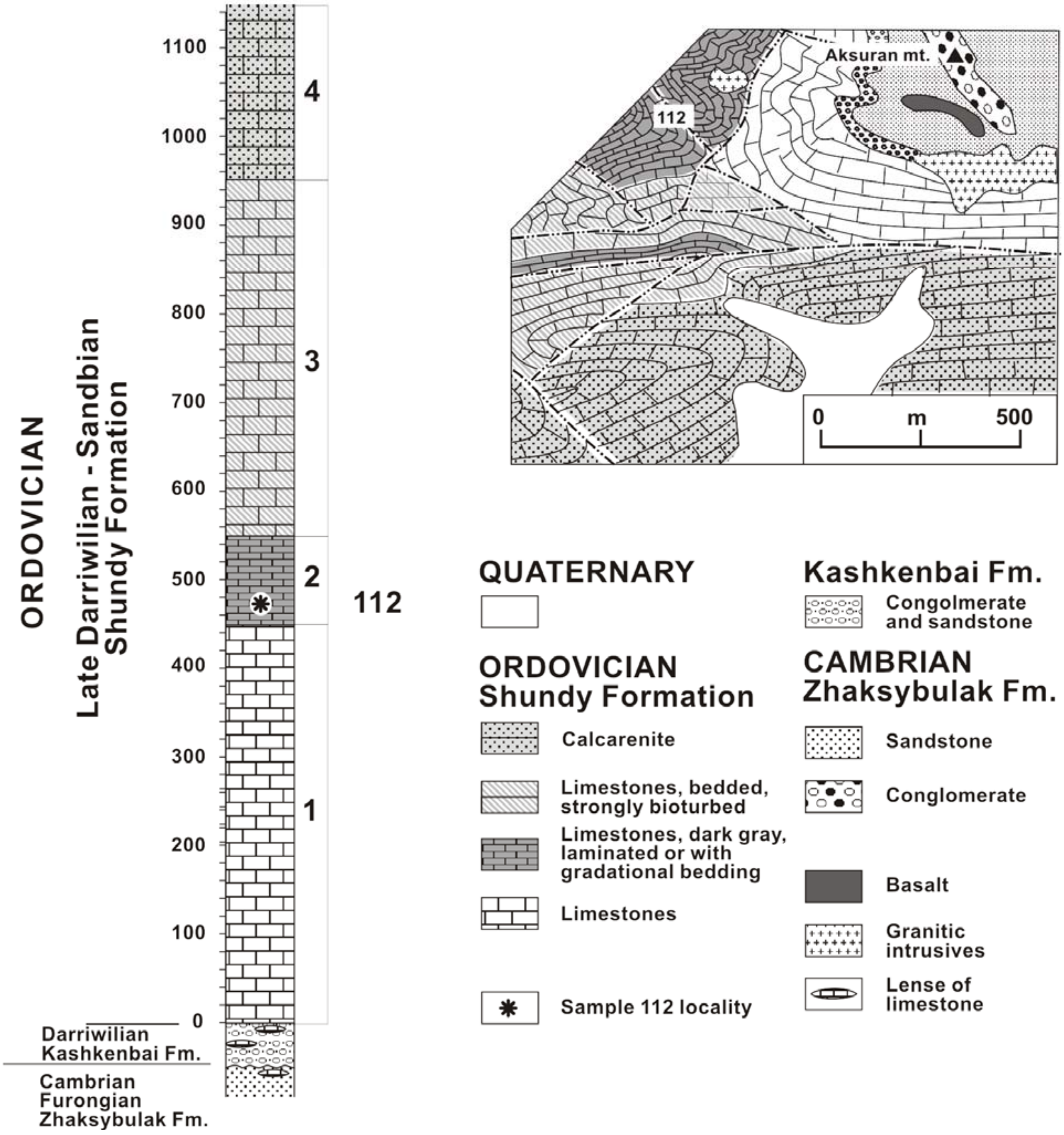

FIGURE 2— Schematic geological map of the Atasu-Zhamshy region (upper right) indicating the location of sample 112 and simplified stratigraphic column of the Shundy Formation (Middle to Upper Ordovician).

MATERIAL AND METHODS

More than 450 specimens were extracted from a black to dark-grey micritic limestone sample after treatment with diluted acetic acid. The sample was crushed into 1-5 cm size blocks and immersed in 30% diluted acetic acid for a maximum of 12 hours. After washing away the acid, the sample residues were sieved through a 50 µm sieve and mounted on SEM stubs. Some specimens were sectioned using Dumitrica's method (e.g., De Wever et al., 2001), but given the fragility of the radiolarian specimens in our material, most of which are highly recrystallized, very few clear images were obtained.

Trilobites were collected from the same level as the radiolarian-bearing sample 112.

All the types described here are housed in the public palaeontological collections of the Earth Sciences Department (SN5) of the University of Lille 1 (France).

SYSTEMATIC PALAEONTOLOGY

—*Radiolaria* (L. Pouille and T. Danelian)

Family INANIGUTTIDAE Nazarov and Ormiston, 1984

Type genus. Inanigutta Nazarov and Ormiston, 1984

1984 Inaniguttidae NAZAROV AND ORMISTON, p. 72 [in Russian], p. 86 [in English]

1995 Inaniguttidae Nazarov and Ormiston; NOBLE AND AITCHISON, p. 21.

2003 Inaniguttidae Nazarov and Ormiston; DANELIAN AND POPOV, p. 332.

Remarks.— The family is characterised by spherical radiolarians composed of one or several latticed to irregularly porous concentric cortical shells bearing six or more rod-like spines. Their innermost structure consists of a small hollow sphere (the microsphere) or a polyhedron from which the rod-like outer spines radiate. Following the initial taxonomic scheme of Nazarov, genera in this family are distinguished by two major criteria: the number of shells and the number of outer spines that can range from 6 to 20. The internal structure of the siliceous skeleton is difficult to decipher as the fragile inner structure is rarely preserved and it is difficult to examine the inner shell and microsphere without breaking the specimen. Moreover, as mentioned by a number of authors (e.g. Maletz, 2011), the number of shells as a genus diagnostic character needs to be re-evaluated as it may depend on the ontogenic stage of the specimen. The inner framework was described initially by Nazarov as an internal structure in the form of a polyhedron located in the centre of the test. Only a few species with a central skeletal structure in the form of a microsphere have been described so far, such as *Triplococcus acanthicus* Danelian and Popov, 2003, *Inanigutta penrosei* (Ruedemann and Wilson, 1936), *Kalimnasphaera maculosa* Webby and Blom, 1986, *Inanigutta complanata* (Nazarov, 1975) and species belonging to the genus *Plussatispila* MacDonald, 2006 (Danelian and Popov, 2003; MacDonald, 2006; Maletz and Bruton, 2007; Noble and Webby, 2009).

Genus TRIPLOCOCCUS Danelian and Popov, 2003

Type species. Triplococcus acanthicus Danelian and Popov, 2003

2003 *Triplococcus* DANELIAN AND POPOV, p 333.

Emended diagnosis.— Inaniguttid Radiolaria composed of three almost perfectly spherical shells placed around a small microsphere (Ø: 40-55 µm) from which originate 5 to 12 outer spines. These outer spines emerge from the bars of the microsphere, initially as thin spines, becoming thicker rod-like spines from the median shell (second after the microsphere) onwards. Numerous beams originate either from the surface of the inner or from the median shell. Outer spines can bear more or less developed apophyses. The microsphere and inner shell's wall structure consist of a thin layer, pierced irregularly,whereas median and outer shells are regularly perforated. The genus *Triplococcus* differs from *Plussatispila* (another three-shelled Inaniguttid genus) by its more closely spaced inner and median shells, its smaller size (outer shell Ø: ca. 290-330 µm) and the wall structure of its shell (*Triplococcus* has a thin microsphere, surrounded by an inner shell, followed by thick, porous median and outer shells, whereas *Plussatispila* has latticed inner shells and a latticed to « gossamer » outer shell).

Occurrence. —Upper Dapingian (?) to upper Darriwilian from Kazakhstan and Argentina.

Remarks.— The term "microsphere" is here used in the sense of Maletz and Bruton (2007) for the hollow sphere (Ø : ca. 40-55 µm) that is located in the centre of the test. The number of outer spines can be up to 12 (instead of 6 in the original definition). Beams not only originate from the surface of the inner shell (as in *Triplococcus acanthicus*) but also from the surface of the median shell.

Based on material from the Lower Silurian Canadian Arctic, MacDonald (2006) compared *Triplococcus* with *Plussatispila* and established a number of new species based essentially on the number of cortical shells: *Plussatispila delicata* MacDonald, 2006 which possesses a microsphere and two additional shells (Fig. 3. 9), *Plussatispila cornwallisensis* MacDonald, 2006 for forms with three shells (Fig. 3. 11) or *Plussatispila magnilimax* MacDonald, 2006 for forms with four concentric shells (Fig. 3. 12).

He distinguished the two genera based on the fact that *Triplococcus* was described as possessing only five or six spines, while *Plussatispila* displays seven or more spines. The material of this study contains specimens with up to 12 spines and thus casts doubt on MacDonald's hypohtesis. However, *Triplococcus* can still be distinguished from *Plussatispila* by its shell's wall structure and by its smaller dimensions compared with three to four-shelled *Plussatispila* (outer shell Ø: ca. 290-330 µm for *Triplococcus* in our material; 414-475 µm for *P. magnilimax*; 384-495 µm for *P. cornwallisensis*). Moreover, a greater distance separates the inner shell from the median shells of *Plussatispila* while in *Triplococcus* they are more closely spaced. The genus *Plussatispila* also differs from *Triplococcus* in the occasional presence of apophyses on the rays between the inner and median shells.

The number of shells and spines are often taken as genus-level characters in radiolarian taxonomy (Nazarov and Ormiston, 1984, 1993; Nazarov, 1988; Furutani, 1990; Noble, 1994; Danelian and Popov, 2003). *Triplococcus* is distinguished from other genera of the family Inaniguttidae chiefly by its greater number of shells. However, the significance of using the number of shells as a genus-level diagnostic character is still under debate (e.g. discussion in MacDonald, 2006); in addition some recent ontogenetic studies on Cenozoic radiolarians revealed that the number of concentric shells can vary with the ontogenic stage (Suzuki, 2006). It has also been observed that some three-shelled actinommid species developed into four-shelled specimens during growth (Cleve, 1899; Petrushevskaya, 1967; Björklund, 1974; Itaki et al., 2003; Nishimura, 2003; Suzuki, 2006). In 2006, MacDonald included all Inaniguttidae present in his Silurian material of the Cape Phillips Formation in a single genus (*Plussatispila*), independent of their number of shells (two to four). However, since the ontogenetic growth of Ordovician Inaniguttids is not yet fully understood, for the moment we prefer to use a more traditional (although imperfect) taxonomic scheme. Thus, *Triplococcus* can still be distinguished from other Inaniguttid genera by the number of its spines or its dimensions. For example, although *Triplococcus'* features are fairly close to the ones of *Inanihella* Nazarov and Ormiston, 1984, the two genera can be differentiated by their shell number and dimensions.

TRIPLOCOCCUS AKSURANENSIS new species

Figures 3.1, 4.1-4.14

Diagnosis.— The skeleton consists of concentric shells around a central microsphere. The latter and the inner shell are made of a thin layer that is irregularly pierced by uneven pores. The median and outer shells are made of a regularly pierced pore frame. Six to eight outer spines originate at the microsphere. Numerous beams are present between median and outer shells.

Description.— The internal frame consists of a microsphere at which six to eight outer spines originate. The test surrounding the microsphere consists of three encapsulated shells, the inner, median and outer shells. The thin outer spines turn into thicker rod-like spines starting from the outer surface of the median shell. They emerge as straight (more rarely curved) rod-like spines from the surface of the outer shell. The microsphere is ca. 40-55 µm in diameter. The inner sphere and microsphere are thin and irregularly pierced by uneven pores. The median and outer shells have a thick pore-frame which is regularly perforated. The pores are numerous, with a hexagonal to sub-circular shape and with a diameter of 5-15 µm. Numerous needle-like beams originate from the pore-frame junctions of the median shell to connect to the outer shell. Beams joining the inner and median shell can be found on some specimens. Very thin, pointed and short secondary spines originate from the pore-frame of the outer shell. Rod-like outer spines emerge from the surface of the outer shell surface and are usually broken but can be up to 197 µm when well-preserved. They often display weakly developed apophyses.

Etymology. — Named after the Aksuran mountains of Kazakhstan, where sample 112 is located.

Types. — Holotype: Figure 4.3a (USTL1173/048), Paratypes: Figure 4.1 (USTL1178/035) Figure 4.4 (USTL1142/011), Figure 4.6a (USTL1142/075) and Figure 4.10 (USTL1142/031).

Measurements (in micrometers; μm).— Diameter of the outer shell: 290-350; diameter of the median shell: 180-230; diameter of the inner shell: 90-130; diameter of the microsphere: 40-55; diameter of the pores: 5-15; outer spines up to 197.

Material examined.— 83 specimens.

Occurrence. — Upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan.

Remarks.— The entire microsphere is rarely preserved in our material. It is often found as relic fragments at the end of the outer spines and there is no evidence of a continuity of these

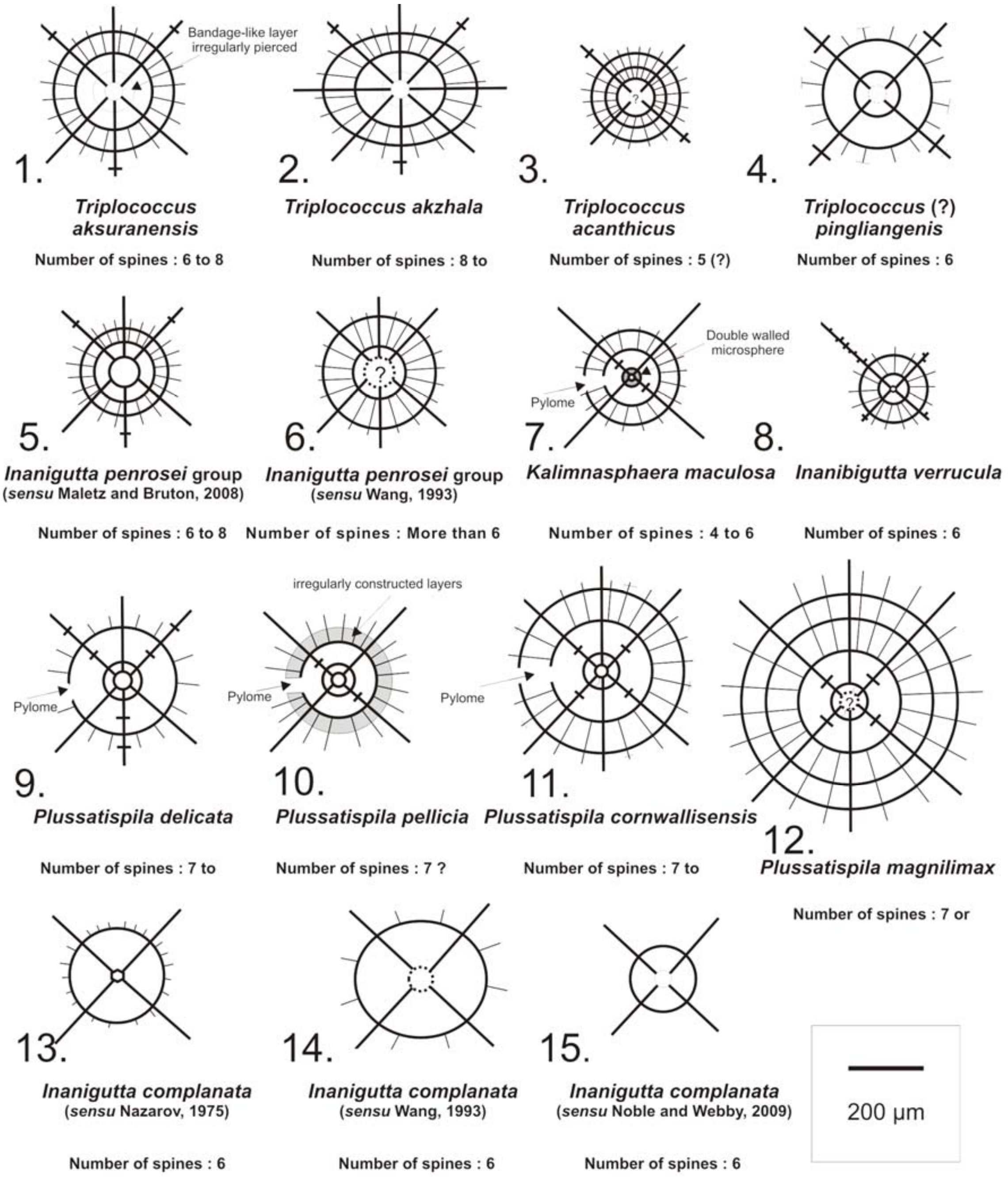

FIGURE 3— Schematic drawings of a number of Inaniguttid species compared with *Triplococcus aksuranensis* in the species discussion. Scale bar (200 µm) is the same for all drawings. *1*, *Triplococcus aksuranensis* Pouille and Danelian n.sp.; *2*, *Triplococcus akzhala* (Danelian and Popov, 2003); *3*, *Triplococcus acanthicus* Danelian and Popov, 2003; *4*, *Triplococcus* (?) *pingliangensis* (Wang, 1993); *5*, *Inanigutta penrosei* group (Ruedemann and Wilson, 1936) drawn after the material of Maletz and Bruton (2008); *6*, *Inanigutta penrosei* group (Ruedemann and Wilson, 1936) drawn after the material of Wang, 1993); *7*, *Kalimnasphaera maculosa* Webby and Blom, 1986 ; *8*, *Inanibigutta verrucula* (Nazarov, 1975) ; *9*, *Plussatispila delicata* MacDonald, 2006; *10*, *Plussatispila pellicia* MacDonald, 2006; *11*, *Plussatispila cornwallisensis* MacDonald, 2006 ; *12*, *Plussatispila magnilimax* MacDonald, 2006 ; *13*, *Inanigutta complanata* (Nazarov, 1975) drawn after the material of Nazarov, 1975; *14*, *Inanigutta complanata* (Nazarov, 1975) drawn after the material of Wang, 1993; *15*, *Inanigutta complanata* (Nazarov, 1975) drawn after the material of Noble and Webby, 2009.

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spines into the microsphere. The rarity of the microsphere could be attributed to preferential dissolution due to its fragility and small size. *Triplococcus aksuranensis* (Fig. 3. 1) differs from *T. acanthicus* (Fig. 3. 3) in having six or eight outer spines (*T. acanthicus* is described as having five to six outer spines) and in bearing numerous beams that originate at the surface of the median shell rather than the surface of the inner shell. However, it should be emphasized that rare beams may be present on the innermost shell of some specimens of *T. aksuranensis*. It also differs from *T. acanthicus* in its larger size (outer shell Ø: ca. 290-330 µm for our material; 214-257 µm for *T. acanthicus*). Despite some morphological similarities, *Triplococcus* (?) *pingliangensis* (Wang, 1993; Fig. 3. 4) differs from *T. aksuranensis* in its larger size. Indeed, even though their inner shells are of approximately the same size (Ø: 100-140 µm for *T.* (?) *pingliangensis* and 90-130 µm for *T. aksuranensis*), the median shell of *T.* (?) *pingliangensis* (Ø: 220-360 µm) is much larger than that of *T. aksuranensis* (Ø: 180-230 µm). Moreover, the dimensions of *T.* (?) *pingliangensis* median shell are closer to the dimensions of *T. aksuranensis* outer shell (Ø: 290-350 µm). Therefore, *T.* (?) *pingliangensis* inner and median shells are not as closely spaced as in *T. aksuranensis*.

Some of the *Triplococcus* specimens encountered in our material possess only two shells (certainly due to poor preservation) but can still be distinguished from other two-shelled Inaniguttids (i.e. *Inanihella*) by their larger size (outer shell Ø: 270-350 µm, median shell Ø: 180-260 µm).

T. aksuranensis differs from all species of *Plussatispila* in its shell structure and dimensions (e.g. discussion under the genus *Triplococcus*) and in the relative arrangement of its inner and median shells which are more closely spaced than in any species of *Plussatispila* (distance between inner and median shells of a minimum of 160 µm for *Plussatispila magnilimax*, of 142 µm for *Plussatispila cornwallisensis*, of 162 µm for *Plussatispila delicata*, of 118 µm for *Plussatispila pellicia* MacDonald, 2006 and 50 µm for *T. aksuranensis*). *T. aksuranensis* also differs from *P. cornwallisensis*, *P. delicata* and *P. pellicia* (Fig. 3. 10) in the absence of a pylome.

Moreover, our material differs from all species cited herein (*T. aksuranensis*, *T.* (?) *pingliangensis* and all the *Plussatispila* species) in displaying a variation in the wall structure of the microsphere and the inner shell, both made of a very thin irregularly porous layer, and the median and outer shell, the wall of both of which consists of a regularly porous thick pore-frame. *T. aksuranensis* displays some morphological similarities with the *Inanigutta penrosei* group *sensu* Maletz and Bruton (2008) (Fig. 3.5-3.6) by the presence of two to three shells and a microsphere. However, *I. penrosei* possesses a microsphere of a wide mesh made of bars nearly twice as large as those found in our material (ca. 80 µm ≠ 40-55 µm). Moreover, all the spheres in *I. penrosei*, including the inner shell, are produced by thin, cylindrical bars which form an irregular to hexagonal meshwork. Forty specimens of *I. penrosei* have also been identified by Wang (1993) from Chinese material but as the shape of their outer shell varies from spherical to sub-spherical and their dimensions range from 240 to 440 µm (a gap of 200 µm while in Maletz and Bruton's material outer shells range from 220 to 240 µm) Wang may have included within the *I. penrosei* larger species such as *T. aksuranensis* or *Triplococcus akzhala* (Danelian and Popov, 2003; Fig. 3. 2) which are difficult to differentiate from *I. penrosei* when intact. The species *Inanigutta complanata* (described initially by Nazarov, 1975 and reported by Nazarov and Popov, 1980; Nazarov and Ormiston, 1984; Wang, 1993; Noble and Webby, 2009; Fig. 3.13-3.15) currently incorporates great morphological differences and different dimensions (outer shell Ø: 250-253 µm for Nazarov's material; 310-350 µm for Wang's material and 165-185 µm for Noble and Webby's material). Nazarov described his material as mostly spherical, sometimes slightly flattened, with small spines in the form of a trihedral pyramid on the outer shell and inner framework consisting of a hexahedron. Wang's material is described as more usually elliptical and rarely spherical and with many slender spines emerging from the outer shell. Nothing is mentioned concerning the internal framework. Noble and Webby's material has no spines radiating from the outer shell and an inner framework consisting of a spherical microsphere. The morphotype illustrated by Noble and Webby (2009) as *I. complanata* displays the same

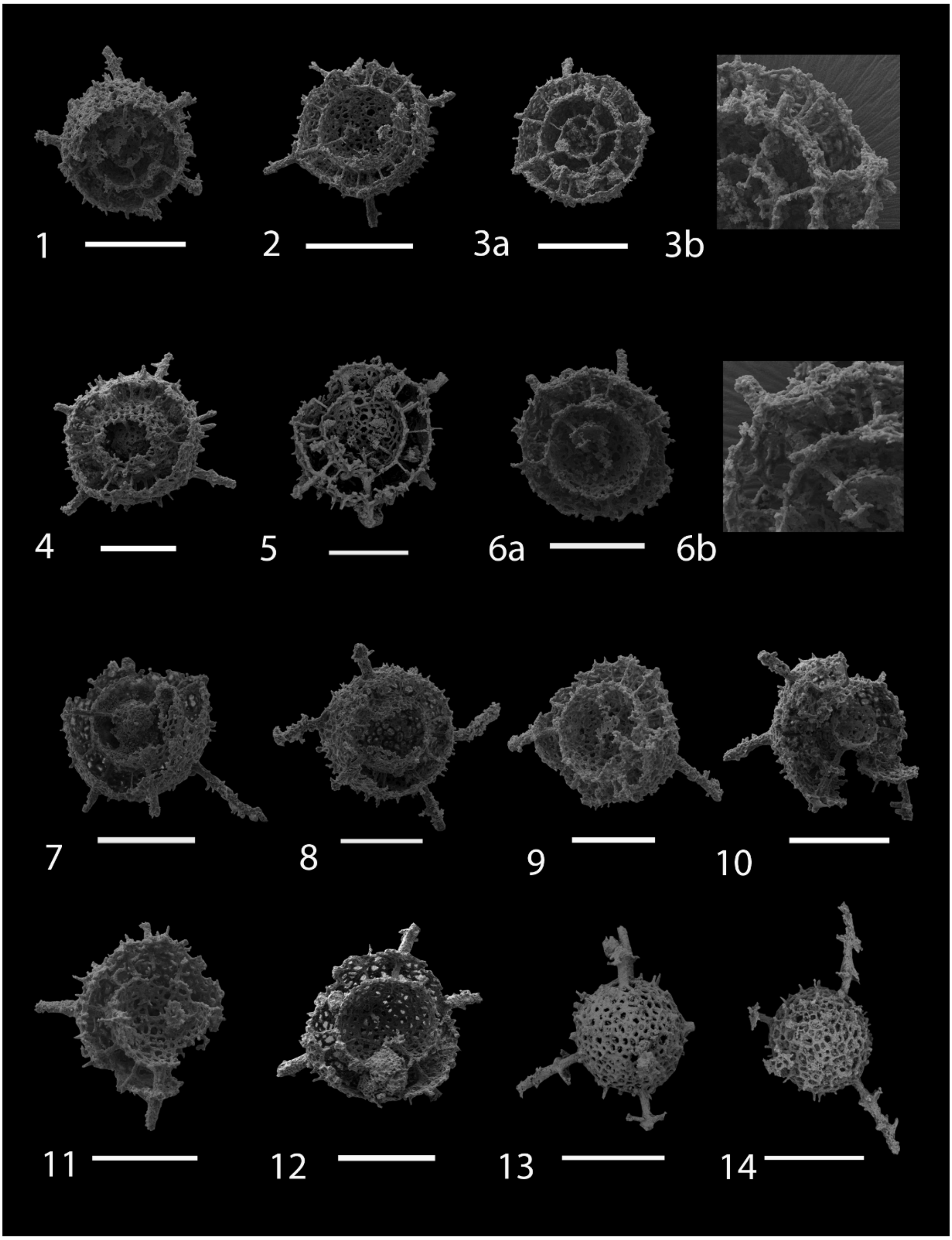

FIGURE 4— Scanning Electron Micrographs of *Triplococcus* radiolarian specimens yielded from Shundy Formation, locality 112, Shundy Mountains, North Balkhash Region. Scale bar corresponds to 200 µm on all figures. *1-14*, *Triplococcus aksuranensis* Pouille and Danelian n.sp.; *2*, Broken specimen bearing relic fragments of the inner shell and the microsphere (USTL1157/004); *3a*, Holotype of *Triplococcus aksuranensis* (USTL1173/048); *3b*, Magnified view of the internal structure of the holotype, showing the inner sphere and

relic fragments of the microsphere from which two of the secondary spines originate; *1*, *4*, *6a*, *10*, Paratypes of *Triplococcus aksuranensis* (USTL1178/035; USTL1142/011; USTL1142/075; USTL1142/031); *1*, Broken specimen showing the thin layer of the inner shell; *6b*, Magnified view of the three shells and the microsphere of *6a*; *10*, Note the thin layered framework composing the microsphere and the inner shell; *5*, (USTL1140/065); *7-9*, (USTL1173/002; USTL1141/015; USTL1183/024); *11-12*, (USTL1142/074; USTL1184/033); *13-14*, Juvenile or broken specimens of *Triplococcus aksuranensis*, lacking the third shell (USTL1180/063; USTL1185/010).

internal structure as our *Triplococcus* specimens. It is composed of a small microsphere (35-55 µm) of a single layer. However, these *I. complanata* cannot be confused with juvenile forms of *T. aksuranensis* because the shell dimensions do not correspond and their inner shells display a rounded pore-frame while in our material the inner shell also consists of a single layer.

Kalimnasphaera maculosa (Fig. 3. 7) has been described by Webby and Blom (1986) as a spherical to subspherical radiolarian composed of three to four concentric shells. In fact, the two innermost shells, termed by Webby and Blom as first and second medullary shells can be confused with a microsphere due to their very small size (respectively 13 and 40 µm). Those two medullary shells were later described by Noble and Webby (2009) from Katian material as one “double walled latticed medullary shell”. Measurement of the illustrated figures indicates that this double walled medullary shell ranges from 20 to 55 µm in size. Therefore, *K. maculosa* corresponds to a two-shelled radiolarian with a double walled microsphere and so cannot be confused with *Triplococcus*. Besides its peculiar inner framework consisting of a double walled microsphere, *K. maculosa* also differs from *T. aksuranensis* in having a microsphere of pore-bars with rounded cross section and slightly polygonal outline, in having a large pylome on the outer shell, in the presence of apophyses between the microsphere and the inner sphere and in its smaller dimensions (outer shell Ø: 198-307 µm and inner shell: 111-189 µm in *K. maculosa*; outer shell Ø: 270-350 µm, median shell 180-260 µm and inner shell: 90-130 µm in *T. aksuranensis*)

Juvenile or broken morphotypes of *T. aksuranensis* composed of only two shells (inner and median shell) that were found in our material can still be differentiated from other Inaniguttidae by the peculiar layered-like structure of their microsphere and inner sphere. However, some unbroken specimens showing only the median shell can be easily confused with *Inanibigutta verrucula* (Nazarov, 1975; Fig. 3. 8). The dimensions of *T. aksuranensis* median shell (Ø: 180-230 µm) are very similar to the outer shell dimensions of *I. verrucula* (Ø: 180-260 µm) as described by Wang (1993). Four unbroken specimens in our material display some morphological similarities with *I. verrucula* having one or two long, straight or gently curved outer spines from which branch randomly distributed apophyses (Fig. 4.13-4.14). However, rare small fragments of a porous shell also branch on some spines, testifying to the presence of a third shell of the same dimensions as *T. aksuranensis* outer shell (Ø: 280-326 µm herein; 290-350 µm for *T. aksuranensis*).

TRIPLOCOCCUS AKZHALA (Danelian and Popov, 2003)

Figures 3.2, 5.1-5.8

2003 *Inanihella* (?) *akzhala* DANELIAN AND POPOV, p.333, fig. 5n-r
2009 ?*Inanihella* (?) *akzhala* Danelian and Popov, MALETZ et al., p.59, fig. 4.1–12

Emended diagnosis.— Test made of encapsulated shells around a microsphere from which radiate 8 to 12 outer spines. Most internal shell surrounding the microsphere consists of a thin layer, irregularly pierced. Median and outer shells display a thick pore-frame regularly perforated by polygonal to oval pores. Outer shell varies from sub-spherical to strongly ellipsoidal shape. Outer spines can bear small apophyses. Numerous beams are present between the median and outer shell.

Measurements (in micrometers; µm).—Diameter of the outer shell: 270-330 (minor axis) / 370-450 (major axis); diameter of the median shell: 180-260; diameter of the inner shell: 90-100; diameter of the microsphere: 45-55; length of outer spines: ≤ 324.

Material examined.— 67 specimens.

Occurrence.— From the upper Dapingian (?) of the Akzhal Formations, Balkhash Region, Kazakhstan to the upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan and the Yerba Loca Formation, Western Precordillera, Argentina.

Remarks.— The internal structure of *Inanihella* (?) *akzhala* had never been observed before and this species was tentatively assigned to the *Inanihella* genus but its attribution remained uncertain. The new material allowed the observation of three encapsulated porous shells surrounding a microsphere which is characteristic of the genus *Triplococcus*. The microsphere is broken in every observed specimen but relic fragments still present at the innermost ends of the outer spines testify to its former presence. The presence of apophyses at the outermost ends of the outer spines may indicate the presence of an incomplete fourth shell.

The observed material shows that an inner sphere consists of a thin, irregularly pierced, layer while the median and outer shells are made of a thick pore-frame that is regularly pierced by polygonal, rounded or strongly elongated pores. It differs from the material described by both Danelian and Popov (2003) and Maletz et al. (2009) in its larger size (outer shell Ø: ca. 216-268 µm for Danelian and Popov's material; 220-300 µm for Maletz's material; 270-450 µm here). Like the Argentinian material recovered by Maletz et al. (2009), the shape of our specimens ranges from sub-spherical to strongly ellipsoidal.

Maletz suggested that the elongated specimens could have been distorted by partial compaction of the sediment. However, in this case, all specimens would have been distorted, regardless of their genus assignment. Yet, on over 450 specimens recovered in our material only those that can be assigned to *Triplococcus akzhala* display such an elongated shape. The peculiar shape of the shell should therefore be considered as charateristic for this species.

T. akzhala bears the same inner wall structure as *T. aksuranensis* with its layered microsphere and inner sphere. However, it differs from *T. aksuranensis* in its ellipsoidal shape, its larger size (Ø: up to 350 µm for *T. aksuranensis*; up to 450 µm for *T. akzhala*) and its larger number of spines (max. eight outer spines in *T. aksuranensis*, max. 12 outer spines in *T. akzhala*)

TRIPLOCOCCUS sp. cf. T. AKZHALA (Danelian and Popov, 2003)

Figure 5.9-5.11

Cf. 2003 *Inanihella* (?) *akzhala* DANELIAN AND POPOV, p.333, fig 5n-r

Description.— Outer shell oval to sub-spherical, irregularly perforated by oval to elongated pores. Eight to 12 outer spines arranged radially. Internal frame consists of a microsphere from which the outer spines originate. Beams are present between the median and outer shell. Numerous short beams emerge at the surface of the outer shell.

Measurements (in micrometers; µm).— Diameter of the outer shell: 190-240; length of outer spines: 15-25.

Material examined.— 12 specimens.

Occurrence.— Upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan.

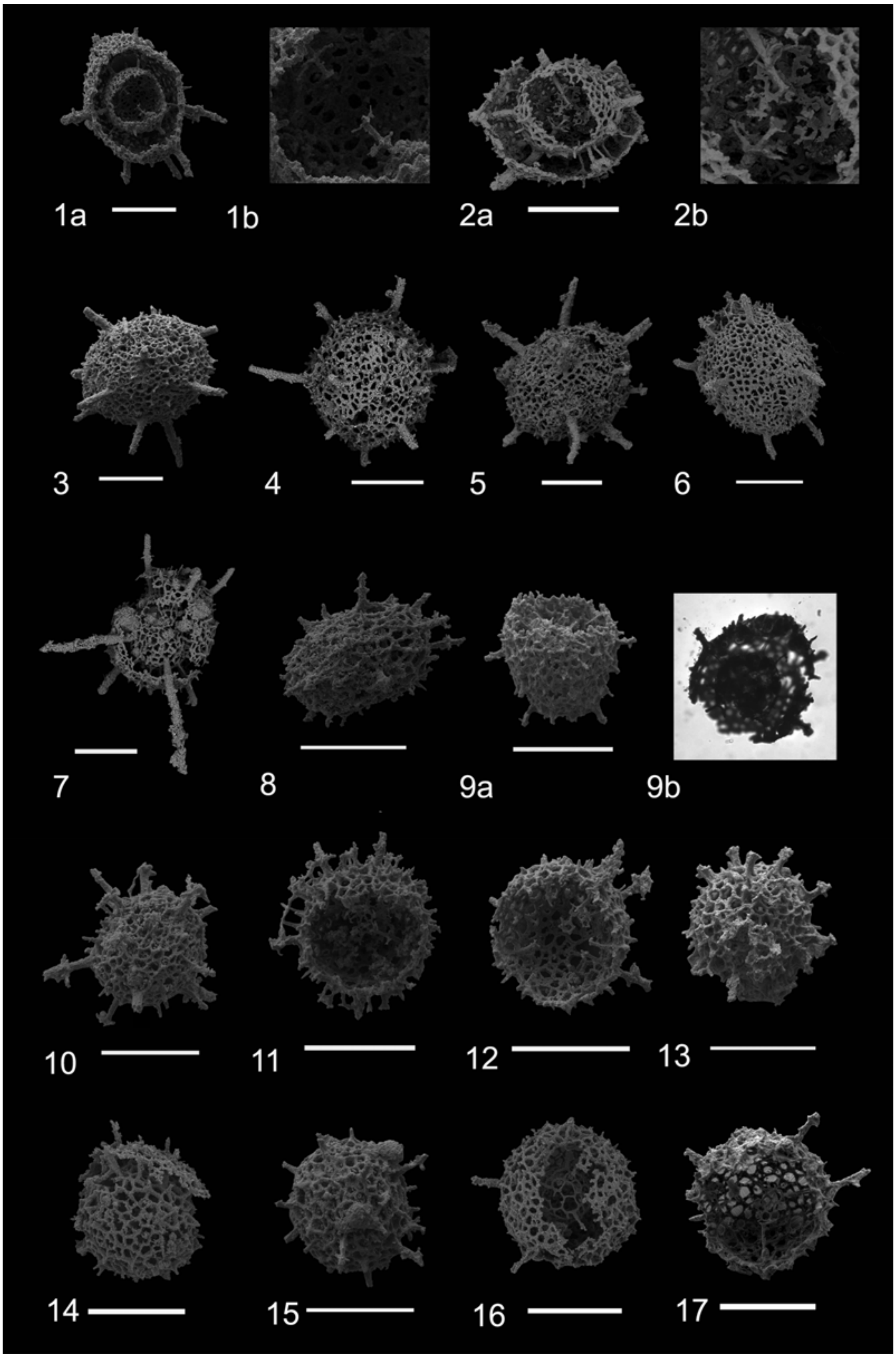

FIGURE 5— Scanning Electron Micrographs of Inaniguttidae radiolarian specimens yielded from from Shundy Formation, locality 112, Shundy Mountains, North Balkhash Region. Scale bar corresponds to 200 µm on all figures. *1-8*, *Triplococcus akzhala* (Danelian and Popov, 2003); *1a*, *2a*, Broken specimens showing the internal

structure of *Triplococcus akzhala* (USTL1157/036; USTL1184/027); *1b*, Magnified view of 1a internal structure showing relic fragments of the inner sphere and the microsphere. It is obvious from this picture that the secondary spines do not spread inside the microsphere; *2b*, Magnified view of 2a internal structure showing the thinly-layered inner shell wall's structure; *3-7*, Complete specimens showing an oval shape and numerous outer spines (USTL1144/005; USTL1143/002; USTL1180/053; USTL1143/020; USTL1145/033); *8-10*, *Triplococcus* sp. cf. *T. akzhala* (Danelian and Popov, 2003) (USTL1160/001; USTL1144/001; USTL1173/036); *9b*, View under the optical microscope of the sectioned specimen illustrated in Fig. 5. 9a. Two shells can be clearly observed. The microsphere is only faintly visible; *11*, *12*, *Triplococcus* sp. A (USTL1142/072; USTL1170/008); *13-15*, *Inanihella bakanasensis* (Nazarov, 1975) (USTL1140/53; USTL1146/014; USTL1147/007); *16*,*17*, *Inanibigutta* sp. A (USTL1146/006; USTL1179/002).

Remarks.— It differs from *Triplococcus akzhala* in its very small dimensions (outer shell Ø: 190-240 µm for *Triplococcus* sp. cf. *T. akzhala* against 270-450 µm for *T. akzhala*), in having a looser outer shell structure with wider and more elongated pores and in having more beams which emerge from the surface of the outer shell. *T.* sp. cf. *T. akzhala* might possibly be a juvenile form of *T. akzhala* as the dimensions of *T.* sp. cf. *T. akzhala* outer shell (Ø: 190-240 µm) are the same as *T. akzhala* median shell (Ø: 180-260 µm) and some specimens have been found bearing relic fragment of a third shell on their outer spines.

TRIPLOCOCCUS sp. A
Figure 5.12-5.13

Description.— The internal frame consists of a microsphere from which 8 to 10 outer spines originate. The test surrounding the microsphere consists of three encapsulated spherical shells. The inner shell and the microsphere are delicate and thinly latticed. The median shell is regularly porous and displays sub-circular to angular pores. The outer rays become thin rod-like spines beginning at the external surface of the median shell. The outer shell is broken in every observed specimen but relic fragments of a third shell can still be observed at the distal ends of the outer spines. Numerous beams originate from the pore-frame junctions of the median shell to connect to the outer shell.

Measurements (in micrometers; µm).— Diameter of the microsphere: 55-60; diameter of the inner shell: 100-105; diameter of the median shell: 222-241; diameter of the outer shell: 265-285.

Material examined.— 7 specimens.

Occurrence.— Upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan.*Remarks.*— It differs from *Triplococcus aksuranensis* and *Triplococcus acanthicus* in its larger number of outer spines and its dimensions (outer shell Ø: 265-285 µm here; 290-350 µm in *T. aksuranensis*; 214-257 µm in *T. acanthicus*) and also in its more closely spaced median and outer shell (distance between outer and median shell of a maximum of 63 µm for *Triplococcus* sp. A; of 170 µm for *T. aksuranensis*; of 102 µm for *T. acanthicus*). It also differs from *Triplococcu*s (?) *pingliangensis* in its larger number of outer spines and its smaller dimensions (median shell Ø: 222-241 µm herein; 220-360 µm in *T.* (?) *pingliangensis*).

Genus INANIHELLA Nazarov and Ormiston, 1984

Type species. Entactinia unica Nazarov, 1975

INANIHELLA BAKANASENSIS (Nazarov, 1975)

Figure 5.14-5.16

1975 *Helioentactinia* ? *bakanasensis* NAZAROV, p. 89, pl. 19, fig. 9-13.

1980 *Helioentactinia bakanasensis* Nazarov; NAZAROV AND POPOV, p. 48, pl. 16, fig. 7-8.

1993 *Inanihella bakanasensis* (Nazarov); NAZAROV AND ORMISTON, pl. 2, fig. 3.

2003 *Inanihella bakanasensis* (Nazarov); DANELIAN AND POPOV, p. 332, fig. 5a–f.

Diagnosis.— see Nazarov, 1975, p.89

Description.— Our material displays two spherical shells closely connected by numerous beams; the inner shell is irregularly perforated with rounded to angular pores distributed evenly on the shell surface. Numerous short thin outer spines emerge from the outer shell surface. Small conical secondary spines, which may be the prolongation of connecting beams between the two shells, emerge sporadically from the surface of the outer shell, which is often not preserved.

Measurements (in micrometers; µm).— Diameter of the outer shell: 290-320; diameter of the inner shell: 210-250.

Material examined.— 23 specimens.

Occurrence. — From the upper Dapingian (?) of the Akzhal Formation, Balkhash Region, Kazakhstan to the upper Darriwilian of the Shundy and Bestamak Formations, Balkhash Region, Kazakhstan and the Yerba Loca Formation, Western Precordillera, Argentina.

Remarks.— Our material differs from the material described by Nazarov (1975) in its larger size (outer shell Ø: 115-169 µm and inner shell Ø: 86-131 µm for Nazarov's material; outer shell Ø: 270-320 µm and inner shell Ø: 210-250 µm here). The specimens in our material are of approximate size to those of Danelian and Popov (2003) and Nazarov and Popov (1980) (outer shell Ø: 292-332 µm and inner shell Ø: 220-263 µm for Nazarov and Popov's material; outer shell Ø: 300-344 µm and inner shell Ø: 171-275 µm for Danelian and Popov's material). However, our material is much smaller than the *Inanihella* sp. cf. *Inanihella bakanasensis* species described by Maletz et al. (2009) from Argentina (outer shell Ø: ca. 350-420 µm).

INANIHELLA HIRTA (Nazarov *in* Nazarov and Popov, 1980)

Figure 6.16-6.19

1980 *Entactinosphaera? hirta* NAZAROV in Nazarov and Popov, p. 39, pl. 16, fig.1-3

1988 *Inanibigutta? hirta* (Nazarov); NAZAROV pl. 9, fig.15

Diagnosis, Description.— see Nazarov in Nazarov and Popov, 1980, p.39

Measurements (in micrometers; µm).—Diameter of the outer shell: 220-308 (average: 230-250); diameter of the inner shell: 86-97; diameter of the mesh: from 6 to 40 µm; length of outer spines: up to 13.

Material examined.— 27 specimens.

Occurrence.— From the lower Darriwilian of the Kurchilik Formation to the upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan.

Remarks.— Nazarov in Nazarov and Popov (1980) described the outer shell structure as "sponge-like". However, we prefer to use the term "three-dimensional meshwork" as the meshes are widely spaced and distinct. The inner framework had not been observed by Nazarov who discussed the possible presence of a six-rayed or a multi-rayed primary spicule inside the inner shell. The fragment of a microsphere present at the end of an outer ray protruding into the inner shell in one of our specimens argues in favour of a small microsphere as internal structure (Fig 6. 16b). The exact number of outer spines is still unclear as outer spines cannot be easily distinguished from secondary spines or beams. Indistinct outer and secondary spines are a common feature in *Inanihella* (*Inanihella magnifica* Maletz and Bruton, 2008, *Inanihella bakanasensis*, *Inanihella* sp. A and *Inanihella* sp. B). Therefore, as it stands, this species is assigned to *Inanihella*.

INANIHELLA MAGNIFICA (Maletz and Bruton, 2008)

Figure 6.4

2008 *Inanigutta magnifica* MALETZ AND BRUTON, Fig. 7N, R-U

Diagnosis, Description.— see Maletz and Bruton, 2008, p.1193

Measurements (in micrometers; µm).—Diameter of the outer shell: 202-211; diameter of the inner shell: 90-100; diameter of the bars: 4-6; diameter of the mesh width of the outer sphere: 16-30 (exceptionally, up to 45).

Material examined.— 2 specimens.

Occurrence.— From the lower Darriwilian of the Valhallfonna Formation, Spitsbergen to the upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan.

Remarks.— The material displays an inner and outer shell formed by a mesh of widely spaced bars. The unusual arrangement of the outer shell mesh, made of bars that are occasionally curved and sometimes arranged in a three-dimensional way, gives the impression of a spiral arrangement. Maletz and Bruton (2008) also mentioned that in their material the outer sphere often appears slightly spiraliform. Our material differs from that of Maletz and Bruton in the absence of outer spines. However, this is most likely due to bad preservation as the bars are covered with recrystallized material and the presence of numerous outer rays (up to 20) is clearly visible. *Inanigutta magnifica* has been assigned here to the genus *Inanihella* because of the presence of the two adjacent spherical shells and numerous outer spines, as described by Maletz and Bruton.

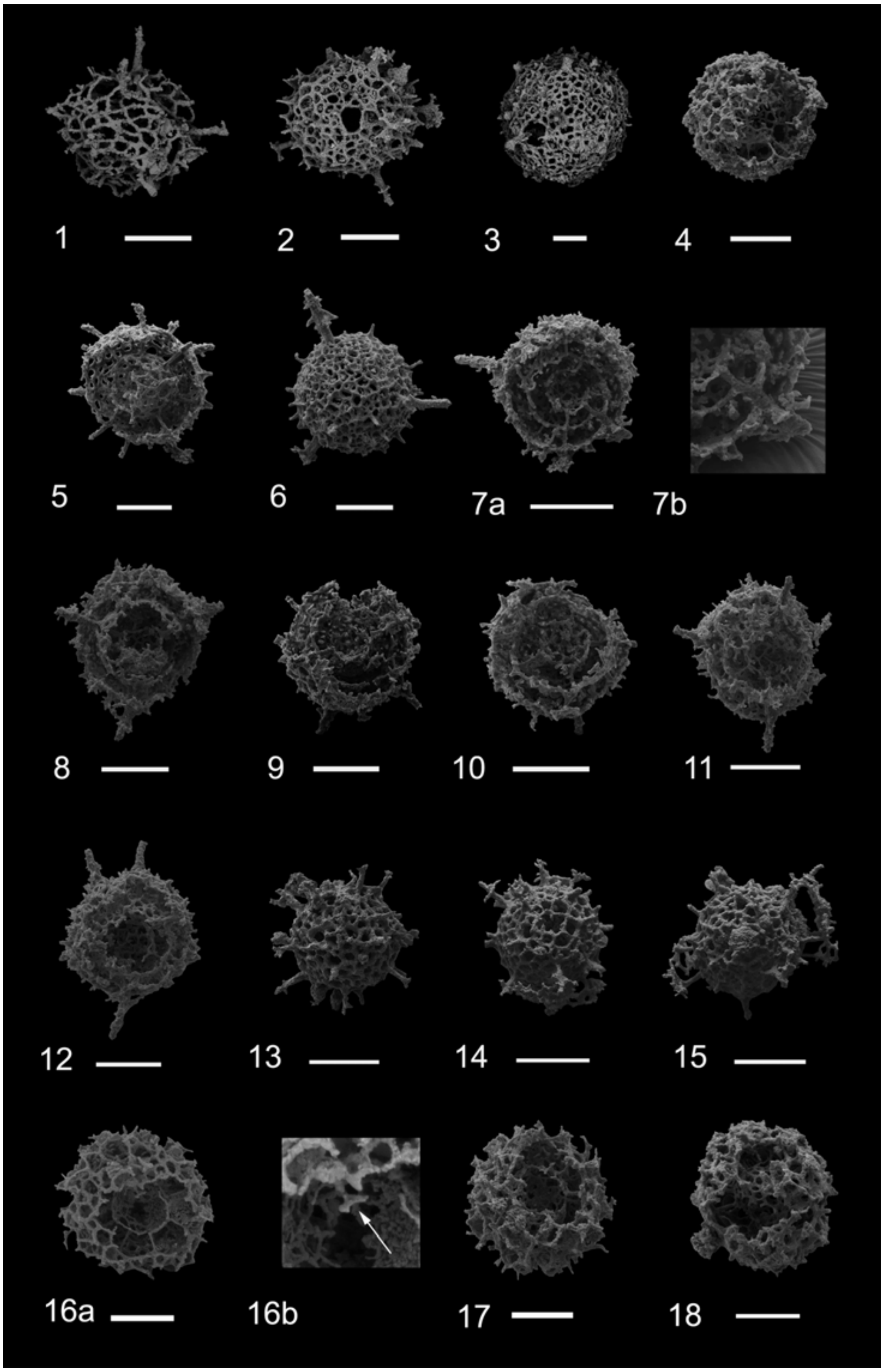

FIGURE 6— Scanning Electron Micrographs of radiolarian specimens yielded from from Shundy Formation, locality 112, Shundy Mountains, North Balkhash Region. Scale bar corresponds to 100 µm on all figures. *1*, *Haplentactinia juncta* (Nazarov, 1975) (USTL1142/071); *2*, *Kalimnasphaera* sp. aff. *K. aperta* (Nazarov, 1975) (USTL1146/012); *3*, *Kalimnasphaera* sp. A (USTL1180/052); *4*, *Inanihella magnifica* (Maletz and Bruton,

2008) (USTL1142/082); *5*, *Inanihella* sp. A (USTL1142/027); *6*, *Inanigutta gansuensis* Wang, 1993 (USTL1152/003); *7-12*, *Inanibigutta maletzi* Pouille and Danelian n.sp; *7a*, Holotype of *Inanibigutta maletzi* (USTL1178/025); *7b*, Magnified view of the Holotype spiraliform arrangement showing the dissymetricaly arranged apophyses forming the shells; *8-10*, Paratypes of *Inanibigutta maletzi* (USTL1142/026; USTL1142/035; USTL1173/040); *11-12*, (USTL1173/042; USTL1183/020); *13-15*, *Inanihella* sp. B (USTL1184/024; USTL1140/079; USTL1140/069); *16-19*, *Inanihella hirta* (Nazarov in Nazarov and Popov, 1980); *16b*, Magnified view of *16a* internal structure, arrow showing relic fragments of the microsphere at the end of a outer ray protruding inside the inner shell (USTL1173/042; USTL1183/020).

INANIHELLA sp. A

Figure 6.5

Description.— Skeleton consists of two encapsulated spherical shells and a microsphere from which 8 to 12 outer rays originate. Inner shell formed of irregularly porous widely spaced bars. Outer shell differs from the inner shell by having more regular and smaller pores. Numerous tiny outer spines are present (from 12 to 16), tapering gently at the distal part. They originate either from the microsphere (outer spines) or from the inner shell surface (secondary spines). They can be up to 80 µm-long and they are often slightly curved. Inner and outer shells are connected by the outer and secondary spines. Occasional beams are present. Some spines emerge from the surface of the outer shell.

Measurements (in micrometers; µm).— Diameter of the outer shell: 195-230; diameter of the inner shell: 115-125; diameter of the microsphere: 50-65; length of the spines: up to 80.

Material examined.— 2 specimens.

Occurrence.— Upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan

Remarks.— It differs from *Inanihella magnifica* in the smaller pore-frame of the outer shell, in the size of the microsphere (Ø: 50-60 µm herein; 80 µm for *I. magnifica*) and in the absence of any three-dimensionally organized meshwork. It differs from *Inanihella bakanasensis* in the structure of its inner shell, in its larger number of outer spines and in its shell size (*Inanihella* sp. A outer shell Ø: 195-230 µm; *I. bakanasensis* outer shell Ø: 115-169 µm for Nazarov's (1975) material; 220-263 µm for Nazarov and Popov's (1980) material and 300-344 µm for Danelian and Popov's (2003) material). In general, it differs from other

Inaniguttidae in the very high number of outer spines (12 to 16) and in its inner shell structure.

INANIHELLA sp. B

Figure 6.13-6.15

Description.— Very small spherical shell. Numerous outer spines are present. Very well-developed apophyses branch out of the distal end of the outer spines and join to form a second shell. On some specimens, broken fragments of a former porous cortical shell are still present. Pores can be rounded or angular and vary in size.

Measurements (in micrometers; µm).— Diameter of the outer shell: 202-220; diameter of the inner shell: 130-168.

Material examined.— 46 specimens.

Occurrence.— Upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan

Remarks.— Our material is assigned to genus *Inanihella* because of the high number of outer spines and the presence of two shells. When apophyses are not present, this species can be easily confused with *Oriundogutta miscella miscella*, which has an outer shell of nearly the same size (Ø: 140-180 µm) as the inner shell of *Inanihella* sp. B (Ø: 130-168 µm). As the internal framework is not accessible, it is difficult to determine whether a smaller internal shell is present or not.

Genus INANIBIGUTTA Nazarov, 1988

Type species. Inanibigutta aksakensis (Nazarov, 1975)

INANIBIGUTTA MALETZI new species

Figure 6.7-6.12

Diagnosis.— Skeleton consists of two porous shells surrounding a large latticed microsphere formed of loosely spaced bars. Six outer spines originate from the microsphere. Apophyses forming the shells are sometimes staggered along the outer spine. Shell displays an irregular outline. Additional spongy meshwork of latticed bars may interweave three-dimensionally on the outer shell.

Description.— The frame consists of two spherical shells surrounding a large latticed microsphere (Ø: 60-70 µm). The latter is formed of loosely spaced bars, at which six outer spines originate. The microsphere may be eccentrically placed on some specimens. No beams are present between the microsphere and the inner shell. The inner and outer shells are regularly perforated with rounded to oval pores. The pores of the outer shell are usually small (8-15 µm) but can be very wide (up to 30 µm). The inner and outer shells are interconnected by tiny beams. The shell is rarely a perfect sphere; it often displays an irregular outline. Apophyses that originate from the outer spines to form the median and outer shells are occasionally staggered along the spine, leading to a spiraliform arrangement of the shell (Fig. 6.7b). At some places on the outer shell surface, a meshwork of latticed bars may interweave three-dimensionally, giving the outer shell a spongious aspect. It usually branches from the outer spines and may develop into an additional irregular layer. Simple apophyses can branch from the outer spines to join the outer shell surface. On some specimens small secondary spines emerge from the wall surface.

Etymology : Named in honour of Jörg Maletz for his contribution to the knowledge of Ordovician Radiolaria.

Types. — Holotype: Figure 6.7a (USTL1178/025); Paratypes: Figure 6.8 (USTL1142/026), Figure 6.9 (USTL1142/035) and Figure 6.10 (USTL1173/040).

Measurements (in micrometers; µm).— Diameter of the outer shell: 190-220; diameter of the inner shell: 120-130; diameter of the microsphere: 60-70; diameter of the pores: 8-15 (exceptionally, up to 30)

Material examined.— 12 specimens.

Occurrence. — Upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan

Remarks.— This species is assigned to the genus *Inanibigutta* because of its two distinct porous shells which enclose a latticed microsphere. However, the presence of assymmetrically arranged apophyses on both sides of the outer spines distinguishes it from other species. This character is more similar to the shell structure of *Gyrosphaera* (Noble and Maletz, 2000). The latter has been synonymized by MacDonald (2006) with the genus *Haplotaeniatum*, but Jones and Noble (2006) chose to keep the two genera separate, as *Gyrosphaera* can be distinguished from *Haplotaeniatum* in its well-defined spiraliform layering and its wall structure. *Gyrosphaera* possesses an irregularly porous wall structure forming three or more strongly spiraled layers. This spiraliform layering of the shell has been well illustrated by the figures of *Gyrosphaera cavea* (Jones and Noble 2006; Pl. 4.2-4.3), *Gyrosphaera raneatela* (Noble and Maletz, 2000; Pl.

2.1-2.3) and *Gyrosphaera siljanenis* (Noble and Maletz, 2000; Pl. 2.4-2.5). The three-dimensional spongy meshwork, developped partly on the outer shell of *Inanibigutta maletzi* recalls to some extent the outer shell structure of *Haplotaeniatum* Nazarov and Ormiston, 1993

INANIBIGUTTA sp. A

Figure 5.17-5.18

Description.— Two-shelled radiolarians with a perfectly spherical inner latticed shell, which consists of widely spaced bars forming a mesh of large polygonal pores (Ø up to 30 µm). The outer shell is formed of a spherical mesh of small sub-circular pores (average Ø 8 to 15 µm; exceptionally up to 34 µm). At some places, the bars interweave. Numerous thorn-like small beams are present at the outer shell surface. They possess a bifurcated or trifurcated base. Six outer rays originate from the inner framework and emerge from the surface of the outer shell as thin rod-like outer spines. Numerous apophyses branch from the base of the outer spines and merge into the latticed shell. Simple apophyses can be present on the outer spines and rare beams connect the inner and outer shell. The innermost framework is not preserved in any of the specimens.

Measurements (in micrometers; µm).— Diameter of the inner shell: 110-121; diameter of the outer shell: 277-309; diameter of the pores of the inner shell: 7-30 (mostly 23-30); diameter of the pores of the outer shell: 8-34 (mostly 8 to 15)

Material examined.— 8 specimens.

Occurrence. — Upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan

Remarks.— It differs from other *Inanibigutta* species by the large pore-size of the inner shell, by the presence of numerous bifurcated and trifurcated beams and the presence of numerous apophyses branching from the base of the outer spines.

Genus INANIGUTTA Nazarov and Ormiston, 1984

Type species. Entactinia unica Nazarov, 1975

INANIGUTTA GANSUENSIS Wang, 1993

Figure 6.6

1993 *Inanigutta gansuensis* WANG, p. 99; pl. 7, fig. 1-8; pl. 8, fig. 1-11.

Diagnosis, Description.— see Wang, 1993, p.99.

Measurements (in micrometers; µm).— Diameter of the outer shell: 200-240; length of spine: up to 100 µm.

Material examined.— 12 specimens.

Occurrence.— From the upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan to the lower Sandibian of the Pingliang Formation, Gansu Province, China.

Remarks.— The specimens found in our material bear a larger number of secondary spines than the species described by Wang (1993). The six rod-like spines emerging out of the spherical outer shell are often broken. Short branch apophyses are common on the pore-bar junctions. Pores are rounded to oval, rarely angular.

Genus KALIMNASPHAERA Webby and Blom, 1986

(syn. Cessipylorum Nazarov and Ormiston, 1984 nomen nudum; Cessipylarum Nazarov in Afanasieva, 1986; e.g. discussion in Noble and Webby, 2009)

Type species. Kalimnasphaera maculosa Webby and Blom, 1986

KALIMNASPHAERA sp. aff. K. APERTA (Nazarov, 1975) n. comb.

Figure 6.2

Aff. 1975 *Pylentonema aperta*; NAZAROV in Nazarov, Popov and Apollonov, p. 102, fig. 1, 2.

Aff.1988 *Cessipylorum apertum* (Nazarov); NAZAROV, p. 70, pl. 10, fig. 6.

Description.— Test made of a spherical to subspherical pylomate cortical shell with seven or more rod-like outer spines. Two of them are located around the pylome which has a sub-circular opening. The rim of the pylome opening is fringed with a small ridge (5 to 7 µm thick). The cortical shell is thick and irregularly latticed with oval to angular-oval pores (more rarely rounded). The size of the pores is very variable (from 3 to 30 µm). The latticed bars are thick and irregular and interweave in some places. Straight or curved rays may branch from the base of the outer spine and merge into the latticed shell. Numerous small conical secondary spines emerge from the pore-bar junction. The outer spines often bear well-developed apophyses. The inner framework is not visible.

Measurements (in micrometers; µm).— Diameter of the outer shell: 210-250; diameter of the pylomate opening: 32-42; thickness of the pylome ridge: from 5 to 7; diameter of the pores: from 3 to 30; length of secondary spines: up to 30.

Material examined.— 6 specimens.

Occurrence.— Upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan

Remarks.— For the moment, only three species of *Kalimnasphaera* are known from the Darriwilian of Kazakhstan: *Kalimnasphaera insueta* (Nazarov and Popov, 1980), *Kalimnasphaera rimata* (Nazarov and Popov, 1980) and *Kalimnasphaera aperta* (Nazarov, 1975). Our material resembles *K. aperta* morphologically though it differs from it in having a smaller outer shell (Ø: 210-250 µm in our material; 260-290 µm in *K. aperta*) and a slightly thinner pylome ridge (5-7 µm in our material; 8-10 µm in *K. aperta*). It differs from *K. insueta* by having mostly oval or angular-oval pores, in the smaller dimensions of its outer shell (Ø: 210-250 µm in our material; 260-300 µm in *K. insueta*) and in the size of its pylomate opening (Ø: 32-42 µm in our material; 45-80 µm in *K. insueta*). They also differ in the thickness of the pylome ridge (5-7 µm in our material; 10-20 µm in *K. insueta*). *Kalimnasphaera* sp. aff. *K. aperta* shares nearly the same dimensions as *K. rimata* (Ø: 210-250 µm for *K.*sp. aff. *K. aperta*; 245-260 µm for *K. rimata*). Yet, it differs from it in having smaller secondary spines but mostly by the more varied shape of its pores (Pores Ø: 3-30 µm in *K.*sp. aff. *K. aperta*; 2-12 µm in *K. rimata*). It also differs from all *Kalimnasphaera* species in the presence of apophyses branching from the outer spines which occasionally might develop into a second outer shell. This feature is present in *Kalimnasphaera maculosa* (Katian; Webby and Blom, 1986; Noble and Webby, 2009). However, our material differs from *K. maculosa* in the larger number of outer spines, the larger size of its outer shell (Ø: 204-225 µm in our material; 111-189 µm in *K. maculosa*) and the pores shape (rounded in *K. maculosa*; angular to oval here).

KALIMNASPHAERA sp. A

Figure 6.3

Description.— Test made of a spherical pylomate cortical shell from which rod-like outer spines emerge. Two of the spines are located around the pylome which has a large irregularly circular opening (60-70 µm width). The rim of the pylome opening is fringed with a small

ridge of 5 to 10 µm thick. The cortical shell is thick and regularly latticed with rounded to angular-oval pores. The size of the pores is mostly uniform. A few tiny conical secondary spines emerge from the pore-bar junction. The outer spines are all broken in the specimen.
Measurements.—(in micrometers; µm) Diameter of the outer shell: 354-360; Diameter of the pylomate opening: 60-70; Thickness of the pylome ridge: from 5 to 10; Diameter of the pores: from 6 to 40; Length of secondary spines: up to 18.
Material examined.— 1 specimen.
Occurrence. — Upper Darriwilian of the Shundy Formation, Balkhash Region, Kazakhstan
Remarks.— This specimen differs from other *Kalimnasphaera* species in its very large size and large pylomate opening (outer shell Ø: 354-360 µm; pylomate opening Ø: 60-70 µm). It also differs from other species by having tiny secondary spines.

—*Trilobites* (M. Ghobadi Pour and L. Popov)

The studied and illustrated trilobite specimens are deposited in the Department of Geology, National Museum of Wales, Cardiff (NMW). Abbreviations for parameters measured on specimens are (in millimetres): Cl, Cw = maximum cranidium length and width; Gl, Gw = maximum glabellar length and width; GTw = width of glabellar tongue; ORl = length (sag.) and width of occipital ring; Pl, Pw = maximum pygidial length and width; Al, Aw = length and width of pygidial axis; sag. = sagittal, exsag. = exsagittal, tr. = transverse.

Family OLENIDAE Burmeister, 1843
Subfamily TRIARTHRINAE Ulrich, 1930
Genus PORTERFIELDIA Cooper, 1953

Type species. Triarthrus caecigenus Raymond, 1920, Upper Ordovician, Sandbian, Athens Shale, north of Salem, Virginia, USA.

PORTERFIELDIA sp. aff. P. DELICATA Kolobova in Klishevich and Kolobova, 1990
Figure 7.5-7.10

Description.— The ranidium is semioval in outline, slightly wider than long. The glabella is subquadrate, almost as long as wide (without occipital ring), distinctly elevated above the fixigenae, bounded by strongly impressed, narrow, gently arcuate axial and preglabellar furrows. S1 and S2 are strongly impressed, almost parallel to each other, arcuate, bend evenly posteriorly adaxially. L1 and L2 are of about equal length. The occipital ring is convex (sag.), slightly narrower than the maximum glabellar width with a posterior margin bowed posteriorly. The median tubercule is strong, situated close to the posterior margin of the occipital ring. The occipital furrow is deep, almost transverse, slightly curved anteriorly abaxially. The fixigenae are narrow, with maximum width (trans.) at the posterior cranidial margin. The posterior border is narrow (exsag.), bounded by a narrow, deep posterior border furrow slightly curved anteriorly abaxially. The anterior border furrow is shallow merged adaxially with the preglabellar furrow. The anterior border is narrow, about as wide (sag., exsag.) as a sutural ridge. The palpebral lobes are small, anteriorly placed, with a posterior termination situated in opposite or slightly anterior to S2. The furrow delineating the palpebral lobe merges with a furrow outlining the sutural ridge. The posterior branches of the facial suture are gently diverge outwards posteriorly, becoming almost parallel posterior to S1. The librigenae and hypostome were not observed.

The thorax bears at least 10 segments. Axis is wide, convex, occupying ca. 45% of thoracic width. The axial furrows are almost parallel anteriorly, gently tapering in five posterior thoracic segments. The pleurae are blunter-tipped with pleural furrows slightly curved anteriorly abaxially.

The pygidium is incompletely preserved, small, with at least four axial rings and at least three pairs of pleural ribs. The axis is broad, tapering posteriorly, occupying about two-fifths of anterior pygidial width, bounded by deep axial furrows. The pleural furrows are shallow and narrow, almost straight, strongly inclined posteriorly abaxially. Interpleural furrows are absent.

Material examined.— NMW 2012.5G.2 (Cl=3.7,Gl=2.9, Gw=3.5, ORl=0.65), NMW 2012.5G.3, (Cl=1.7, Cw~1.9,Gl=1.3, Gw=1.25, ORl=0.3), NMW 2012.5G.4-7, cranidia; NMW 2012.5G.1, pygidium with attached thorax; all specimens from Shundy Formation, locality 112, Shundy Mountains, North Balkhash Region, Kazakhstan.

Remarks.— Specimens from the Shundy Formation show very close similarity to *Porterfieldia delicata* Kolobova in Klishevich and Kolobova, 1990 from the lower part of the Zyndan Formation (Middle Ordovician, upper Darriwilian) of the North Tien Shan, Kyrgyzstan, but differ in having more arcuate glabellar furrows, a more strongly impressed furrow delineating the sutural ridge, and probably a lesser number of the axial rings and pleural ribs on the pygidium. The studied Kyrgyz specimens are preserved in argillite and they are strongly flattened, therefore differences in convexity of the cranidium and glabella are mainly due to their distortion.

P. sp. aff. *P. delicata* differs from *Porterfieldia sinensis* (Chang and Fan, 1960) from **t**he upper part of the Yinggou Group (middle Darriwilian, *Amplexograptus confertus* Biozone), Angzanggou, southwest Yumen, Gansu Province, South China, in the complete absence of preglabellar field and eye ridges. The pygidial morphology cannot be compared due to any report on the pygidium in the original description of the species.

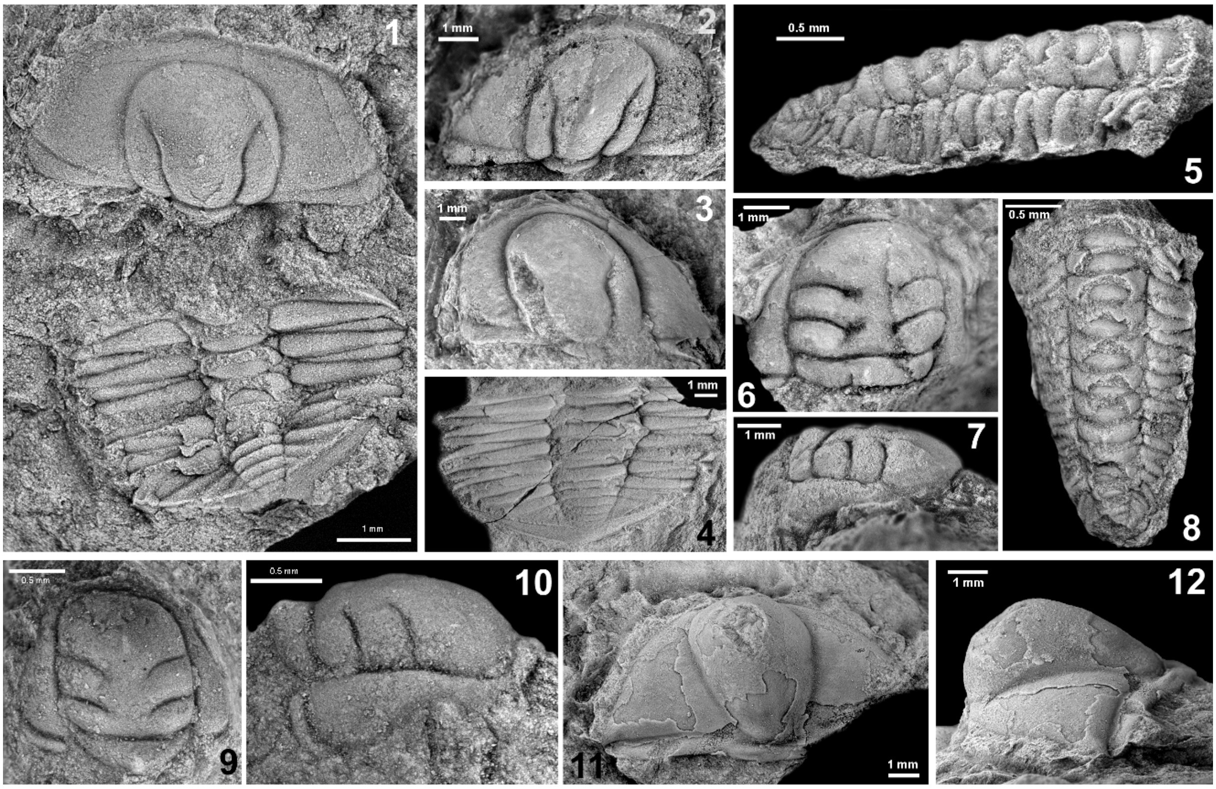

FIGURE 7— All specimens from Shundy Formation, locality 112, Shundy Mountains, North Balkhash Region: *1-4*, *Endymionia semielliptica* Chang and Fan, 1960; *1*, NMW 2012.5G.8, disarticulated exoskeleton; *2*, NMW 2012.5G.9, cranidium; *3*, NMW 2012.5G.10, cranidium; *4*, NMW 2012.5G, pygidium with attached thorax; *5-10*, *Porterfieldia* sp. aff. *P. delicata* Kolobova *in* Klishevich and Kolobova, 1990; *5*, *8*, NMW 2012.5G.1, pygidium with attached thorax, dorsal and lateral views; *6*, *7*, NMW 2012.5G.2, cranidium, dorsal and lateral views; *9*, *10*, NMW 2012.5G.3, cranidium, dorsal and lateral views; *11*, *12*, *Nambeetella*? sp., NMW 2012.5G.12, cranidium, dorsal and lateral views.

The specimens from the Shundy Formation closely resemble *Porterfieldia goldwyerensis* (Legg, 1976) from the Middle Ordovician, Darriwilian, Goldwyer Formation, Canning Basin, Western Australia in general cranidial morphology, shape and outline of the glabella and characters of the glabellar furrows. The main differences are the complete absence of preglabellar field and interpleural furrows on the pygidium; the latter has also fewer axial rings and pleural ribs.

There are two other species of *Porterfieldia* presently documented from the Darriwilian of neighbouring Northern Kyrgyzstan (Weber, 1948; Klishevich and Kolobova, 1990), but they are definitely not conspecific. *Porterfieldia turkestanica* (Weber, 1948) differs in having a wider (sag.), a strongly swollen medially anterior cranidial border and a spine on the occipital ring. *Porterfieldia sponisa* Kolobova in Klishevich and Kolobova, 1990, unlike Kazakhstanian specimens, have almost straight, converging closely, but not merging glabellar furrows, and a prominent median spine in front of the cranidium.

Family RAPHIOPHORIDAE Angelin, 1854

Subfamily RAPHIOPHORINAE Angelin, 1854

Genus NAMBEETELLA Legg, 1976

Type species. Nambeetella firroyensis Legg, 1976, Lower Ordovician, Floian, Emanuel and Namber formations, Canning Basin, West Australia.

NAMBEETELLA? sp.

Figure 7.11-7.12

Material examined.— NMW 2012.5G.12, cranidium, NMW 2012.5G.13, external mould of pygidium and incomplete thorax.

Remarks.— A single cranidium resembles *Nambeetella* (Legg, 1976) in its subsemicircular shape and the absence of an anterior border with a strongly convex, flask-shaped glabella; the latter is slightly overhanging above a steeply inclined preglabellar field, but it is not crossing the anterior cranidial margin. An anterior part of the glabella is slightly damaged, thus the absence of a glabellar spine cannot be proved, which explains the tentative identification of the specimen.

Subfamily ENDYMIONIINAE Raymond, 1920

Genus ENDYMIONIA (Billings, 1865)

Type species. Endymion meeki Billings, 1862, Middle Ordovician, Levis Formation, Quebek Canada.

ENDYMIONIA SEMIELLIPTICA Chang and Fan, 1960

Figure 7.1-7.4

1960 *Endymionia semielliptica* CHANG AND FAN; p. 129, pl. 7, figs 5-7.
1965 *Endymionia semielliptica* Chang and Fan; Lu et al., p. 609, pl. 127, figs 11-13.
1990 *Endymionia kazakhstanica* Balashova (*nomen nudum*); APOLLONOV et al., 1990, p. 15.

Description.— The cranidium is semioval in outline, about three-fifths as long as wide, with an evenly curved anterior margin. The glabella is gently convex (trans.), subcircular to subquadrate in outline, and almost as long as wide (including occipital ring); it is bounded by equally deep axial and preglabellar furrows, which occupy ca. 85% of the cranidial length and slightly less than half of the cranidial width. Median tubercle is situated slightly posterior to glabellar mid length. The glabellar lateral lobes taper outwards; they are separated from the median glabellar lobe by deep, sigmoidal glabellar furrows sharply terminated anteriorly, at a short distance from the axial furrows. The occipital ring is narrow, bordered by a deep occipital furrow running almost parallel to the cranidial margin.

The fixigena is broad and tapers gently outwards, but more sharply at the proximity of the facial sutures.

The preglabellar field is fairly broad, slightly widening (exsag.) laterally. The anterior border is very narrow and defined by a shallow border furrow. The posterior border is narrow (trans.) adaxially, to widen gradually (trans.) abaxially, to narrow slightly at its lateral extremity. The posterior border is furrow, narrow, well defined and slightly curved forward abaxially.The librigena is unknown. Facial sutures are gently curved and converge anteriorly.

The thoracic axis is about one fourth as long as the thoracic width; pleural furrows are deep and curved slightly forward. The posterior pleural band is more prominent and becomes wider adaxially.

The pygidium is three to four times as wide as long, with its axis occupying 25-30% of the pygidial width at the anterior margin. The axis is truncated conical tapering posteriorly, with five axial rings of approximately equal length (sag.) and a short (sag.) terminal piece crossing the margin of the posterior border. The pleural fields are almost flat, bordered by a distinct rim, with three pairs of pleural ribs, separated by broad, straight pleural furrows that are slightly inclined posteriorly abaxially. The posterior border is flattened and tapers strongly downwards; it is ornamented by faint subparallel terrace lines.

Holotype.— Cranidium figured by Chang and Fan (1960, pl. 7, fig. 5), Ordovician, Darriwilian, Datouyanggou, Da Qaidam, north-west China.

Material examined.— NMW 2012.5G.8 (Cl=2.6, Cw=4.9, Gl=2.1, Gw=2.1, Pl=1.2, Pw=3.6, Al=0.95, Aw=0.85), disarticulated exoskeleton lacking free cheeks; NMW 2012.5G.9 (Cl=4.0, Cw=6.8, Gl=3.35, Gw=3.3); ; NMW 2012.5G.10 (Cl=4.6, Cw=7.3, Gl=4.2, Gw=3.9); cranidia; NMW 2012.5G.11 (Pl=2.7, Pw=10.5, Al=2.2, Aw=3.2), pygidium with attached thorax; all specimens from Shundy Formation, locality 112, Shundy Mountains, North Balkhash Region, Kazakhstan.

Remarks.— The specimens from the Shundy Formation show close similarity in their cranidial morphology to *Endymionia semielliptica* Chang and Fan, 1960 known from the Darriwilian of northern Qinghai; in particular, they have a subcircular to subquadrate glabella with sigmoidal glabellar furrows that are not merged anteriorly with axial furrows; they also have strongly impressed posterior border furrows that are not fading adaxially. The sigmoidal glabellar furrows are not merged anteriorly and the axial furrows can be considered as the most distinctive feature of *E. semielliptica*, which is uknown from any other species referred to the genus (e.g., Fortey, 1975 and Whittington, 1965). The closest species is *E. canningi* Legg, 1976 from the Darriwilian, Goldwyer Formation, Canning Basin of Western Australia; it has similar proportions and shows a similar cranidial and glabellar outline. However, unlike *E. semielliptica,* the glabellar furrows present in the Australian species are only slightly curved and they almost reach the axial furrows; moreover, Kazakhstanian specimens have a significantly wider pygidium with only five axial rings (instead of 12) and three pleural ribs (instead of five). Our specimens differ from the type species *Endymionia meeki* (Billings, 1862) in cranidial morphology, including the sigmoidal glabellar furrows, which do not approach the axial furrows and their glabella that is less rounded.

DISCUSSION

The studied radiolarian assemblage is dominated by the family Inaniguttidae, which is represented by five genera and 14 species: *Triplococcus aksuranensis* n. sp., *Triplococcus akzhala*, *Triplococcus* sp. cf. *T. akzhala*, *Triplococcus* sp. A, *Inanihella bakanasensis*, *Inanihella hirta*, *Inanihella magnifica*, *Inanihella* sp. A, *Inanihella* sp. B, *Inanibugutta maletzi* n. sp., *Inanibugutta* sp. A, *Inanigutta gansuensis*, *Kalimnasphaera* sp. aff. *K. aperta* and *Kalimnasphaera* sp. A. Representatives of genus *Triplococcus* are particularly abundant, representing half of the Inaniguttidae found in this fauna. Ordovician Radiolarian biostratigraphy is still in its infancy. Based on the Inaniguttid species discussed here, the radiolaria of sample 112 could be correlated with the *Triplococcus akzhala - Inanihella bakanasensis* assemblage described by Danelian and Popov (2003) from upper Dapingian (?) (e.g., Maletz, 2011) limestones in Kazhakstan and possibly with the radiolarian assemblage described by Maletz et al. (2009) from Lower Darriwilian carbonates in Argentina. Based on the low diversity of this assemblage, Maletz (2011) suggested that it may represent "a depauperate fauna" of the Lower Darriwilian *Proventocitum procerulum* assemblage. We also report the presence of *Haplentactinia juncta* (Fig. 6. 1) in the fauna studied here, which is one of the characteristic species of the *Haplentactinia juncta-Inanigutta unica* assemblage, correlated with the uppermost Darriwilian (e.g., discussion in Nazarov and Ormiston, 1993; Danelian and Popov, 2003; Maletz, 2011). Moreover, pylomate radiolarians of the genus *Kalimnasphaera* are known to first occur in this assemblage (Nazarov and Popov, 1980).
In addition to the radiolarian assemblage, sample 112 also contains three species of trilobites (*Endymionia semielliptica*, *Nambeetella*? sp. and *Porterfieldia* sp. aff. *P. delicata*), which form an oligotaxic association characteristic of the deep water olenid biofacies (Fortey in Webby et al., 2004), reflecting a basinal, offshore depositional environment, below the strongest storm wave base. *E. semielliptica* was originally described from the uppermost part of the Duoquanshan Formation (Ordovician, Darriwilian) of the Qaidam Terrane in north-west China, where argillites, overlying the trilobite-bearing unit, contain the mid-Darriwilian graptolites of the *Pterograptus elegans* Subzone of the *Didymograptus murchsoni* Biozone (Chang and Fan, 1960; Zhou and Dean, 1996). *P.* sp. aff. *P. delicata* from the Shundy Formation is fairly similar and possibly conspecific to specimens described by Klishevich and Kolobova (1990) from the Upper Member of the Zyndan Formation of the Toluk river valley in North Tien Shan (Kyrgyzstan), which also contains a graptolite assemblage (*Cryptograptus*

sp. cf. *C. tricornis* (Carruthers, 1858), *Glossograptus* sp. cf. *C. hincksii* (Hopkinson, 1872), *Hustedograptus* ex gr. *teretiusculus* (Hisinger, 1840) and *Pseudoclimacograptus* ex. gr. *scharenbergi* (Lapworth, 1876) transitional in age from the late Darriwilian to the Sandbian. Finally, the stratigraphic level from which sample 112 was collected also contains the graptolite species *Hustedograptus* ex gr. *teretiusculus* (identification Tsai in Apollonov et al., 1990), which confirms and further narrows the age of the radiolarian-bearing sample to the latsest Darriwilian.

In conclusion, the fossil record taken as a whole suggests a late Darriwilian age for radiolarian sample 112. It appears to be somewhat older than the radiolarian-bearing beds of the Bestomak Formation in the Chingiz Range (sample 553a), which are overlain by graptolites of the *Nemagraptus gracilis* biozone (lower Sandbian) and from which Nazarov and Popov (1980) described the diverse radiolaria that defined the *Haplentactinia juncta- Inanigutta unica* assemblage. Radiolarian sample 112 of this study is also older than the radiolarian assemblage described by Wang (1993) from the Pingliang Formation of Gansu Province, China, of early Sandbian age, dated by graptolites of the *Nemagraptus gracilis* to *Climacograptus bicornis* biozones (Maletz, 2011).

CONCLUSION

A rich and well-preserved radiolarian assemblage from a Middle Ordovician sample from Kazakhstan is composed essentially of representatives of the family Inaniguttidae. They are represented by five genera and 14 species, two of which are new. The Trilobite fauna found in the sample suggests a late Darriwilian age, which is supported by graptolite species found previously. The presence of the radiolarian species *Haplentactinia juncta* corroborates this age. The trilobite fauna is characteristic of the deep water olenid facies. This work provides a significant contribution regarding the family Inaniguttidae, especially by providing a more detailed examination of the internal structure of *Triplococcus*. It also refines our knowledge of Ordovician radiolarian biostratigraphy using the identification of co-occurring trilobites and graptolites which provide a reliable age constraint for the assemblage.

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Article 4:

A new diverse Radiolarian assemblage from the Upper Darriwilian (Ordovician) Shundy Formation of Kazakhstan: a key fauna to better evaluate Radiolarian diversity trends in the context of the Great Ordovician Biodiversification Event

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A new diverse Radiolarian assemblage from the Upper Darriwilian (Ordovician) Shundy Formation of Kazakhstan: a key fauna to better evaluate Radiolarian diversity trends in the context of the Great Ordovician Biodiversification Event.

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ABSTRACT - We here report on a new diverse and well-preserved radiolarian assemblage from uppermost Darriwilian. The fauna was extracted from a carbonate sample (sample 112) coming from the Shundy Formation of the Aksuran Mountain, North Balkhash Region, Kazakhstan. This sample displays a well-preserved and highly diversified fauna with the presence of 4 families (Inaniguttidae, Haplotaeniatidae, Haplentactinidae and Polyentactinidae), nine genera (*Inanihella, Inanigutta, Triplococcus*, *Inanibigutta, Kalimnasphaera, Haplotaeniatum, Syntagentactinia, Polyentactinia* and *Haplentactinia*) and 32 species (including nine new species). It is dominated by a rich *Triplococcus* and *Inanihella* fauna. Representatives of the Inaniguttidae family are particularly abundant, representing 69% of the studied assemblage. Identified trilobites, radiolaria and graptolites suggest an assignment to the *Hustedograptus teretiusculus* zone. This assemblage is correlated to the *Inanihella bakanasensis*- *Triplococcus akzhala* assemblage but also shares characteristic species and genera of the *Haplentactinia juncta*-*Inanigutta unica* assemblage.

KEYWORDS: *Radiolaria, Darriwilian, Ordovician, Kazakhstan*

INTRODUCTION

In spite of the major progress achieved recently in understanding the “Great Biodiversification Event” (Webby *et al*. 2004; Servais *et al*. 2011) our understanding of the biodiversity dynamics of some biotic groups is still very fragmentary. This is more particularly the case for polycystine Radiolaria, a major component of the oceanic heterotrophic plankton in the Early Paleozoic marine ecosystem. Yet only a few radiolarian assemblages have been recognized so far in the Ordovician.

Lower Ordovician assemblages are mainly known from Spitzbergen and Western Newfoundland (Maletz, 2007a, 2007b; Maletz & Bruton, 2005); they differ considerably from Middle Ordovician faunas which have been mainly recovered from Kazakhstan.

Three distinct Middle Ordovician (Dapingian-Darriwilian) assemblages have been recognized from a few radiolarian localities, dispersed around lake Balkash in Kazakhstan (Danelian & Popov, 2003; Nazarov & Ormiston, 1993; Nazarov & Popov, 1980; Nazarov *et al*., 1977; Nazarov, 1975, 1988):

- The *Inanihella bakanasensis*- *Triplococcus akzhala* Assemblage, described by Danelian & Popov (2003) from sample 8807-A of the Akzhal Formation in Kazakhstan, was initially considered as Floian in age. Since, it was also recovered from the lower Darriwilian of Argentina (Maletz *et al*., 2009) and was considered as covering the upper Dapingian-lower Darriwilian interval (Maletz, 2007a, 2011)
- The *Proventocitum procerulum* Assemblage was described by Nazarov & Popov (1980) from the middle Darriwilian of Kazakhstan (sample 19). It was also recorded from Spitsbergen (Fortey & Holdsworth, 1971; Holdsworth, 1977; Maletz & Bruton, 2008) and Scotland (Aitchison, 1998). The *Proventocitum procerulum* faunas were at first thought to range from early Floian to early Darriwilian (Nazarov & Popov, 1980; Danelian & Popov, 2003) but it is now referred to a strict Darriwilian age (Maletz & Bruton, 2007, 2008; Maletz, 2011).
- The *Haplentactinia juncta*- *Inanigutta unica* assemblage was described by Nazarov & Popov (1980) from the Bestomak Formation in the Chingiz Range (sample 553a) in Kazakhstan. This assemblage, overlain by the *Nemagraptus gracilis* biozone (Lower Sandbian) appears to be somewhat a bit younger than our assemblage which has been dated of an uppermost Darriwilian age.

The new, diverse and well-preserved radiolarian assemblage from the uppermost Darriwilian in Kazakhstan studied here displays an entirely new fauna including some characteristic species of the two radiolarian assemblages *Haplentactinia juncta*- *Inanigutta unica* and *Inanihella bakanasensis*- *Triplococcus akzhala*. This assemblage, dominated by the family Inaniguttidae and represented by five genera (*Triplococcus*, *Inanihella*, *Inanigutta, Inanibigutta* and *Kalimnasphaera*) and 14 species (including the two new species *Triplococcus aksuranensis* and *Inanibigutta maletzi*), have been described in detail in Pouille *et al.*, 2012b. This paper focuses essentially on the taxonomic study of the rest of the fauna including representatives of the Haplentactiniidae, Haplotaeniatidae and Polyentactinidae with the description of 18 species, seven of which are new.

It allows to improve considerably our understanding of the Radiolarian palaeodiversity during the Darriwilian, a critical interval in the context of the Ordovician diversification (Servais *et al.*, 2008, 2009).

STRATIGRAPHIC SETTINGS AND AGE

Stratigraphic settings

Middle to Upper Ordovician outcrops are represented by two Formations: The Kurchilik Formation (upper Dapingian-Darriwilian) and the Shundy Formation (Upper Darriwilian to Sandbian) which include a wide spectre of deposites representing a sequence of lithofacies from a shallow shelf to an outer fan and fan ridge.

The Shundy Formation can be divided into four informal units (Apollonov *et al*, 1990) representing the slope of a carbonate platform margin. There is an evidence of an important deepening of water environment from Unit 1 to Unit 4:

- Unit 1 (up to 450 m thick) is composed of Breccia (often formed by submarine debris flows), characteristic of the base of a slope
- Unit 2 (up to 100 m thick) is composed of bedded, black or dark grey limestones (carbonate turbidites with well-defined Boma cycles, possibly representing lower fan environment) with dark grey cherts (up to 1-3mm thick) on the lower part of the Unit, representing pelagic layers on the top of Boma cycles
- Unit 3 comprises bedded limestone, strongly bioturbated

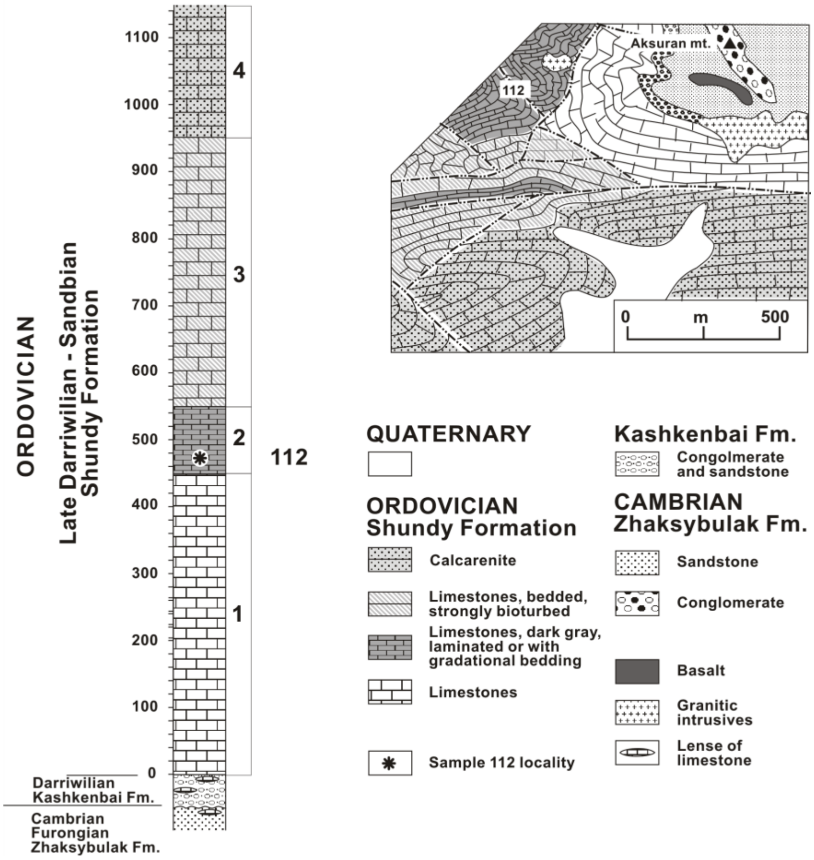
- Unit 4, at the top of the sequence, is made of calcarenite and represents a shallow water environment.

The radiolarian-bearing sample was collected from locality 112 about1100 m west-southwest from the Aksuran Mountain (north-west of Lake Balkhash) of the Atasu-Zhamshy Region (47°32'40.77"C, 73° 2'47.34"E; Fig.1). It has been sampled from the middle of Unit 2 of the Shundy Formation which consists of deep-water, black or dark grey bedded limestones intercalated with thin dark grey cherts. Carbonate turbidites with well-defined Bouma cycles also present in this unit, suggest a possible base-of-slope carbonate apron system (Fig. 2).

Figure 1: Schematic map of central Kazakhstan indicating the location of the Radiolarian and Trilobite bearing strata of this study in the Atasu-Zhamshy region (after Pouille *et al*., 2012b).

Age

Graptolites, identified by Tsai (*in* Apollonov *et al*., 1990) as *Hustedograptus* ex gr. *teretiusculus* occurring in the same stratigraphic level as the radiolarian-bearing sample 112 suggest an uppermost Darriwilian age. The trilobite fauna (*Endymionia semielliptica*, *Nambeetella*? sp. and *Porterfieldia* sp. aff. *P. delicata*) found associated with the sample confirms this upper Darriwilian age. *E. semielliptica* is known to occur in the mid-Darriwilian *Pterograptus elegans* graptolites Subzone (*Didymograptus murchsoni* Biozone ; Chang & Fan, 1960; Zhou & Dean, 1996) and *P.* sp. aff. *P. delicata* from the Shundy Formation is fairly similar and possibly conspecific to specimens occurring in the graptolite assemblage (*Cyrtograptus* sp. cf. *C. tricornis* (Carruthers, 1858), *Glossograptus* sp. cf. *C. hincksii* (Hopkinson, 1872), *Hustedograptus* ex gr. *teretiusculus* (Hisinger, 1840) and *Pseudoclimacograptus* ex. gr. *scharenbergi* (Lapworth, 1876)) transitional in age from the late Darriwilian to the Sandbian.



Schematic geological map of the Atasu-Zhamshy region (upper right) indicating the location of sample 112 and simplified stratigraphic column of the Shundy Formation (Middle to Upper Ordovician) (after Pouille *et al.*, 2012b).

Moreover, two radiolarian genera commonly present in sample 112 (*Syntagentactinia* and *Kalimnasphaera*) are known to first occur in the *Haplentactinia juncta*- *Inanigutta unica* assemblage which can be best correlated with the uppermost Darriwilian–lowermost Sandbian (e.g., discussion in Nazarov & Ormiston, 1993; Danelian & Popov, 2003; Maletz, 2011). Our assemblage also contains *Haplentactinia juncta*, one of the characteristic species of the *Haplentactinia juncta*-*Inanigutta unica* assemblage.

MATÉRIAL AND MÉTHODS

Radiolarians were extracted from a black to dark-grey micritic limestone sample after a standard treatment with 30% diluted acetic acid. Taxonomic study of this assemblage was made on the basis of SEM observation on over 450 specimens. This newly discovered assemblage is highly diversified, with a good state of preservation. All the types described here are housed in the public palaeontological collections of the Earth Sciences Department (SN5) of the University of Lille-1 (France).

FAUNAL COMPOSITION

The taxonomic study conducted on this assemblage shows the presence of 4 families (Inaniguttidae, Haplotaeniatidae, Haplentactinidae and Polyentactinidae), nine genera (*Inanihella, Inanigutta, Triplococcus*, *Inanibigutta, Kalimnasphaera, Haplotaeniatum, Syntagentactinia, Polyentactinia* and *Haplentactinia*) and 32 species.

The radiolarian fauna is here dominated by the Inaniguttidae which represent more than two-thirds of the fauna (69%) with the presence of five genera (*Inanihella, Inanigutta, Triplococcus*, *Inanibigutta* and *Kalimnasphaera*) and 14 species. The rest of the fauna is composed at 15% of *Haplotaeniatum*, at 13% of *Syntagentactinia*, and at 3% of *Polyentactinia* and rare *Haplentactinia* (Fig. 3).

The Inaniguttidae family is dominated by the genus *Triplococcus* which represents half of the Inaniguttidae (54%) and 37% of the whole assemblage. The genus *Triplococcus* is represented at 89% by two species: *Triplococcus aksuranensis* (49%) and *Triplococcus akzhala* (40%). These two species are here predominant, representing one-third (33%) of an assemblage composed of 32 species. The Inaniguttidae are also composed for a large part of the *Inanihella* (32%) which are dominated by 3 species (*Inanihella* sp. B, *Inanihella hirta* and *Inanihella bakanasensis*) and represent 22% of the whole assemblage. The rest of the Inaniguttidae family is composed of *Inanibigutta* (8%), *Inanigutta* (4%) and *Kalimnasphaera* (2%).

The Haplotaeniatidae are composed for a large part of *Haplotaeniatum* sp. cf. *H. tegimentum*, representing half of the *Haplotaeniatum* present in the sample (54%), *Haplotaeniatum noblae* (24%) and *Haplotaeniatum circulum* (10%).

The Haplentactinidae are composed at 98% of representatives of *Syntagentactinia*, dominated by *Syntagentactinia excelsa* (47%). The genus *Haplentactinia* is represented by only one species: *Haplentactinia juncta*, which represent 2% of the Haplentactinidae.

The Polyentactinidae family is dominated at 73% by *Polyentactinia spinulenta*.

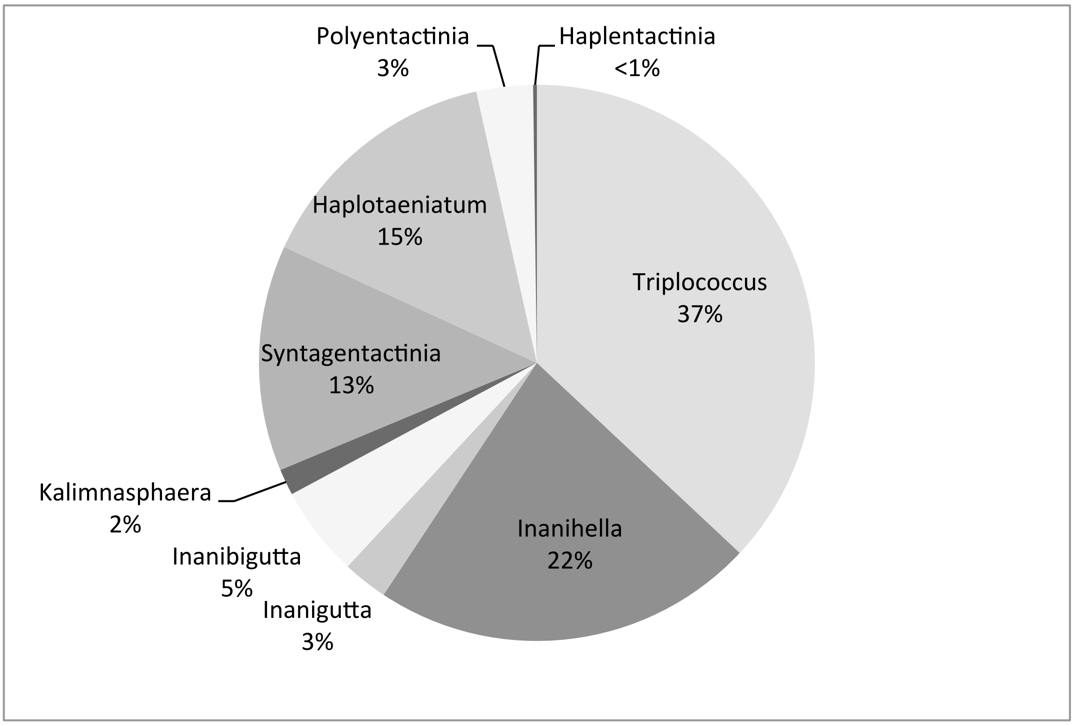


Figure 3**:** Pie diagrams showing the % relative abundance of radiolarian taxa composing the radiolarian assemblage of sample 112.

SYSTEMATIC PALAEONTOLOGY

Order **Entactinaria** Kozur and Mostler, 1982

Family **Haplentactiniidae** Nazarov *in* Nazarov & Popov, 1980

Genus *Syntagentactinia* Nazarov *in* Nazarov & Popov, 1980

Type species. Syntagentactinia biocculosa Nazarov *in* Nazarov & Popov, 1980.

Syntagentactinia excelsa Nazarov and Ormiston, 1993

(Pl. 1. figs. 1-4)

1993 *Syntagentactinia excelsa* n. sp.*;* Nazarov & Ormiston, p. 40, pl. 6, fig. 13-14.

2000 *Syntagentactinia excelsa* Nazarov & Ormiston; Kurihara & Sashida, p. 153, Figs. 7. 19, 7.20; 8.1-8.7

Material. 29 specimens.

Description. The inner framework consists of a distinct spherical to subspherical loosely latticed inner sphere, centrally or slightly eccentrically located inside an internal cavity. The outer shell consists of a thick spherical spongious meshwork formed of three to four latticed shell layers closely interconnected in a three-dimensional way by many radial beams. In some cases it can be very difficult to distinguish the different shell layers and the outer shell forms a very complex sponge-like ball. The inner shell is connected to the outer shells by rare beams. Primary spines are very thin, weakly developed and commonly indistinguishable from the exterior as most of the specimens lack them on the external surface of the outermost shell. The internalmost structure inside is not preserved in our material.

Dimensions (µm). Diameter of the cortical shell: 231-283; diameter of the inner shell: 76-97; Thickness of the outer shell: 45-75.

Remarks. It differs from the two other Ordovician *Syntagentactinia* species (*S. biocculosa*, *S. pauca*) described by Nazarov & Popov (1980) by possessing a thick multi-layered spongious outer shell, by the absence of rod-like outer spines and by its larger size (outer shell Ø: 231-283 µm herein; 175-225 µm for *S. biocculosa*; 110-160 µm for *S. pauca*; inner shell Ø: 76-97 µm herein; 35-65 µm for *S. biocculosa*; 50-82 µm for *S. pauca*). Our specimens only differ from *S. excelsa* as described Nazarov & Ormiston's material by their inner shell dimensions (76-97 µm herein; 40-42 µm for Nazarov & Ormiston's material), though it matches the dimensions defined by Kurihara & Sashida (40-90 µm). It differs from *S. afflicta* found in the same strata as *S. excelsa* by the absence of long, robust rod-like spines and of internal half-closed shells.

Syntagentactinia biocculosa Nazarov *in* Nazarov & Popov, 1980

(Pl. 1, figs. 5-7)

1980 *Syntagentactinia biocculosa* n. sp.; Nazarov *in* Nazarov & Popov, p. 56, pl. 12, fig. 1-3.

Material. 5 specimens.

Description. Internal structure consists of a five to six-rayed primary spicule incorporated in a small latticed inner shell. Six primary rays originate from a median-bar and turn into long rod-like outer spines (up to 200 µm) from the outer shell surface. These primary spines can be straight or slightly curved on their proximal part. A small internal cavity of an irregular outline separates the inner shell from the outer shell. The outer shell structure consists of three to four spongious shell layers of an irregular outline, closely interconnected by numerous radial beams in a very complex three-dimensional arrangement. The different spongious layers of the shells are hardly distinct. The outer shell is mostly spherical (rarely sub-spherical) and displays a sponge-like external aspect. Inside the inner cavity, rare apophyses can branch from the primary rays to join the inner shell surface.

Dimensions (µm). Diameter of the outer shell: 232-277; Diameter of the inner shell: 76-98; length of primary spines: 120-220; thickness of the outer structure: 80-110.

Remarks. The skeleton structure and dimensions of *S. biocculosa* are very close to *S. excelsa* (outer shell Ø: 232-277 µm herein; 231-283 µm for *S. excelsa*; inner shell Ø: 76-98 µm herein; 76-97 µm for *S. excelsa*). However, it differs from it by possessing six long, robust rod-like spines, a less loosely latticed inner shell and by having a less distinct inner cavity. It differs from *S. pauca* by possessing a thick multi-layered spongious outer shell and by its larger size (outer shell Ø: 232-277 µm herein; 110-160 µm for *S. pauca*). It differs from *S. afflicta* as described by Nazarov & Ormiston (1993) by the larger size of its inner shell (inner shell Ø: 76-98 µm herein; 40-42 µm for Nazarov & Ormiston's material) and from *S. afflicta* as described by Kurihara & Sashida (2000) by its smaller size (outer shell Ø: 232-277 µm herein; 280-300 µm for Kurihara & Sashida's material; inner shell Ø: 76-98 µm herein; 160-200 µm for Kurihara & Sashida's material). It also differs from *S. afflicta* by the absence of internal half-closed shells.

Syntagentactinia radiata nov. sp.

(Pl. 1, figs. 8-11)

Derivation of name. From the latin word "radiatus" meaning with rays, radiating

Holotype. Plate 1, figure 8 (USTL1157/045)

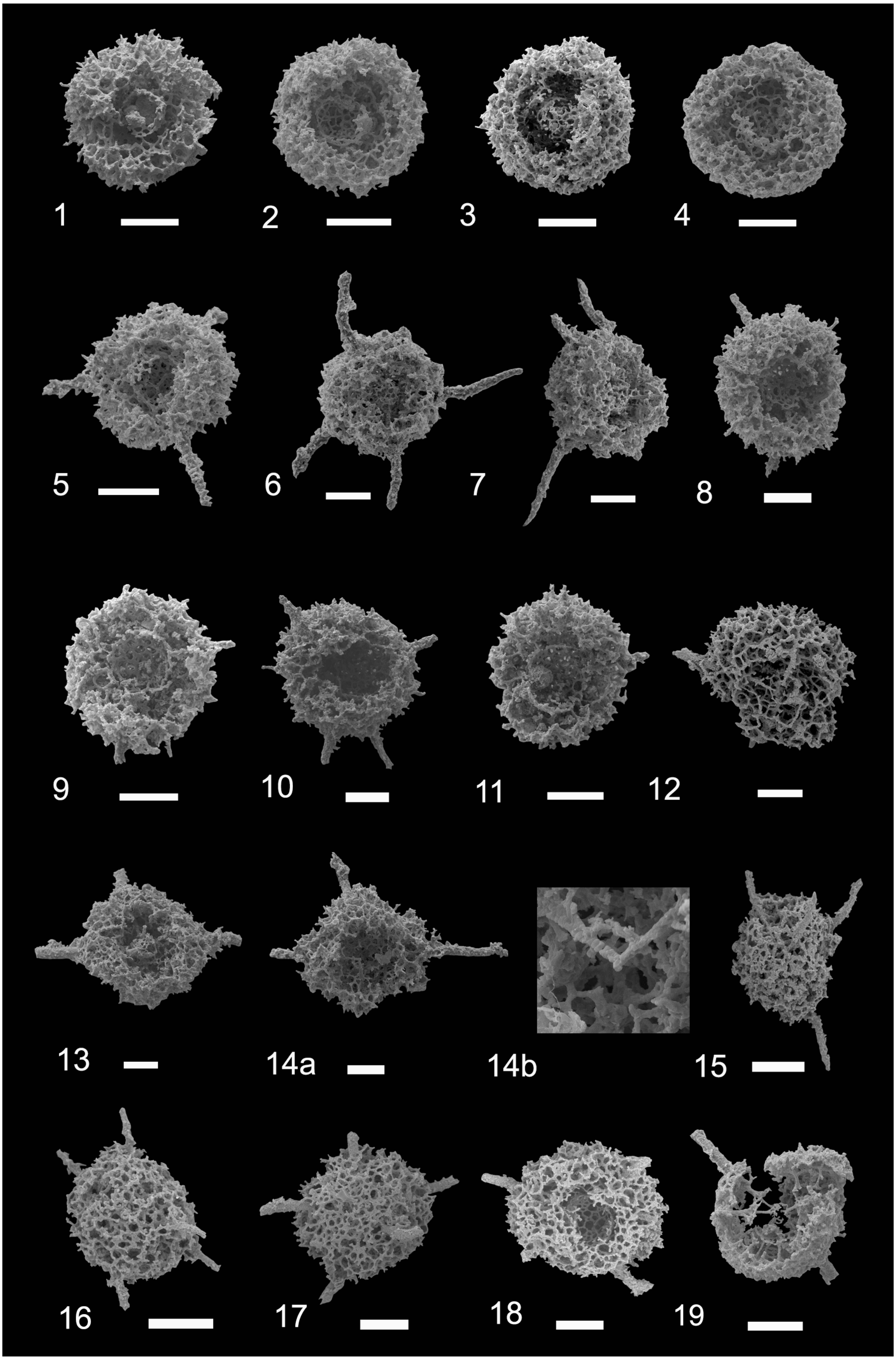
Paratype. Plate 1, figure 9 (USTL1182/044)

Material. 7 specimens.

Description. Spherical radiolarian with an outer shell structure formed of two (rarely three) spongious shell layers closely interconnected by many radial beams and arranged in a thick spongious three-dimensional way. The thickness of the spongious meshwork is variable. The internal framework consists of a large latticed inner shell with well-defined pores located inside a small hollow cavity. Inner shell is connected to the outer shells by short beams. Six primary rays protrude radially as very thin and short rod-like outer spines outside the outer shells. Thin secondary spines are present on the surface of the outer shell. The internalmost framework is broken in every specimen but primary rays have been observed to protrude inside the inner shell. Moreover, this species differs from Haplotaeniatumidae by the absence of any labyrinthine or spiraliform structure and from Ianinguttidae by the presence of a thick spongious meshwork.

Dimensions (µm). Diameter of the cortical shell: 260-330; diameter of the inner shell: 100-120; thickness of the outer structure: 32-70

Explanation of Plate 1. Scanning Electron Micrographs of *Syntagentactinia* yielded from from Shundy Formation, locality 112, Shundy Mountains, North Balkhash Region. Scale bar corresponds to 100 µm on all figures. 1-4. *Syntagentactinia excelsa;* 5-7. *Syntagentactinia biocculosa*, 5. Specimen showing broken internal spicule; 8-11. *Syntagentactinia radiata*, 8. Holotype of *Syntagentactinia radiata* (USTL1157/045); 9. Paratype of *Syntagentactinia radiata* (USTL1182/044); 12-14. *Syntagentactinia angulata,* 13. Holotype of *Syntagentactinia angulata* (USTL1142/048), 14a. Paratype of *Syntagentactinia angulata* (USTL1142/058), 14b. Magnified view of the paratype internal structure showing broken internal spicule and apophyses branching to form the innermost shell. 15-18. *Syntagentactinia polaspinata,* 15. Holotype of *Syntagentactinia polaspinata* (USTL1183/018), 17-18. Paratypes of *Syntagentactinia polaspinata* (USTL1185/008; USTL1184/015); 19. *Syntagentactinia* ? sp. A.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Remarks. It differs from *S. excelsa* and *S. biocculosa* by its larger size (outer shell Ø: 260-330 µm herein; 231-283 µm for *S. excelsa*; 232-277 µm for *S. biocculosa*; inner shell Ø: 100-120 µm herein; 76-97 µm for *S. excelsa*; 76-98 µm for *S. biocculosa*). It also differs from them by possessing thin secondary spines emerging at the surface of the outer shell. It differs from *S. pauca* by its thick spongious outer shell and by its larger size (outer shell Ø: 260-330 µm herein; 110-160 µm for *S. pauca*; inner shell Ø: 100-120 µm herein; 50-82 µm for *S. pauca*).

Syntagentactinia angulata nov. sp.
(Pl. 1, figs. 12-14b)

Derivation of name. From the latin word ”angulatus” meaning angular, bony

Holotype. Plate 1, figure 13 (USTL1142/048)

Paratype. Plate 1, figure 14a (USTL1142/058)

Material. 9 specimens.

Description. The internal framework consists of a six-rayed point-centered spicule from which six primary rays originate. Apophyses are branching from the primary rays at a distance of about 20-40 µm from the spicule centre to form a small irregularly latticed inner shell (Ø 68-85 µm). The inner shell is unevenly porous and located inside a hollow cavity. The cavity is formed of a very irregular outline and clearly separates the inner and outer shell. Outer shell is formed from different groups of apophyses which branch from the primary rays to form a very thick, irregular and dense spongious meshwork (up to 130 µm thick). The outer shell displays a polygonal to quadrangular shape. Primary rays are separated by an angle of 90° and emerge as thick rod-like outer spines from the surface of the outer shell.

Dimensions (µm). Diameter of the cortical shell: 346-400; diameter of the inner shell: 64-85; length of primary spines: up to 200; diameter of the inner cavity: 60-85.

Remarks. Due to its small size, the inner shell surrounding the primary spicule can be mistaken with a microsphere on unbroken specimens. This species differs from other *Syntagentactinia* species previously cited by its much larger size (outer shell Ø: 346-400 µm herein; 240-310/280-300 µm for *S. afflicta*, 231-283 µm for *S. excelsa*; 232-277 µm for *S. biocculosa*, 260-330 µm for *S. angulata*; 110-160 µm for *S. pauca*). It also differs from them by its polygonal to quadrangular shape, its wide inner cavity and its thick and complex three-dimensional non-layered meshwork.

Syntagentactinia polaspina nov. sp.

(Pl. 1, figs. 15-18)

Derivation of name. From the latin words ”polus” meaning polar, and “spinus” meaning spine

Holotype. Plate 1, figure 15 (USTL1183/018)

Paratype. Plate 1, figure 17 (USTL1185/008); Plate 1, figure 18 (USTL1184/015)

Material. 10 specimens.

Description. The spongious outer shell displays an ovoid shape with six primary spines. Two spines are located on the margin of one pole of shell. The four other horn-like spines are situated on the opposite pole of the sphere and are curved inwardly. The outer shell consists of a thick multi-layered three-dimensional meshwork. The inner framework consists of a latticed inner shell. Internalmost framework is unknown.

Dimensions (µm). Diameter of the outer shell: 190-318; diameter of the inner shell: 117-134; length of the outer spines: up to 150.

Remarks. It differs from other *Syntagentactinia* by its ovoid shape, by the peculiar position of its primary spines and by the size of its inner shell (inner shell Ø: 117-134 µm herein; 42-56/160-200 µm for *S. afflicta*; 76-97 µm for *S. excelsa*; 76-98 µm for *S. biocculosa*; 100-120 µm for *S. radiata*; 64-85 µm for *S. angulata*; 50-82 µm for *S. pauca*).

Syntagentactinia? sp. A

(Pl. 1, fig. 19)

Material. 1 specimen.

Description. This morphotype displays a primary spicule located inside a very small sphere (Ø about 33-38 µm) surrounded by an inner and an outer shell. Six or more primary rays originate from the primary spicule and turn into thick rod-like spines from the surface of the outer one. Numerous beams connect the latticed inner shell with the outer shell. The external framework consists of two latticed shell layers closely interconnected in a three-dimensional arrangement. The outermost shell layer displays a thick spongious aspect.

Dimensions (µm). Diameter of the innermost sphere: 33-38; Diameter of the inner shell: 91-98; Diameter of the outer shell: 229-238; Length of the outer spines: up to 95; Thickness of the outer shell wall: 33.

Remarks. The small sphere inside the inner shell can only be distinguished from a microsphere by the presence of primary rays protruding inside it. As the primary spicule is broken it is difficult to know the exact number of primary rays that originated from it. It differs from all other *Syntagentactinia* species by its regular outline, the presence of a very small sphere surrounding the primary spicule and the presence of numerous beams connecting the inner and outer shells. It also differs from all the species described in this paper by possessing a much thinner outer shell wall.

Genus *Haplentactinia* Foreman, 1963

Type species. Haplentactinia rhinophyusa (Foreman, 1963)

Haplentactinia juncta (Nazarov, 1975)

(Pl. 2, fig. 1)

1975 *Haplentactinia juncta* sp. nov; Nazarov, pl. 20, fig. 5, 6.
1980 *Haplentactinia juncta* Nazarov, Nazarov & Popov, pl.4, fig. 2; pl. 6, fig. 3-5
1988 *Haplentactinia juncta* Nazarov, Nazarov, pl. 10, fig. 4
1994 *Haplentactinia juncta* Nazarov, Gorka, pl.2, fig. E, F.

Material. 1 specimen from sample 112.

Description. See Nazarov, 1975

Dimensions (µm). Diameter of the shell: 177-205; Diameter of the meshes width: 20-45, Length of the spines (from median bar): up to 150 µm.

Remarks. It differs from *Haplentactinia armillata* by its wider and more loosely constructed mesh, its smaller size (shell Ø: 177-205 µm herein; 320-400 µm in *H. armillata*) and absence of a bifurcated primary spine, characteristic of *H. armillata* species. It differs from *H. infida* and *H. baltica* by its more rounded outline. *H. infida* differs also from *H. juncta* by possessing one spine considerably larger than the others and by having apophyses on this spine located closer to the inner spicule whereas other apophyses are at equal distance from it.

Family **Polyentactiniidae** Nazarov, 1975

Genus *Polyentactinia* Foreman, 1963

Type species. Polyentactinia craticulata Foreman 1963

Polyentactinia spinulenta nov. sp.

(Pl.2, figs. 2-8)

Derivation of name. From the latin word “spinulentus” meaning thorny.

Holotype. Plate 2, figure 7 (USTL1140/008)

Paratype. Plate 2, figure 5a (USTL1140/074); Plate 2, figure 6a (USTL1142/068)

Material. 11 specimens, all from sample 112.

Description. Internal framework consists of a primary spicule formed of a short median bar (10-15 µm) from which six primary rays originate. The median bar is eccentrically located in the spherical skeleton and it may often appear point-centered depending on its orientation.

Due to the eccentric position of the median bar not all the primary rays have the same length. The six primary rays become more robust and thicker when protruding outside the spherical shell as they become rod-like outer spines. They can be straight or slightly curved. Two perpendicular whorled rays originate at the distal parts of the primary rays and are connected to the spherical skeleton. The shell is formed from a latticed meshwork with angular meshes formed from interwoven bars of various thickness. On well-preserved specimens numerous small simple or bifurcated spinules are present on the shell surface.

Dimensions (µm). Diameter of the shell: 227-305 (average; 262-284); length of primary spines: up to 120; length of the median bar: 10-15; Thickness of the inner elements of the skeleton: up to 10.

Remarks. This species differs from *Astroentactinia* by the absence of pores and of any conical secondary spines on its cortical shell. Its internal frame and shell structure suggest an assignement to *Polyentactinia*. *P. spinulenta* differs from the other upper Darriwilian species *P. offerta* described from the *Haplentactinia juncta- Inanigutta unica* assemblage by possessing no more than 6 thin rod-like external spines and a shell formed from a meshwork of interwoven bars forming angular meshes and covered by small spinules whereas *P. offerta* displays a porous latticed shell with more than 12 external spines. It differs from Upper Ordovician *Polyentactinia? estonica* by possessing thinner, longer and less numerous outer spines and by its less massive shell structure.

It differs from Silurian species *P. stelcki* and ?*P. leeorum* by its larger size (outer shell Ø: 227-305µm herein; ca. 200 µm for ?*P. leeorum*, 70-135 µm for *P. stelcki*), by its more angular mesh structure and the presence of interwoven bars.

Most *Polyentactinia* species are described from the Devonian to Permian interval. As for the Devonian, *P. spinulenta* is easily distinguished from *P. kossistekensis*, *P. rudihispida* and *P. propinga* by its internal structure and number of primary spines (6-rayed median-bar herein, 7 to 8 rays for *P. kossistekensis*; 7 to 10 rays for *P. propinga* and *P. rudihispida*). *P. circumretia* differs from *P. spinulenta* by having a 6 to 7-rayed point-centered spicule centrally located and bi or tri-furcated outer spines. *P. spinulenta* differs from *P. polygonia*, *P. craticulata* and *P. leptosphaera* by its larger size (outer shell Ø: 227-305 µm herein; 90-180 µm in *P. polygonia*; 115-150 µm in *P. craticulata*; 160-240 µm in *P. leptosphaera*) but also possessing a short median-bar instead of a double spicule. The shell structure of *P. spinulenta* also differs from *P. invenusta* and *P. tenera* which display a thinly and delicately shell structure constructed in a three-dimensional way and which display a thick spongy tissue. *P. spinulenta* can be easily distinguished from all younger *Polyentactinia* species (Carboniferous to Permian) by lacking three-bladed spines.

Polyentactinia. sp. cf. *P. spinulenta*

(Pl. 2, fig. 9)

Material. 2 specimens from sample 112.

Description. Internal framework consists of an initial spicule formed of a very short median bar (about 8 µm) eccentrically located that may appear point-centered depending on its orientation. Five primary rays emerge from the median bar and turn into thick rod-like outer spines from the outer shell surface. Two primary rays are longer than the others and bear at their distal ends two long perpendicular whorled rays connected to the outer shell meshwork. Some of them can emerge from the shell surface as secondary spines. Simple apophyses can be present at the distal end of these whorled rays and be merged with the bars of the shell meshwork. The shell is formed of a loosely meshwork of thick straight and curved bars disorderly interwoven or fused. Numerous simple or bi- to tri-furcated spinules are present on the shell surface.

Dimensions (µm). Diameter of the shell: 330-365; length of the median bar: about 8; thickness of the inner elements of the skeleton: up to 20.

Remarks. This species differs from *P. spinulenta* by having much thicker primary rays, a thicker skeleton structure, larger dimensions (shell Ø: 330-365µm herein; 227-305 µm in *P. spinulenta*) and the presence of numerous spinules on the shell surface. It also differs from *P. spinulenta* by possessing whorled rays on only two primary spines and by having only five primary spines and a much shorter median bar (length of the median bar: 8µm herein; 10-15 µm for *P. spinulenta*).

Polyentactinia sp. A

(Pl. 2, figs. 10a-10b)

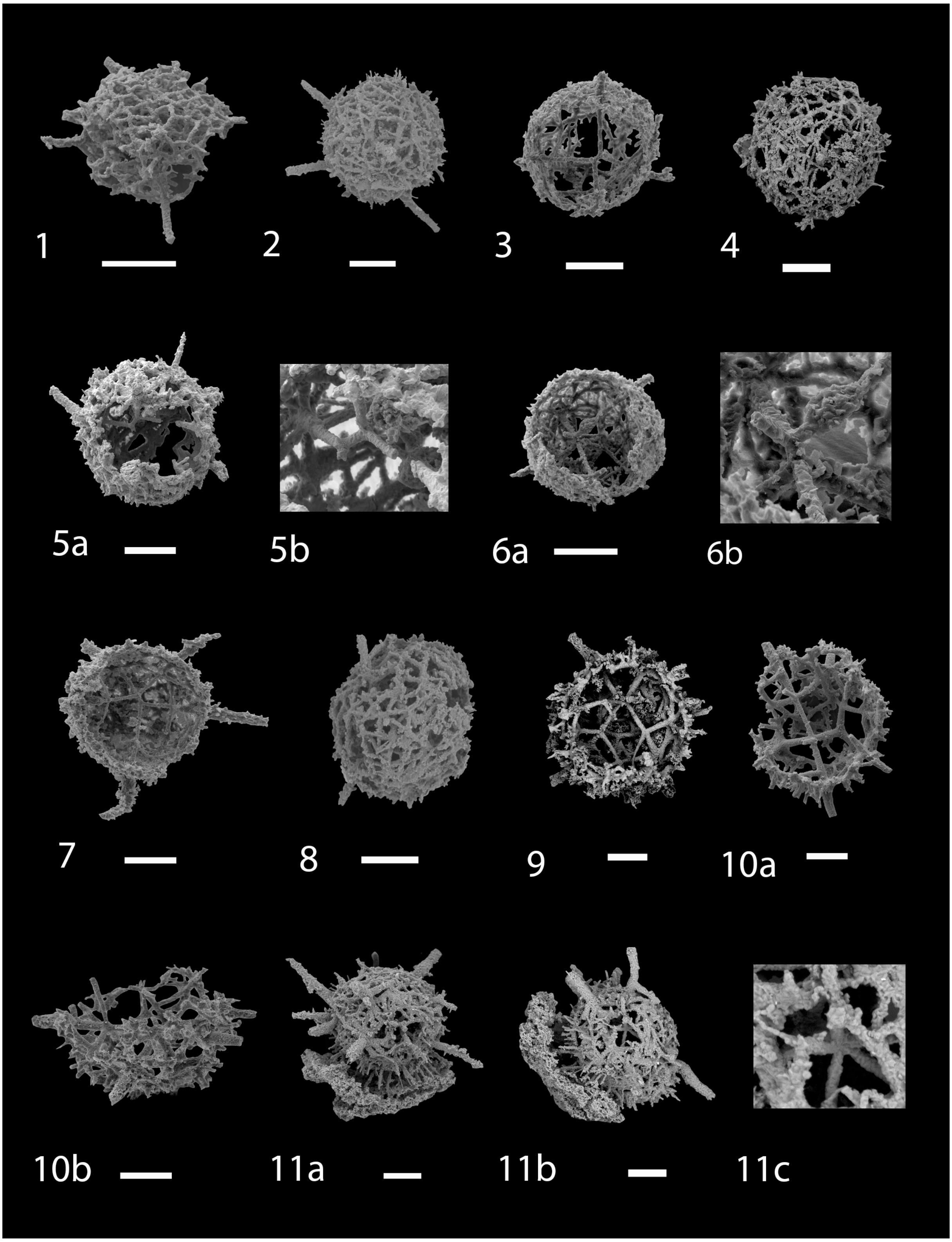
Material. 1 specimen from sample 112.

Description. Internal framework consists of an initial spicule formed of a long median bar (about 60 µm) eccentrically located from which five (six?) primary rays originate. The primary rays turn into thick rod-like straight outer spines when protruding outside the spherical shell. Two to three perpendicular whorled rays originate at the distal parts of each primary rays and fuse with the spherical skeleton. Some of them can emerge from the shell surface as rod-like secondary spines. Apophyses are branching from the primary spines to form an irregular spherical loosely meshwork formed of thick straight and curved bars disorderly interwoven or fused. Numerous simple or bi- to tri-furcated spinules are present on the shell surface.

Dimensions (µm). Diameter of the shell: 325-365; length of the median bar: about 60; thickness of the inner elements of the skeleton: up to 20.

Remarks. It only differs from *Polyentactinia.* sp. cf. *P. spinulenta* by possessing up to three whorled rays on the primary spines and also by the larger size of the median bar (length of the median bar: 60 µm herein; 8µm for *Polyentactinia.* sp. cf. *P. spinulenta*).

Explanation of Plate 2. Scanning Electron Micrographs of *Haplentactinia* and *Polyentactinia* yielded from Shundy Formation, locality 112, Shundy Mountains, North Balkhash Region. Scale bar corresponds to 100 µm on all figures. 1. *Haplentactinia juncta*; 2-8. *Polyentactinia spinulenta,* 7. Holotype of *Polyentactinia spinulenta* (USTL1140/008), 5a, 6a. Paratypes of *Polyentactinia spinulenta* (USTL1140/074; USTL1142/068). 5b, 6b. Magnified view of *Polyentactinia spinulenta* paratypes showing the primary spicule and the median bar; 9. *Polyentactinia.* sp. cf. *P. Spinulenta*; 10a-b. *Polyentactinia* sp. A; 11a-c. . *Polyentactinia* sp. B, 11c. Magnified view of the internal spicule.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Polyentactinia sp. B
(Pl. 2, figs. 11a-11c)

Material. 1 specimen from sample 112.

Description. The outer shell displays an ovoid outline and is characterized by an intergrowth of strongly fused bars. The skeleton is very compact and made of thick elements. From eight to ten thick rod-like outer spines emerge from the shell surface and can bear small simple apophyses. Numerous thin and long spinules are present on one side of the shell surface. The internal framework is hidden except for a six-rayed point centered spicule visible from a wide opening.

Dimensions (µm). Diameter of the shell: 282-335; length of the outer spines: up to 122.

Remarks. The inner structure of the shell is not entirely visible. The six-rayed point centered spicule may be considered as the initial skeleton but none of the thick rod-like outer spines seems to be connected to the rays of this spicule. The outer shell of *Polyentactinia* sp. B clearly differs from all other *Polyentactinia* species by its characteristic intergrowth of strongly fused bars and the more developed long spinules covering the shell surface. The skeletal structure of *Polyentactinia* sp. B displays some affinities with the Silurian genus *Palaeophippium* but it differs from it by not showing a saddle shaped internal spicule with apical and basal hemispheres.

Order **Spumellaria** Ehrenberg, 1875

Family **Haplotaeniatidae** (Won *et al*., 2002)

Genus *Haplotaeniatum* Nazarov and Ormiston, 1993, emend. Won *et al*., 2002, emend. Jones & Noble, 2006

Type species. Haplotaeniatum labyrintheum Nazarov & Ormiston, 1993

Haplotaeniatum circulum nov. sp.
(Pl. 3, figs. 1-2b)

Derivation of name. From the latin word ”circulus” meaning circle

Holotype. Plate 3, figure 2a (USTL1142/061)

Material. 6 specimens, from sample 112.

Description. *Haplotaeniatum* formed of five to six irregularly circular pseudospongy latticed shells arranged in a slightly spiraliform fashion. Internal framework consists of a small latticed microsphere centrally located. Four visible primary rays originate from the microsphere. They turn into massive rod-like long outer spines (up to 350 µm or more) from the outer shell. Apophyses branch from the primary spines to form the different latticed shells surrounding the microsphere. A few apophyses can be irregularly placed giving the shell a spiraliform arrangement. The shells are connected together by thin beams irregularly placed forming a “cellular-wall”. The shell layer forms numerous half-loops at the points where it is connected to the radial beams. The outermost shell is formed of a three-dimensional spongious meshwork which originates from two to three groups of apophyses branching from the primary spines. The outer shell displays a spherical shape. No secondary spines are presents.

Dimensions (µm). Diameter of the outer shell: 290-354; diameter of the microsphere: 40-52; length of primary spines: up to 368; thickness of the cortical shell wall: 42-48

Remarks. It differs from Late Ordovician *Haplotaeniatum* by its shell structure formed of four to five irregularly circular pseudospongy shells, its perfectly spherical shape and its large size (outer shell Ø: 336-354 µm in our material; 104-170 µm for *H. spinatum*; ca. 145 µm for *H. fenestratum*; 115-291(?) µm for *H. prolatum*; 180-230 µm for *H. ovatum*). *H. circulum* external appearance can be similar to *H. ovatum* when this latter display a circular outline. However, *H. circulum* can still be easily distinguished from it by the presence of long thick rod-like outer spines and the absence of a pylome. This species shows closer affinities with Lower Silurian species. It shares a similar shell structure with *H. labyrintheum* with the presence of three to five spiraliform shells united by means of transverse cross-beams. Both species share approximately the same size (outer shell Ø: 336-354 µm herein; 296-354 µm for *H. labyrintheum*, microsphere

Ø: 40-52 µm herein; 38-43 µm for *H. labyrintheum*) but *H. circulum* still differs from *H. labyrintheum* by having a centrally positioned microsphere, a thinner meshwork and very thin cross beams. *H. circulum* also differs from *H. labyrintheum* by the length of its primary spines (up to 368 µm herein; up to 100 µm for *H. labyrintheum*). However, this difference here is certainly preservational as *H. labyrintheum*? spine length *sensu* MacDonald (2006) reaches 480 µm. *H. circulum* also displays structural similarities with *H. cathenatum* which possess four to five intermediate shells of an isometric form between the microsphere and outer shell. Though, it differs from it by having a more spherical shape, well-developed massive primary spines (spine length up to 368 µm herein; up to 80 µm for *H. cathenatum*) and by the absence of a pylome.

It also differs from *H. primordialis*? and *H. tegimentum* by its larger size (outer shell Ø: 336-354 µm in our material; 194-208 µm for *H. primordialis*?; 240-264 µm for *H. tegimentum*) and by its well-developed outer spines (spine length up to 368 µm herein; up to 40 µm for *H. primordialis*?; up to 20 µm for *H. tegimentum*). It also differs from *H. tegimentum* by the absence of half-closed shells and conical external spines and by possessing a microsphere centrally located.

Haplotaeniatum noblae nov. sp.

(Pl. 3, figs. 3-4)

Derivation of name. In honor of Paula Noble.

Holotype. Plate 3, figure 4 (USTL1182/033)

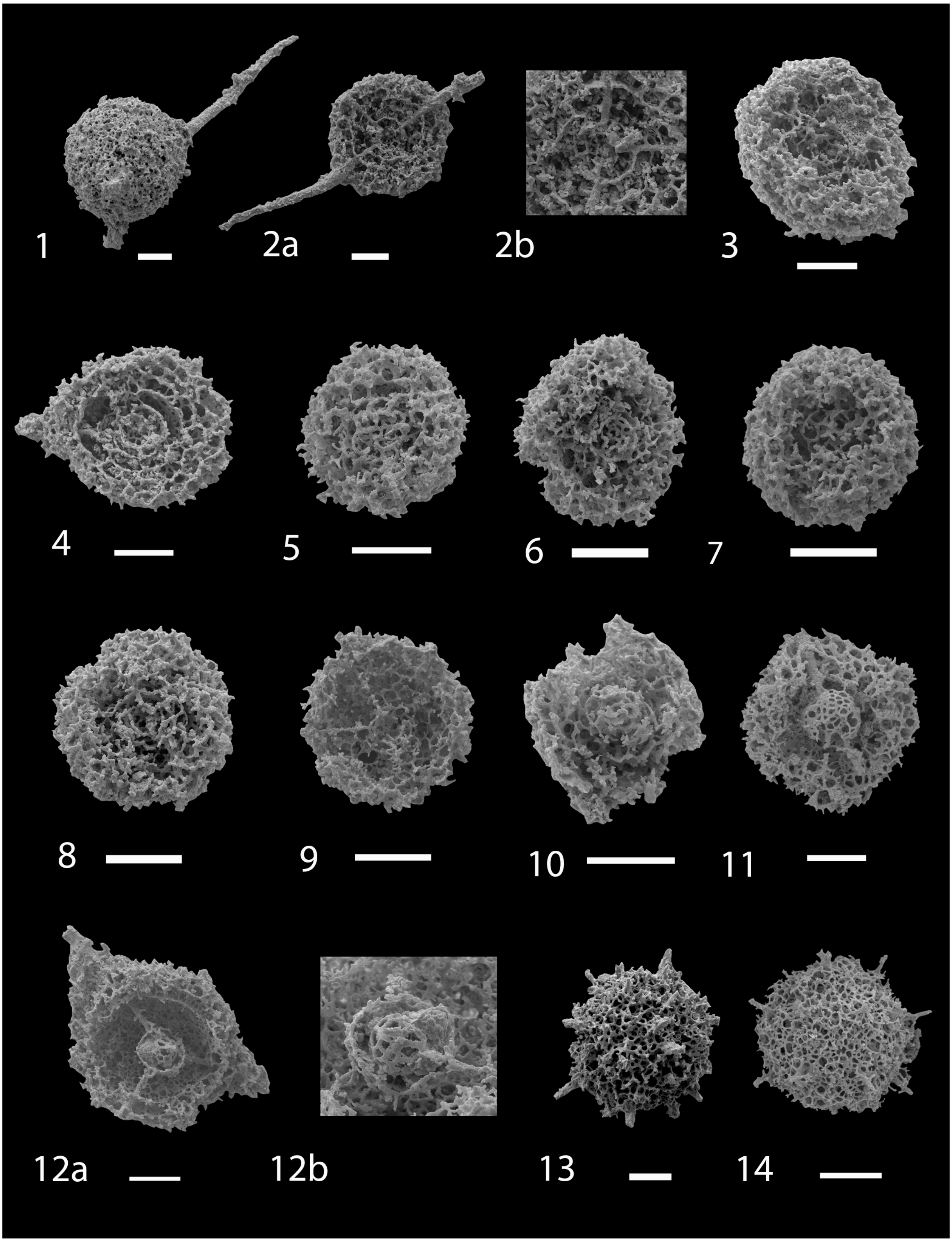
Paratype. Plate 3, figure 3 (USTL1182/030)

Material. 9 specimens, from sample 112.

Description. *Haplotaeniatum* formed of a latticed microsphere, centrally located, surrounded by four to five shells arranged in a spiraliform fashion. Shells are interconnected together by small beams irregularly placed. They display a cellular outline, forming numerous half-loops at the point where they are link to the beams. The outermost shell is egged-shaped and formed of a thin spongious meshwork. At least two primary spines have been observed to originate from the microsphere. Outer spines are thick and covered with spongious accretions that accentuate the ellipsoidal shape. No secondary spines are present.

Dimensions (µm). Diameter of the outer shell: 240-358; Diameter of the microsphere: 50-55

Remarks. This species differs from Upper Ordovician *Haplotaeniatum* by its shell structure formed of four to five irregularly latticed shells and its large size (outer shell Ø: 240-358 in our material; 104-170 µm for *H. spinatum*; ca. 145 µm for *H. fenestratum*; 115-291(?) µm for *H. prolatum*; 180-230 µm for *H. ovatum*). It also differs from *H. ovatum* by its larger size (outer shell Ø: 240-358 µm herein; 180-201 µm for *H. ovatum*). It shows closer affinities regarding its shell structure with *H. circulum*, *H. labyrintheum* and *H. cathenatum*. It differs though from *H. circulum* by its more accentuated spiraliform construction, by its ellipsoidal shape and by its weakly developed primary spines. It differs from *H. labyrintheum* by possessing very thin radial beams, weakly-developed primary spines, a larger microsphere (Ø: 50-55 µm herein; 38-43 µm for *H. labyrintheum*) centrally located and a more distinct layering. It differs from *H. cathenatum* by the absence of a pylome and secondary spines and a more compact shell layers construction but also by its smaller dimensions (outer shell Ø: 240-358 µm herein; 308-394 µm for *H. cathenatum*). It differs from *H. primordialis* and *H. tegimentum* by its larger size (outer shell Ø: 240-358 µm in our material; 194-208 µm for *H. primordialis*?; 240-264 µm for *H. tegimentum*). It also differs from Its external egg-shaped appearance is similar to *H. ovatum* but it differs from it by lacking a pylome, having a less dense labyrinthine shell construction and a more distinct internal layering. *H. primordialis*? by possessing a more important number of shell layers and by *H. tegimentum* by the absence of half-closed shells and conical external spines but also by possessing a centrally located microsphere.



Explanation of Plate 3. Scanning Electron Micrographs of the *Haplotaeniatum* yielded from from Shundy Formation, locality 112, Shundy Mountains, North Balkhash Region. Scale bar corresponds to 100 µm on all figures. 1-2. *Haplotaeniatum circulum*, 2a. Holotype of *Haplotaeniatum circulum* (USTL1142/061); 2b. Magnified view of *Haplotaeniatum circulum* holotype showing the microsphere and inner shell; 3-4. *Haplotaeniatum noblae*,

4. Holotype of *Haplotaeniatum noblae* (USTL1182/033), 3. Paratype of *Haplotaeniatum noblae* (USTL1182/030); 5-10. *Haplotaeniatum* sp. cf . *H. tegimentum*; 11. *Haplotaeniatum?* sp. A; 12. *Haplotaeniatum? giganteum,* 12a. Holotype of *Haplotaeniatum? giganteum*, 12b. Magnified view of *Haplotaeniatum? giganteum* holotype showing the the microsphere and inner shell; 13. *Haplotaeniatum* sp. B; 14. *Haplotaeniatum* sp. C.

Haplotaeniatum sp. cf . *H. tegimentum*
(Pl. 3, figs. 5-10)

Cf. 1993 *Haplotaeniatum tegimentum* sp. nov; Nazarov *in* Nazaov and Ormiston, pl. 3, fig. 14-16.
Cf. 2000 *Haplotaeniatum tegimentum* Kurihara and Sashida, pl. 7, fig. 1-13
CF. 2004 *Haplotaeniatum tegimentum*; Kurihara, pl. 1, fig. 1-2.

Material. 33 specimens, from sample 112.

Description. The internal framework is formed of a microsphere surrounded by a complex meshwork of several latticed layers formed from curved to curled bars developed in a spiraliform way. The curled bars form numerous small half-closed loops around the microsphere. No internal cavity is seen. The microsphere, which is not easily distinct, is generally centrally located. Rare beams are present. From three to four primary rays originate from this microsphere but they are rarely developed externally. The outer shell consists of a thick spongious three-dimensional shell of variable thickness. It displays a spherical to sub-spherical outline.

Dimensions (µm). Diameter of the outer shell: 220-280; Diameter of the microsphere: 26-38

Remarks. This species show a very similar morphology as *H. tegimentum* illustrated by Kurihara (2004). However, it differs from it by its centrally located microsphere and by the absence of any external spines. It differs from co-occuring *H. circulum* and *H. noblae* by its less distinct and less numerous internal shell layers, by its thickest outer shell spongious meshwork and by its denser layering structure formed of numerous small half-closed loops around the microsphere. It also differs by its smaller size (outer shell Ø: 220-280 µm in our material; 290-

354 µm for *H. circulum*; 240-358 µm for *H. noblae*; microsphere Ø: 26-38 µm in our material; 50-55 µm for *H. circulum*; 40-52 µm for *H. noblae*).

It differs from Upper Ordovician *Haplotaeniatum* by its internal shell structure, by its dense and thick three-dimensional spongious outer shell of a spherical shape and by its large size (outer shell Ø: 220-280 µm in our material; 104-170 µm for *H. spinatum*; ca. 145 µm for *H. fenestratum*; 115-291(?) µm for *H. prolatum*; 180-230 µm for *H. ovatum*). It is easily distinguished *H. ovatum* by its more discernable internal layering and the absence of a pylome.

It differs from *H. labyrintheum* and *H. cathenatum* by its smaller size (outer shell Ø: 220-280 µm in our material; 296-354 µm for *H. labyrintheum*; 308-394 µm for *H. cathenatum*) by possessing less internal shell layer that are more densely constructed forming numerous half-closed loops of a very small size around the microsphere and a thick spongious three-dimensional outer shell. It also differs from *H. labyrintheum* by possessing a centrally located microsphere, lacking rod-like external spines and a cellular wall and from *H. cathenatum* by lacking a pylome and thin secondary spines. It differs from *H. primordialis*? by its larger size (outer shell Ø: 220-280 µm in our material; 194-208 µm for *H. primordialis*?) and its denser internal shell structure. It differs from *H. fissura* by the absence of a distinct gap between the microsphere and outer layers of the shell, the absence of a pylome and the weak development of primary spines. It also differs from it by possessing a thick spongious outer shell with no distinct pores. It differs from *H. aperturatum* and *H. adobensis* by lacking large pores on the outer shell surface, by having a more distinct internal spiraliform structure and by lacking a pylome. It differs from the co-occuring species *S. excelsa* by displaing a small microsphere, a spiraliform layering, the presence small half-closed loops around the microsphere and by lacking a distinct gap between the microsphere and outer shell layers. These two species also differ by their outer shell structure which is formed of more or less distinct closely interconnected layers in *S. excelsa* whereas *Haplotaeniatum* sp. cf. *H. tegimentum* is formed of a undistinctly-layered thick three-dimensional spongious meshwork.

Haplotaeniatum? giganteum nov. sp.

(Pl. 3, figs. 12a-12b)

Derivation of name. From the latin word “giganteus” meaning gigantic, huge.

Holotype. Plate 3, figure 12 (USTL1172/085)

Material. 5 specimens, all from sample 112.

Description. Internal framework consists of a centrally located latticed microsphere with uneven pores variable in size (from 5 to 18 μm). This microsphere is encapsulated in a subspherical to oval inner latticed shell. Six primary rays originate from the microsphere and turn into thick rod-like spines from the surface of the outer shell. The inner shell is clearly separated from the outer shell by a large empty cavity. Small and simple apophyses, irregularly placed, can branch from the primary rays between the inner and outer shells. Some apophyses can join the inner shall surface. The outer framework consists of three thinly latticed oval shell layers closely interconnected by numerous short beams in form of a three-layered wall arrangement. The outer shell surface displays a very spongious aspect. Outer spines are thick and covered at their proximal part with numerous apophyses branching to join the outer shell surface which contribute to give the shell a strong ellipsoidal shape.

Dimensions (μm). Diameter of the outermost shell: 336-470; diameter of the inner shell: 90-100; diameter of the microsphere: 55-59; diameter of the inner cavity separating outer and inner shells: 55-74; thickness of the outer structure: 50-62, width of microsphere pores: 5 to 18.

Remarks. The internal part of *Haplotaeniatum? giganteum* has been observed on only two specimens. This species is here assigned to genus *Haplotaeniatum* based on its internal framework consisting of a microsphere. However, this assignement is still ambiguous as it displays some morphological characters more similar to the genus *Syntagentactinia* while at the same time it doesn't display any spiraliform arrangement as in *Haplotaeniatum*. On the contrary, it is formed of concentric shells, with internal and outer shells separated by a wide empty internal cavity as in *Syntagentactinia*. In their emendation of *Haplotaeniatum*, Won *et al*. (2002) included specimens that are definitely separated into outer and inner parts but Jones and Noble (2006) removed forms possessing a distinct inner and outer areas from the genus. Some *Syntagentactinia* possess a very small innermost sphere surrounding the primary spicule that can be mistaken with a microsphere (see *Syntagentactinia angulata* and *Syntagentactinia* ? sp. A). However, as no primary rays were observed to protrude inside the microsphere, this species is tentatively assigned to *Haplotaeniatum*.

Haplotaeniatum? sp. A
(Pl. 3, fig.11)

Material. 1 specimen from sample 112.

Description. Internal framework consists of a centrally located latticed microsphere from which six (?) primary rays originate. The microsphere is surrounded by a spherical inner latticed shell. The inner shell is clearly separated from the outer shell by a small empty cavity. Very thin and tiny beams emerge from the surface of the inner shell to connect the outer shell. The primary rays turn into thick rod-like outer spines from the outer shell wall. Three to four groups of apophyses branch from the primary spines to form a thick three-dimensional spongious meshwork indistinctly layered.

Dimensions (µm). Diameter of the outermost shell: 319-325; diameter of the inner shell: 99-100; diameter of the microsphere: 53-54; diameter of the inner cavity separating outer and inner shells: 28-41; thickness of the outer structure: 40-83.

Remarks. This species is formed of concentric shells, with the internal and outer shells separated by an empty internal cavity as in *Syntagentactinia*. As no primary rays have been observed to protrude inside the microsphere, this species is tentatively attributed to the genus *Haplotaeniatum*. It differs from *Haplotaeniatum? giganteum* by its smaller size (outer shell Ø: 319-325 µm herein and 336-470 µm for *Haplotaeniatum? giganteum*) but also by possessing a smaller inner cavity of an irregular outline and a thick three-dimensional spongious outer meshwork indistinctly layered.

Haplotaeniatum sp. B
(Pl. 3, fig. 13)

Material. 2 specimens, all from sample 112.

Description. This specimen displays a dense three-dimensional mesh of bars disorderly interwoven forming the spherical shell. About 20 thick and short outer spines are irregularly placed on the shell surface. The outer shell displays a subspherical irregular outline. Inner structure is unknown.

Dimensions (µm). Diameter of the outer shell: 313-320; Thickness of the base of the outer spines: 20 to 25.

Remarks. This species differs from other *Haplotaeniatum* by the presence of numerous outer spines. This high number of outer spines is most often encountered in *Oriundogutta* which can possess from 8 to 20 external horns. However, *Oriundogutta* is distinguished by possessing a two-dimensional porous outer shell whereas *Haplotaeniatum* sp. indet. 1 displays a thick three-dimensional disorderly interwoven meshwork.

Haplotaeniatum sp. C

(Pl. 3, fig.14)

Material. 1 specimen from sample 112.

Description. This specimen is formed of a dense three-dimensional mesh of fine bars. It consists of several latticed layers three-dimensionally interwoven which give the shell a spongious aspect. There are about 20 thin short outer spines present. It displays a spherical to hexagonal outline. Apophyses can branch from the proximal part of the outer spines and merge into the outer shell meshwork. Inner structure is unknown.

Dimensions (µm). Diameter of the outer shell: 238-255; Thickness of the base of the outer spines: 5 to 7.

Remarks. This species differs from *Haplotaeniatum* sp. B by having a thinner and more delicate meshwork and thinner outer spines (thickness of the base of the outer spines: 5 to 7 µm herein; 20 to 25 µm for *Haplotaeniatum* sp. B) but also from its smaller size (outer shell Ø: 238-255 µm herein; 313-320 µm for *Haplotaeniatum* sp. B)

DISCUSSION

Our assemblage can be correlated to the upper Darriwilian *Haplentactinia juncta*- *Inanigutta unica* assemblage with which it shares seven genera (*Syntagentactinia*, *Kalimnasphaera, Polyentactinia, Inanihella, Inanibigutta, Inanigutta* and *Haplentactinia*) and one characteristic species (*Haplentactinia juncta*). However, despite their more or less similar age, their high diversity and a number of common genera, the two Kazakhstanian assemblages are very different at the species level. Besides, our assemblage contains two genera unrecovered from the *Haplentactinia juncta*- *Inanigutta unica* Assemblage: *Haplotaeniatum* and *Triplococcus*, which represent more than half of the total number of specimens (52%). It also lacks the presence of *Oriundogutta*, *Bissylentactinia* and *Ceratoikiscum*?. It is interesting to note that despite their high diversity level (9 genera and 32 species in sample 112; 10 genera and 31 species in sample 553a), the two assemblages share only 2 common species (*Haplentactinia juncta* and *Syntagentactinia biocculosa*) and two close morphotypes (*Kalimnasphaera aperta* and *Kalimnasphaera* sp. aff. *K. aperta*, *Inanihella bakanasensis* and *Inanihella* sp. cf. *I. bakanasensis*) (Fig. 4).

Our assemblage can be also be correlated with the *Inanihella bakanasensis*- *Triplococcus akzhala* assemblage described by Danelian and Popov (2003) and Maletz *et al*. (2009) as it contains two of its characteristic species (*Inanihella bakanasensis* and *Triplococcus akzhala*) and shares the particularity to be dominated by representatives of a *Triplococcus* and *Inanihella* (59% in our assemblage). However, Danelian and Popov's and Maletz's assemblages are much less diverse (only 3 species described for sample P10 and A17, 4 species described from sample 8807-a) and do not allow further faunal comparison.

Our assemblage therefore suggests that the two characteristic species of the *Inanihella bakanasensis*- *Triplococcus akzhala* are not restricted to the early-mid Darriwilian but they also extend to the uppermost Darriwilian. Therefore, only the *Proventocitum procerulum* assemblage can be used to define the upper Dapingian-mid-Darriwilian interval.

The uppermost Darriwilian is characterized by the *Haplentactinia juncta*- *Inanigutta unica* assemblage. In the light of our new radiolarian fauna, discovered from the *Hustedograptus teretisculus* biozone, the uppermost Darriwilian can be now better defined by the co-occurrence of genera *Syntagentactinia*, *Kalimnasphaera*, *Inanibigutta*, *Protoceratoikiscum*, which first occur in the *Hustedograptus teretisculus* biozone, and genera *Triplococcus* and *Polyentactinia*. It is also characterized by the absence of genus *Proventocitum*. It displays the following characteristic species: *Haplentactinia juncta*, *Inanigutta unica*, *Triplococcus* *aksuranensis*, *Kalimnasphaera aperta, Syntagentactinia biocculosa* and *Syntagentactinia excelsa*.

The presence of *Haplotaeniatum* species in our material is also of interest because they are known from the Silurian (southern Urals; Nazarov & Ormiston, 1993; Japan; Kurihara & Sashida, 2000; Nunavut; Jones & Noble, 2006; MacDonald, 2006; Sweden; Noble & Maletz, 2000; Umeda & Suzuki, 2005; Alaska; Won *et al*., 2002). Ordovician *Haplotaeniatum* have only been recorded from the Late Floian of Newfoundland (Maletz, 2007), the early Middle Ordovician of China (Li, 1995), the early Darriwilian of Spitzbergen (Maletz & Bruton, 2008), and the Late Ordovician of Australia (Goto *et al*., 1992; Noble & Webby, 2009). The new assemblage described here displays the first record of genus *Haplotaeniatum* in the late Darriwilian of Kazakhstan, including three species new to science. It is also the second record of genus *Triplococcus*, previously known from the upper Dapingian *Inanihella bakanasensis*-*Triplococcus akzhala* assemblage in Kazakhstan (Danelian & Popov, 2003). Our assemblage also brings new data regarding the *Syntagentactinia* with the recovering of three new species.

Before our study, 31 species were known from the uppermost Darriwilian, based on the *Haplentactinia juncta*-*Inanigutta unica* assemblage described by Nazarov & Popov (1980). The new assemblage described here displays an entirely new fauna, including 30 new morphotypes (nine of which are described as new species; Fig. 4) observed for the first time in the Darriwilian strata. Therefore, our study allows to improve considerably our knowledge on radiolarian species in the upper Darriwilian and provides a much better insight of the Radiolarian palaeodiversity at the upper Darriwilian, a critical interval from which well-studied planctonic groups (acritarchs, graptolites or chitinozoans) are known to reach their maximal diversity (Servais *et al*., 2008, 2009).

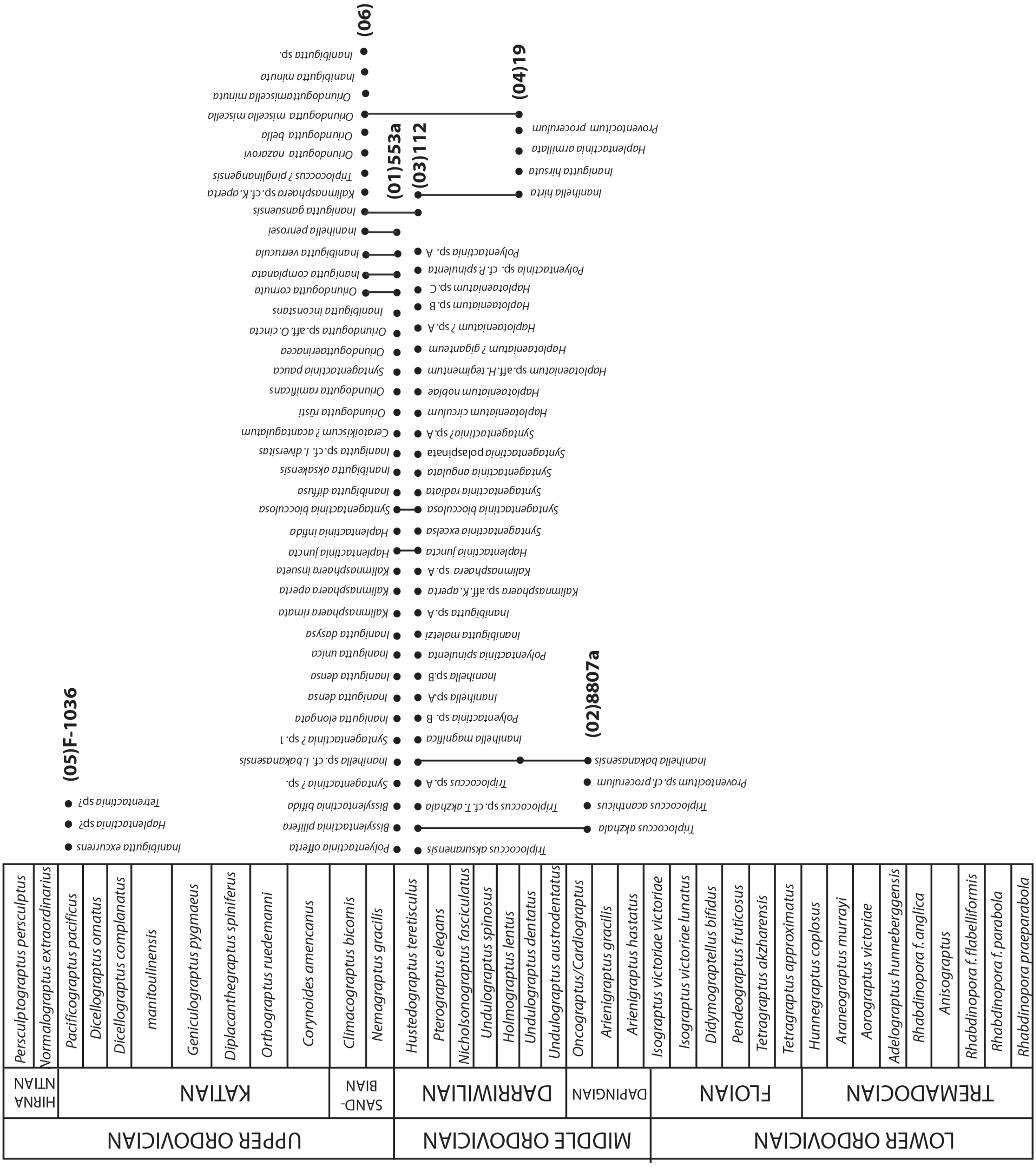


Figure. 4. Ordovician radiolarian records in Kazakhstan and China, biostratigraphy and correlation with graptolites zones. Faunal assemblages from Kazakhstan: 01. (sample553a): *Haplentactinia juncta-Inanigutta unica* Assemblage; Nazarov, 1975; 1980; 02. (sample 8807-a) *Inanihella bakanasensis- Triplococcus akzhala* Assemblage; Danelian & Popov, 2003; 03. (sample 112) Assemblage described in this paper; 04 (sample 19) *Proventocitum procerulum* Assemblage; Nazarov, 1980; 05 (sample F-1036) Nazarov, 1980; faunal assemblage from China: 06. Wang 1993.

CONCLUSION

This new radiolarian assemblage enables us improve considerably our understanding of the palaeodiversity of Upper Darriwilian Radiolaria by the description of 30 new morphotypes, including nine new species (two of which have been described in Pouille *et al.*, 2012b). It also allows us to better understand age range and community structure of Middle Ordovician radiolarian assemblages. It also permits for the first time to record the presence of the genus *Haplotaeniatum* at an upper Darriwilian age and to confirm its presence in Kazakhstanian strata. It also displays the second record of genus *Triplococcus* and highlights its biostratigraphic significance for the upper Dapingian-Darriwilian interval.

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Conclusion et perspectives

I. Conclusion

Ce travail de thèse nous a donc permis d'acquérir de nouvelles données sur l'enregistrement fossilifère des premiers radiolaires biominéralisés, d'approfondir nos connaissances sur la diversité et les changements biotiques intervenus au sein des assemblages à radiolaires de Terre-Neuve au cours de l'intervalle critique de la transition Cambro-Ordovicienne avec la mise en lumière de deux épisodes de changements fauniques et de préciser l'assemblage à radiolaires caractéristique du Jingshanian (Cambrien supérieur). Il nous a également permis d'avoir un meilleur aperçu de la diversité des radiolaires à l'Ordovicien moyen et d'enrichir nos connaissances taxonomiques, en particulier sur la compréhension de la structure interne des Inaniguttidae de l'Ordovicien. Ce travail nous a également permis de décrire un nouveau genre et de définir dix nouvelles espèces. Cependant, de nombreuses lacunes persistent toujours dans notre connaissance de la paleobiodiversité des radiolaires au Paléozoïque inférieur. En guise de conclusion à ce travail de thèse nous avons établi une synthèse de la répartition stratigraphique des familles et des genres au Cambrien-Ordovicien (Fig. 1 et 2). La synthèse de répartition stratigraphique des genres (Fig. 1) met en évidence les intervalles temporels bien documentés ainsi que ceux que notre travail de thèse a contribué à enrichir par l'apport de nouvelles données sur la diversité des radiolaires au cours du Paléozoïque inférieur. Bien que les données actuelles restent encore trop lacunaires au Cambrien inférieur et moyen pour avoir une bonne idée de l'évolution de la diversité générique à cette période, les études menées au cours de ces dix dernières années sur de nombreux assemblages à radiolaires de bonne qualité et bien préservés en Terre-Neuve, au Nevada, au Spitzberg, en Australie et au Kazakhstan nous permettent ici d'entrevoir la tendance générale de l'évolution de la diversité générique du Cambrien supérieur à l'Ordovicien terminal. On peut constater que celle-ci est stable (8-9 genres) du Jingshanien jusqu'au milieu de l'étage 10 du Cambrien supérieur (zone à *C. proavus*). Elle est ensuite suivie d'une très légère baisse à la transition Cambrien-Ordovicien (présence de 6 genres de la partie terminale de l'étage 10 jusqu'au Trémadocien moyen), due au second épisode d'extinction mentionné dans nos travaux. Le Trémadocien supérieur connait ensuite une importante augmentation de diversité avec la présence de 13 genres mentionnés dans la zone à *R. anglica*, soit une diversité générique deux fois plus importante qu'au Trémadocien moyen. Le fait que la diversité des radiolaires du Trémadocien ait été très bien documentée en Terre-Neuve grâce à des assemblages abondants et très bien préservés limite les biais dans l'interprétation de cette évolution de diversité entre le Trémadocien moyen et supérieur.

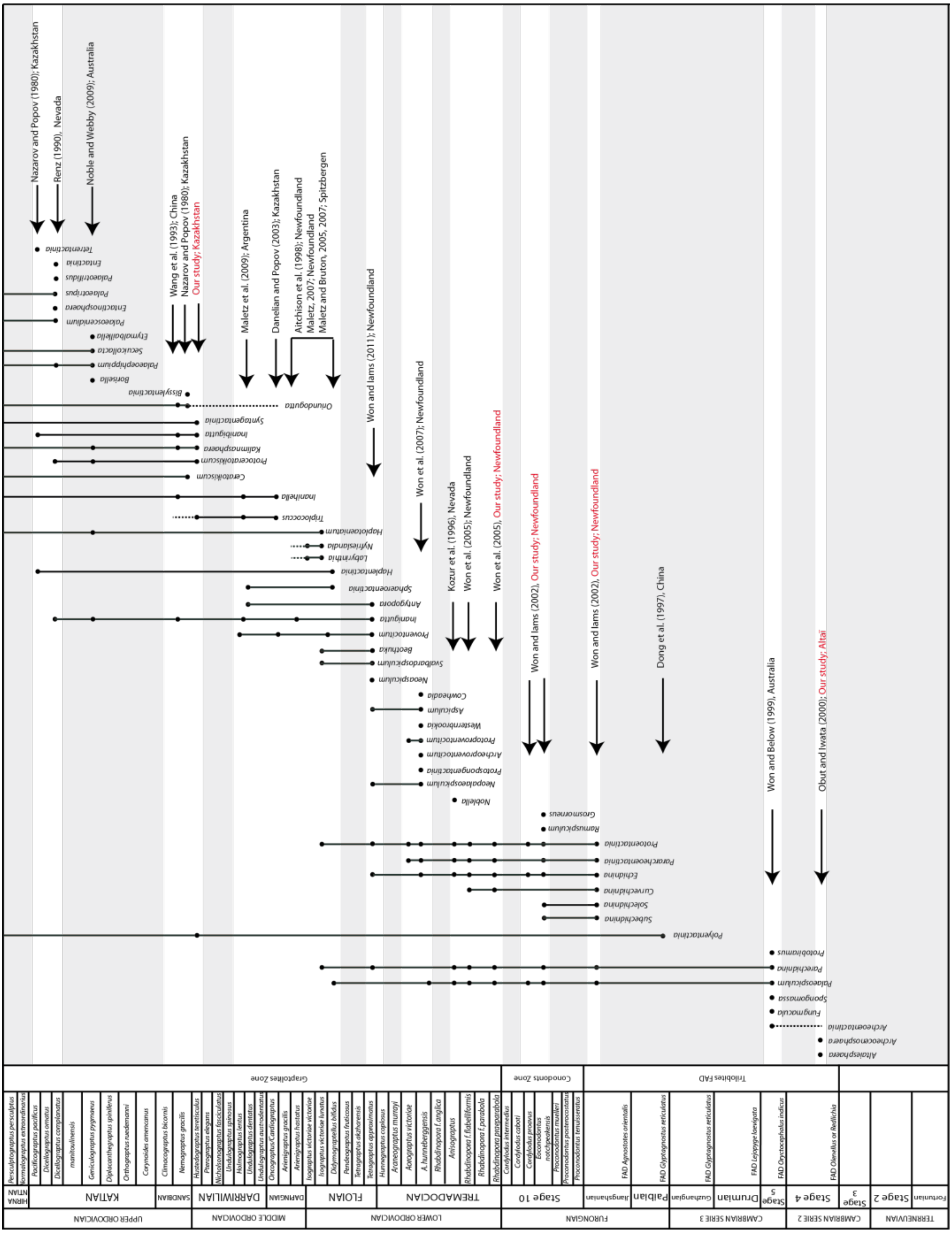

Figure 1 : Tableau de synthèse de la répartition stratigraphique des genres à radiolaires au cours du Cambrien-Ordovicien. Les points représentent les occurrences stratigraphiques des genres et les zones grisées représentent les intervalles temporels dépourvus de données sur l'enregistrement fossile des radiolaires. Les références sur lesquels nous nous sommes appuyés pour construire cette synthèse apparaissent également sur cette figure. Echelle chronostratigraphique d'après l'ISC (2012) et d'après Maletz, 2007b.

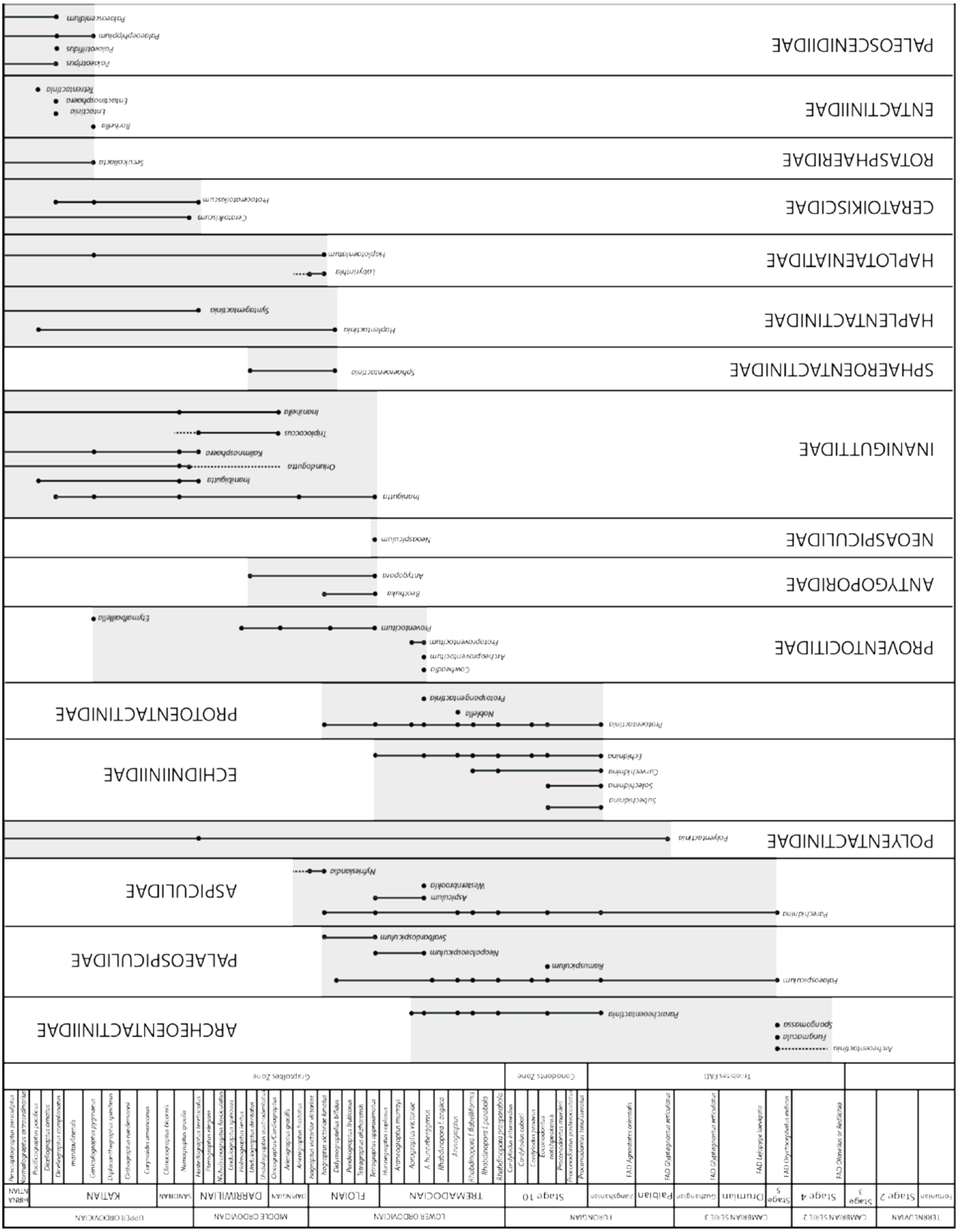

Figure 2 : Tableau de synthèse de la répartition stratigraphique des familles à radiolaires au cours du Cambrien-Ordovicien (zone grisée). Les points représentent les occurrences stratigraphiques des genres au sein des différentes familles.

A l’exception des intervalles temporels dont les assemblages se sont révélés mal préservés ou oligospécifiques (ex : Danelian et Popov, 2003 ; Maletz *et al*., 2009), on constate l’apparition de nouveaux genres en continu dans tous les intervalles temporels documentés entre le Trémadocien supérieur et l’Ordovicien terminal. Le niveau de diversité générique reste cependant quasi-constant au cours du temps (le nombre de genres par intervalle de temps documenté varie entre 11 et 14 genres entre le Trémadocien supérieur et l’Ordovicien terminal) grâce à un équilibre stable entre le nombre d’apparitions et de disparitions des genres. On observe toutefois une légère augmentation de la diversité générique au Katien supérieur avec la présence de 17 genres répertoriés dans la zone à graptolites *D. complanatus*.

La figure 2 nous permet également d’avoir une bonne idée de la répartition stratigraphique des familles dans le temps. On constate ici très nettement une diversification croissante des familles à radiolaires au cours du Cambrien-Ordovicien. Notre travail de thèse mené sur les radiolaires des montagnes de l’Altai nous a donc permis d’identifier la présence des premiers représentant de la famille des Archeoentactinidae au Cambrien inférieur. On peut constater dans cette synthèse que les familles à radiolaires atteignent leur diversité maximale au Floien supérieur avec la présence de 10 familles entre les zones à *I. victoriae lunatus* et *I. victoriae victoriae*. On a donc une croissance continue du nombre de familles du Cambrien inférieur au Floien supérieur (Cambrien inférieur : 1 famille ; Cambrien moyen : 4 familles ; Cambrien supérieur : 6 familles ; Trémadocien : 7 familles, Floien inférieur-moyen : 7 familles ; Floien supérieur : 10 familles). Le nombre de familles ensuite décroit légèrement et se stabilise au Dapingien (Dapingien : 8 familles ; Darriwilien : 8 familles ; Katien moyen : 6 familles; Katien supérieur : 8 familles).

II. Perspectives

La figure synthétique de la répartition stratigraphique des genres (Fig. 1) met également en évidence les intervalles temporels lacunaires (zones grisées) pour lesquels nous manquons encore cruellement de données sur l’enregistrement fossile à radiolaires. On peut observer l’existence de trois grandes lacunes dans notre connaissance de la répartition stratigraphique des genres à radiolaires : l’intervalle temporel du Terreneuvien (Cambrien inférieur), l’intervalle du Drumien au Jingshanien supérieur (Cambrien moyen) et l’intervalle du Sandbien supérieur au Katien moyen. La multiplication des études et des échantillonnages dans des terrains du Cambrien inférieur à moyen et de l’Ordovicien supérieur pourrait donc contribuer à améliorer de façon significative la connaissance de l'origine et de l'évolution de la diversité des radiolaires au Paléozoïque inférieur. Nous avons pu constater dans notre étude que la région de Gorny-Altai présente un grand potentiel pour la découverte de Radiolaires primitifs et mérite d'être explorée davantage. La découverte de nouveau matériel bien préservé dans ces niveaux pourrait accroitre grandement nos connaissances sur la diversité des assemblages à radiolaires au Cambrien inférieur et il serait intéressant à l'avenir de prospecter davantage dans ce sens.

Par ailleurs, il serait également intéressant d'effectuer sur les séries sédimentaires étudiées du Cambrien-Ordovicien (Altaï et Terre-Neuve) des analyses géochimiques (éléments traces et mineurs) combinées avec des observations sédimentologiques qui permettraient de préciser le contexte paléoenvironnemental des niveaux fossilifères à Radiolaires et nous permettrait d'avoir un regard croisé entre les changements biotiques du plancton et les paramètres abiotiques de l'environnement. D'autre part, il serait également intéressant de mener une étude comparée des changements biotiques intervenus à travers divers groupes fossilifères du plancton, comme les Radiolaires (représentant de protistes hétérotrophes), les Acritarches (représentants du phytoplancton) et les Graptolites (plancton colonial) afin d'avoir une meilleur perspective des changements intervenus à travers la chaîne trophique pélagique au Paléozoïque inférieur.

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Annexes

The biostratigraphic and palaeoenvironmental significance of Lower Cambrian (Botomian) trilobites from the Ak-Kaya section of the Altai Mountains (southern Siberia, Russia).

L'importance biostratigraphique et paléoenvironnementale des trilobites du Cambrien inférieur (Botomien) de la coupe d'Ak-Kaya des montagnes de l'Altaï (Sibérie méridionale. Russie)

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Abstract

The presence of one of the oldest records of polycystine Radiolaria in the Lower Cambrian sedimentary sequence of the Ak-Kaya section (Gorny Altai) requires a biostratigraphic dating. The trilobites found recently a few tens of meters below the Radiolarian level belong to *Calodiscus resimus* Repina, *Serrodiscus fossuliferus* Repina and *Alacephalus* aff. *contortus* Repina; they suggest that this part of the Shashkunar Formation can be correlated with the lower part of the Botomian stage. The absence of eyes in the two former species suggests a mode of life buried in the fine pelagic sediments. Indications of the presence of a strongly developed musculature on the third species suggest a palaeoenvironment characterized by a relatively high hydrodynamic regime.

Keywords : Trilobites, Radiolaria, Botomian, Cambrian, Gorny Altai, Siberia, Russia

Résumé

La présence d’un des plus anciens enregistrements de radiolaires polycystines dans la série sédimentaire du Cambrien inférieur de la coupe d’Ak-Kaya (Gorny-Altai) nécessite une datation biostratigraphique précise. Des trilobites ont été trouvés récemment quelques dizaines de mètres sous le niveau à radiolaires. Ils ont été déterminés comme appartenant à Calodiscus resimus *Repina,* Serrodiscus fossuliferus *Repina et* Alacephalus *aff.* contortus *Repina, ce qui suggère, avec certitude, que cet intervalle de la Formation de Shashkunar peut être corrélé avec la partie inférieure du Botomien. L’absence des yeux chez les deux premières espèces suggère un mode de vie enfoui dans les sédiments pélagiques fins. Des indications de la présence d’une musculature bien développée sur la troisième espèce suggère un paléoenvironnement caractérisé par un régime hydrodynamique relativement élevé.*

***Mots-clefs** : Trilobites, radiolaires, Botomien, Cambrien, Gorny-Altai, Sibérie, Russie.*

1. **Introduction**

The Lower Cambrian sedimentary sequences that crop out in the Gorny Altai, southern part of western Siberia (Fig. 1), contain an interesting fossiliferous record preserved in pelagic biogenic sediments that can potentially provide important insights to the biotic changes that occurred in the pelagic ecosystems during the Early Cambrian diversifications. This is especially true for biological groups with a siliceous record, such as siliceous sponges and polycystine Radiolaria (see Zybin et al., 2000; Sennikov et al., 2011), even though siliceous biomineralisation occurred independently in the two eukaryote lineages (Danelian and Morreira, 2004).

The Ak-Kaya section of the Gorny Altai (Fig. 2) has a particular significance because it has yielded one of the oldest fossil records of Polycystine Radiolaria (Fig. 3; Obut and Iwata, 2000; Pouille et al., 2011). The presence of Polycystine Radiolaria in the Lower Cambrian is still regarded with doubts by some authors (i.e. Maletz, 2011). This is partly due to the state of preservation of the yielded material, which impedes sometimes confident recognition of polycystine morphological characters, but it is also due to uncertainties with respect to the age of the radiolarian-bearing sediments.

The Lower Cambrian sequences of Gorny Altai, which crop out along the Katun River (Fig. 1), are mainly dated on the base of trilobites and archaeocyathes studied during the 1960s and 1970s. Trilobites from the Altai Mountains are known since the 1970s; more specifically, Botomian trilobites are known following the work of Repina and Romanenko (1978; see also Zybin et al., 2000, for further details).

However, their presence was not confirmed so far in the Ak-Kaya section, where radiolaria were discovered more recently (Fig. 3; Obut and Iwata, 2000; Pouille et al., 2011); therefore, the exact age of the radiolarian-bearing levels was uncertain.

During a recent field campaign (September 2011) we discovered three trilobite specimens from strata situated a few tens of meters below the radiolarian-bearing levels, which are documented and discussed in the present paper. Their presence establishes clearly the Botomian age of the radiolarian-bearing levels. Finally, the palaeoecological attributes of the found trilobites provide some useful palaeoenvironmental insights.

2. The stratigraphic framework of the Ak-Kaya section

The Ak-Kaya section is situated on the left bank of the Katun River, where a several hundreds meter-thick sequence of thin bedded carbonates intercalated with siliceous rocks can be observed.

The sedimentary sequence belongs to the Shashkunar Formation, represented at its base by conglomerates with poorly rounded pebbles of basalt, tuff, limestone and chert (Fig. 3). The basal conglomerate is overlain by rather thick polymictic sandstone units, which are intercalated with massive and bedded limestones; the latter are often clayey and become dark-colored upward the section. The upper part of the section is composed essentially of thin-bedded grey to dark grey limestones with interbedded varicolored nodular chert levels, which become more frequent towards the top of the section. Massive, dark-colored algal limestones of the Cheposh Formation build up the top of the section. The trilobites of the Ak-Kaya section were collected from the middle part of the Shashkunar Formation, where gray limestones alternate with siliceous limestones (units 18, 20 and 21 on Fig. 3). More precisely, the GPS coordinates of the level which provided the trilobite species *Calodiscus resimus* are N 51° 08´ 14", E 86° 09´ 36". Species *Serrodiscus fossuliferus* Repina *in* Repina et al., 1964 was collected 5 m above sample AK-5 and *Alacephalus* aff. *contortus* Repina, 1960 was collected 1 m above sample AK-6 (Fig. 3).

3. Systematic Palaeontology

Class Trilobita Walch, 1771
Order Agnostida Salter, 1864
Suborder Eodiscina Kobayashi, 1939
Family Weymouthiidae Kobayashi, 1943
Genus *Serrodiscus* Richter and Richter, 1941
Serrodiscus fossuliferus Repina *in* Repina et al., 1964
Pl. 1, fig. 1, 2.

Serrodiscus fossuliferus: Repina et al., 1964, p. 260, pl. XXXVIII, figs. 12-14; 1978, p. 104, pl. I, figs. 7б, 10, 12, 14, 15, 17, 18.

Holotype. Cephalon; № 253/41, CSGM (Central Siberian Geological Museum, Novosibirsk); Lower Cambrian, Botomian Stage, Sanashtykgol Horizon; Altai Mountains, Katun River, Shashkunar stream; Repina et al., 1964, pl. XXXVIII, fig. 14).

Material. One cephalon, good preservation.

Diagnosis. Palpebral lobes and eye ridges absent, glabella narrow, frontal lobe slightly tapered with three pairs of short lateral glabellar furrows, anterior border moderately convex with tubercles located at an equal distance from each other.

Description. Cephalon moderately large for Eodiscina trilobites; length: 9 mm, width: 8 mm. The anterior cephalic margin is curved forward, the posterior margin is straight. Glabella narrow, long, considerably narrowed forward with three pairs of short and wide lateral glabellar furrows. The anterior lobe of glabella rounded, length of glabella: 6 mm, width in middle part of glabella: 2 mm. The glabella is well detached, with deep lateral furrows. The greatest convexity of the glabella is located to her posterior part, near the occipital ring. The latter is slightly separated from the glabella in the middle part; just on the sides there are wide grooves, which pass into an occipital furrow. The genal fields are smooth, moderately convex, and they descend to the margin of the cephalon. The anterior border is moderately convex with tubercles located at an equal distance from each other. The anterior border is separated by a broad anterior marginal furrow.

Discussion. Several species of *Serrodiscus* are known from the Lower Cambrian of the Altay Mountains. *S. fossuliferus* differs from *Serrodiscus pokrovskayae* Poletayeva, 1960 (Poletayeva, 1960, pp. 54, Pl. I, Figs. 1-8) by its narrower frontal lobe of glabella, which does not reach to its anterior border and by its larger tubercles located on the anterior border. *Serrodiscus fossuliferus* Repina, 1964 differs from *Serrodiscus agnostoides* Poletayeva, 1960 (Poletayeva, 1960, p., 56 Pl. I, Figs. 9, 10) by the large size of its cephalon, its wider genal fields and wider anterior border which displays large tubercles. This species differs from *Serrodiscus levis* Repina *in* Repina et al., 1964 (p. 261, Pl. XXXVIII, figs. 15, 16) by its rounded frontal lobe of glabella, the merely deep lateral glabella furrows and its wider anterior border with large tubercles.

Occurrence. Sample AK-6, Ak-Kaya section (Fig. 2)

Family Calodiscidae Kobayashi, 1943

Genus *Calodiscus* Howell, 1935

Calodiscus resimus Repina, 1972

Pl. 1, fig. 4

Calodiscus resimus: Repina, 1972, p.193, Pl. XXX, figs. 4-10.

Holotype. Cephalon; № 382/35, CSGM (Central Siberian Geological Museum, Novosibirsk); Lower Cambrian, Botomian Stage, Bergeroniellus micmacciformis ¨C Erbiella zone, Taryn horizon; Siberian platform, Sukharikha River, Shumnaya Formation; Repina, 1972, pl. XXX, fig. 6).

Material. One cephalon, good preservation.

Diagnosis. Anterior margin of the cephalon round shaped with a wide, flat frontal field. Genal fields with a conical convexity in the middle part. Thin ridges diverge from the anterior part of the glabella towards the sides, merging gradually with the genal fields.

Description. The anterior margin of the cephalon displays a round shape; length: 3 mm, width: 3 mm. The glabella tapers gently towards the anterior margin. Two pairs of lateral glabellar furrows are situated on the sides of the glabella as wide depressions. Length of glabella: 1 mm, width: 0.5 mm. The dorsal furrow is wide and deep. The occipital ring is narrow and tapered backwards. A broken occipital spine can be observed in the middle part of the occipital ring. The frontal field is wide, flat and displays a preglabellar field with a small depression. The anterior border is convex. The genal fields are wide and display a conical convexity in the middle part. Thin ridges diverge from the anterior part of the glabella towards the sides, merging gradually with the genal fields.

Discussion. Three species of genus *Calodiscus* were known previously from the Lower Cambrian strata of the Gorny Altay, but not *Calodiscus resimus* Repina, 1972, which was found previously on the Siberian platform (Repina, 1972). This species differs from *Calodiscus lobatus grandis* Poletayeva, 1960 by its wide frontal field, its narrower anterior border and wider genal fields, which display a conical convexity in the middle part of their genal fields, as well as an occipital spine. *Calodiscus resimus* Repina, 1972 differs from *Calodiscus unflatus* Poletayeva, 1962 by its narrower and less "dismembered" glabella, which displays a conical convexity in the middle part of the genal fields. This species differs from *Calodiscus mirus* E. Romanenko, 1967 by its tapering glabella, the conical convexity in the middle part of its genal fields, a less "dismembered" glabella (*Calodiscus mirus* E. Romanenko, 1967 has two transglabellar furrows) and the smoother surface of its cephalon (*Calodiscus mirus* E. Romanenko, 1967 displays a cephalon surface with small tubercles).

Occurrence. Sample AK-5, Ak-Kaya section (Fig. 2)

Order Corynexochida Kobayashi, 1935

Family Edelsteinaspididae Hupe, 1953

Genus *Alacephalus* Repina, 1960

Alacephalus aff. *contortus* Repina, 1960

Pl. 1, fig. 3

Material. One cranidium, medium preservation.

Description. The cranidium is large in size, trapezoidal, with a moderate convexity, stretched in width; length: 20 mm, width: 35 mm). The anterior and posterior margins of the cranidium are straight. The glabella is large, broad, tapering to the anterior margin with the maximum width in the middle part (glabella length: 18 mm, width in the middle part: 14 mm). Three pairs of lateral glabellar furrows occur on the glabella. The posterior lateral glagellar furrows are long and deep. The other lateral glabellar furrows are broad and shallow and located on the sides of the glabella. The lateral furrows are not expressed. The anterior margin of the glabella reaches almost the anterior border. The occipital ring is separated from the posterior margin of glabella by a broad furrow. The occipital furrow is deeper on the sides. The occipital ring is slightly drawn back into the middle part. The genal fields are slightly convex, wide, especially in the posterior fields. The surface of the genal fields is covered with relatively large tubercles, arranged rarely in chessboard order. The frontal field is expressed only in the preocular fields. The preglabellar field is absent. There is a small depression at the side of the frontal lobe of glabella. The surface of the frontal field is covered with tubercles smaller than on the genal fields. The anterior border is convex, thin, and turned up. The eye ridges are thin and long and they run along the anterior lobe of the glabella. Tubercles are located at equal distance to the eye ridges. The palpebral lobes are short and situated at the anterior third of the glabella. The anterior branches of the facial sutures are short and slightly convergent. The posterior branch of the facial sutures is not preserved, but its was probably long since the posterior parts of the palpebral lobes are far removed from the posterior margin of the cranidium.

Discussion. The morphological characteristics of the described specimen are very similar to *Alacephalus contortus* Repina, 1960 (p. 222, Pl. XI, fig. 11-13). They have the same form of cranidium, a wide fixigenae, long eye ridges, tubercles on the surface of the cranidium. However, there are also some differences, such as the broader and more massive glabella, which is slightly expanded in its middle part.

Alacephalus contortus Repina, 1960 has a narrower, subcylindrical and slightly tapered forward glabella, which is dissected by three identical pairs of lateral glabellar furrows. The described specimen has a deeper posterior lateral glabellar furrow. *Alacephalus contortus* Repina, 1960 has a wider preglabellar field than our specimen, in which the anterior margin of glabella reaches the anterior border.

Occurrence. Sample AK-7, Ak-Kaya section (Fig. 2)

4. Discussion

4.1. Biostratigraphy

Six species of genus *Calodiscus* Howell, 1935 are known from the Siberian platform and three of them (*Calodiscus lobatus grandis* Poletayeva, *Calodiscus unflatus* Poletayeva and *Calodiscus mirus* Romanenko) were also known from the Altay-Sayan area

All three species found in the Altai Mountains were collected from the *Parapagetia-Serrodiscus* layers, which are compared with the Sanashtykgol Horizon of the Altai-Sayan folded area (Decisions all union stratigraphical meeting, 1983) and which correlate with the Taryn Horizon of the Lower Cambrian (in Russian terminology) of the Siberian platform (lower part of the Botomian Stage). This is the first time that *Calodiscus resimus* Repina, 1972 is found in the Altai Mountains. This species is known from the lower part of the Botomian Stage [Lower Cambrian (in Russian terminology) of the NW Siberian platform], from the lower part of the Shumnaya Formation (Repina, 1972).

Five species of genus *Serrodiscus* Richter and Richter, 1941 are known from the Gorny Altay: *Serrodiscus pokrovskayae* Poletayeva, *Serrodiscus agnostiodes* Poletaeva, *Serrodiscus fossuliferus* Repina, *Serrodiscus levis* Repina and *Serrodiscus* cf. *spinulosus* Rasetti. All of them are confined to the beds with *Parapagetia-Serrodiscus*, which are compared with the Sanashtykgol Horizon of the Altay-Sayan folded area (ASFA; lower part of the Botomian Stage; Repina and Romanenko, 1978). *Serrodiscus fossuliferus* Repina, 1964 is a typical representative of the assemblage characteristic for the beds with *Parapagetia-Serrodiscus*; it was previously known from the Shashkunar Formation that crops out at Cheposh section (Repina et al., 1964; Repina and Romanenko, 1978), which is situated about 60 km to the North of the Ak-Kaya section.

Genus *Alacephalus* Repina, 1960 is fairly rare. It was first described from the Cambrian of the Eastern Sayan, near the Kameshki village (Repina, 1960; Repina et al., 1964). The strata in which it was found belong to the Kameshki Horizon of the ASFA (top part of the Atdabanian Stage; Lower Cambrian). In the Tyrga River Section of the Gorny Altay area another species of this genus - *Alacephalus latus* E. Romanenko, 1978- was found, in strata which contain *Sajanaspis* and they underlie the layers with *Parapagetia-Serrodiscus*.

Consequently, the interval of the Ak-Kaya section in which we discovered the trilobites reported in this study can be assigned with certainty to the lower part of the Botomian Stage. This is because two of the three species belong to the beds with *Parapagetia-Serrodiscus.* The discovery of *Alacephalus* Repina, 1960 suggests that this genus had a wider stratigraphic distribution than previously thought.

4.2. Palaeoecology

The eodiscid trilobites *Calodiscus resimus* Repina, 1972 and *Serrodiscus fossuliferus* Repina *in* Repina et al., 1964 are characterized by the absence of eyes. This is explained by their digging mode of life underneath the muddy seafloor. Representatives of these genera inhabited different paleodepths, from the relatively shallow part of the paleobasin to its relatively deeper parts. Trilobites *Alacephalus contortus* Repina, 1960 had previously been found in the Kameshki Formation, in organogenic (detrital) limestone. There they were recovered together with archeocyaths, regarded traditionally as indicators of shallow-water environments. In the Ak-Kaya Section one finds alternations of biogenic, siliceous limestone and lumpy limestone. The trilobites *Alacephalus* aff. *contortus* Repina, 1960 of this section are found in the lumpy limestone. The large and convex cranidium, as well as the sharply dismembered glabella of *Alacephalus* aff. *contortus* Repina, 1960 suggests the presence of strongly developed muscles, which is characteristic of trilobites that used to live in palaeoenvironments influenced by a high hydrodynamic regime.

Conclusions

A recent Russian-French collaborative geological expedition at the Ak-Kaya section of the Gorny Altai led to the collection of three trilobite species a few meters below strata containing one of the oldest Radiolarian records known so far (Obut and Iwata, 2000; Pouille et al., 2011). This is the first report of the trilobite species *Calodiscus resimus* in the entire Gorny Altai (this species was known previously from the Siberian platform). Together with the presence of species *Serrodiscus fossuliferus* they allow to assign these levels to the lower part of the Cambrian stage 4 (Botomian stage in Russian terminology). The presence of *Alacephalus* aff. *contortus* suggests that these sediments accumulated in a high energy environment

Acknowledgments

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CAPTIONS

Fig. 1. a) Map of Russia with the Altai-Sayan area indicated in grey; b) simplified tectonic map of the Altai-Sayan Folded area.

a) Carte géographique de la Russie avec la région de l'Altaï- Sayan (en gris); b) Carte tectonique simplifiée de la région de l'Altaï-Sayan.

Fig. 2. Geological map of the Katun'-Kaspa area, with location of the Ak-Kaya section.

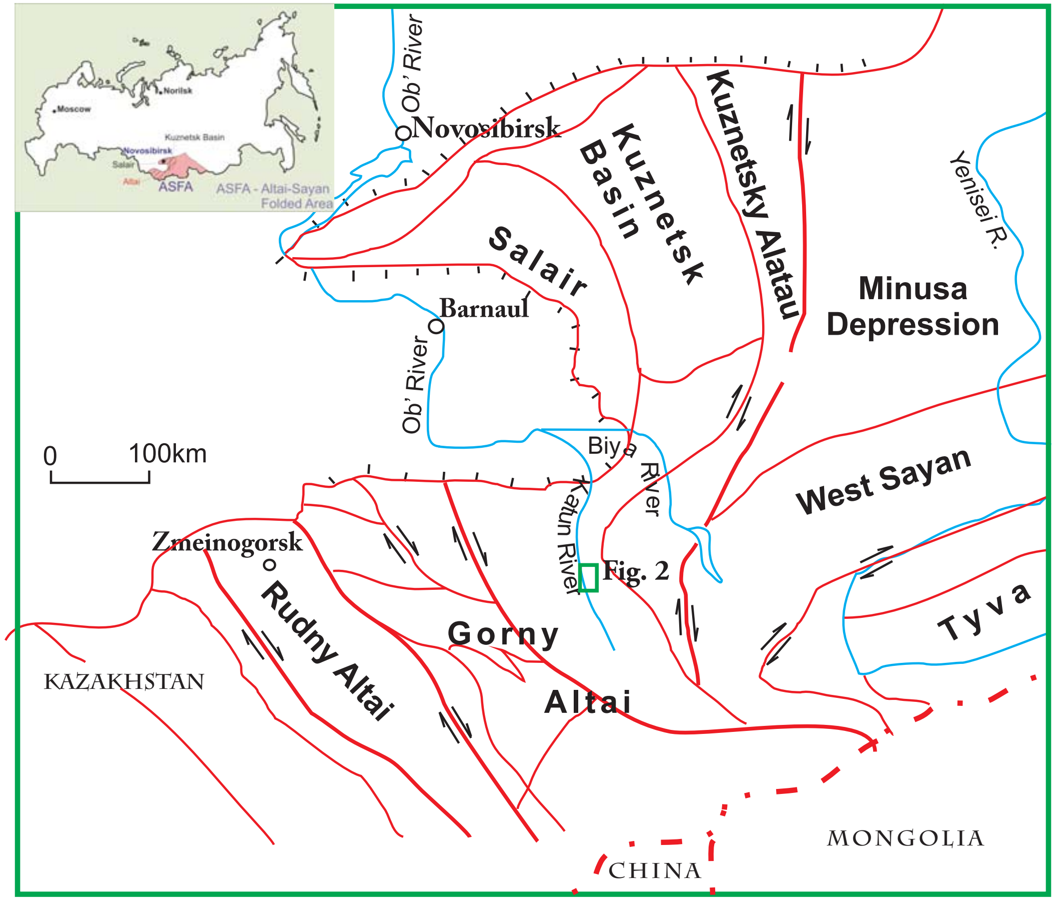
Carte géologique de la région de Katun' -Kaspa, avec localisation de la coupe d'Ak-Kaya.

Fig. 3. Lithostratigraphic column of the sedimentary sequence observed at the Ak-Kaya Section.

Colonne stratigraphique de la série sédimentaire observée à la coupe d'Ak-Kaya.

Plate 1. Lower Cambrian trilobites from the Ak-Kaya section, Gorny Altai. Fig. 1, 2, *Serrodiscus fossuliferus* Repina *in* Repina et al., 1984, cephalon, sample AK-6. Fig. 3, *Alacephalus* aff. *contortus* Repina, cranidium, sample AK-7. Fig. 4, *Calodiscus resimus* Repina, cephalon, sample AK-5.

Trilobites du Cambrien inférieur de la coupe d'Ak-Kaya, Gorny Altaï. Fig. 1, 2, Serrodiscus fossuliferus *Repina* in *Repina et al., 1984, céphalon, échantillon AK-6. Fig. 3,* Alacephalus *aff.* contortus *Repina, 1960, cranidium, échantillon AK-7. Fig. 4,* Calodiscus resimus *Repina, 1972, céphalon, échantillon AK-5.*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ASFA - Altai-Sayan Folded Area
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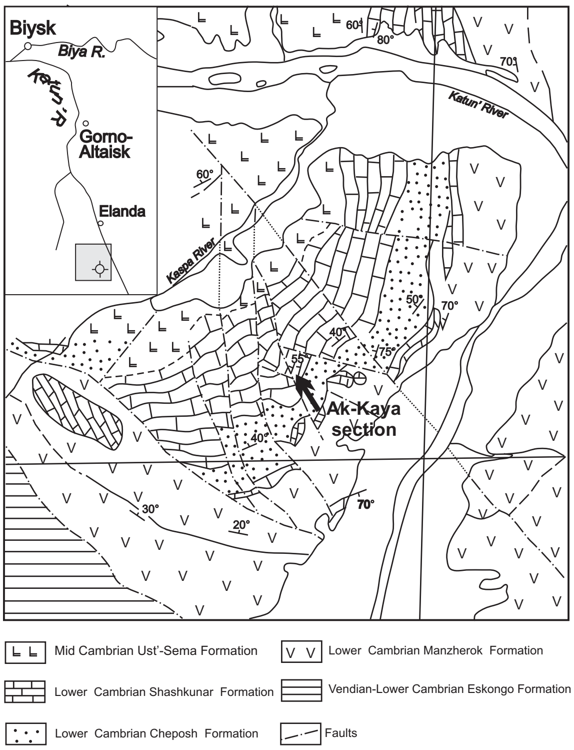
Kuznetsk Basin
Kuznetsky Alatau
Yenisei R.
Salair
Minusa Depression
Barnaul
Ob' River
0
100km
Biya River
Katun River
West Sayan
Zmeinogorsk
Fig. 2
Rudny Altai
Gorny Altai
Tyva
KAZAKHSTAN
MONGOLIA
CHINA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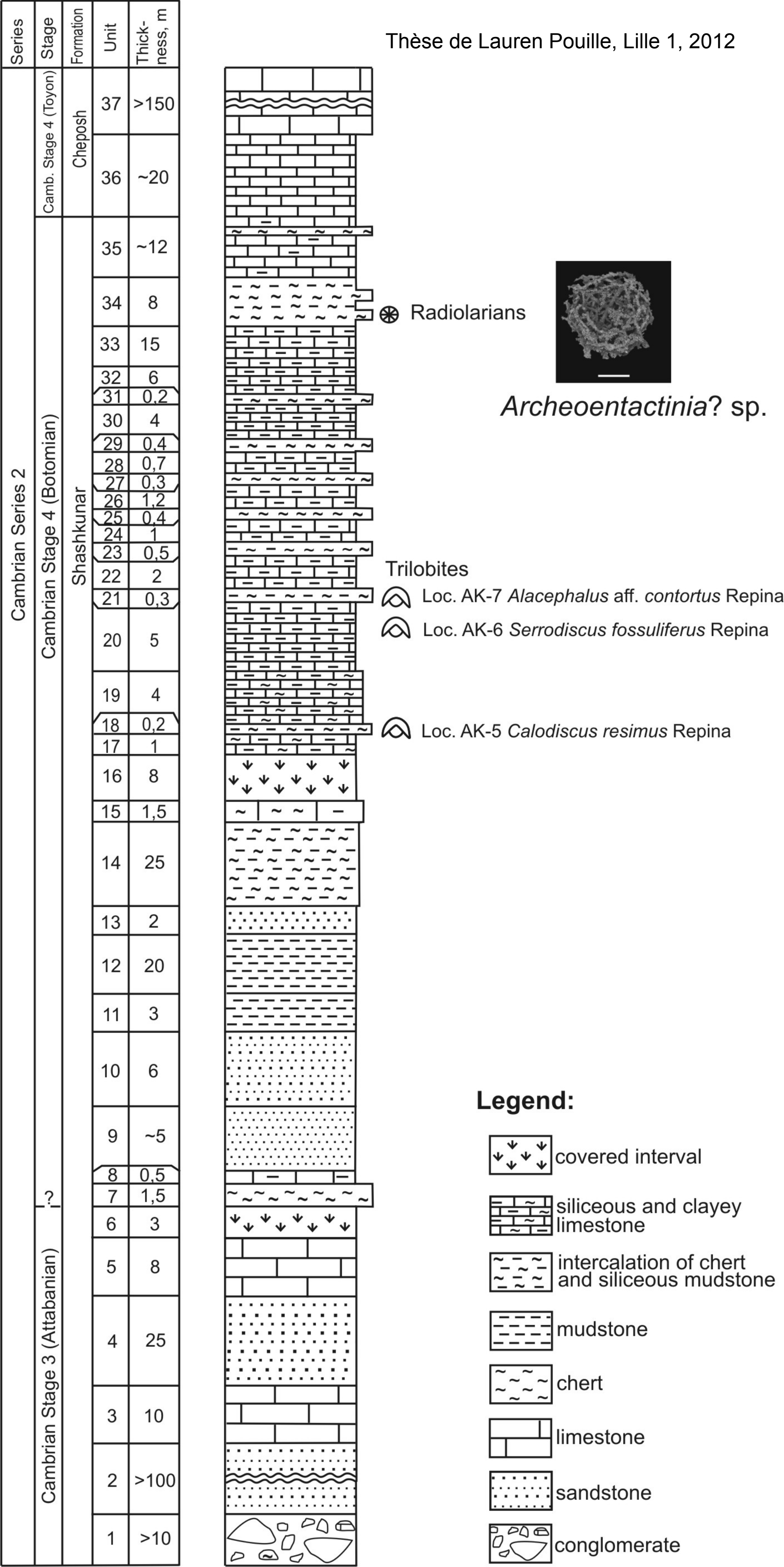
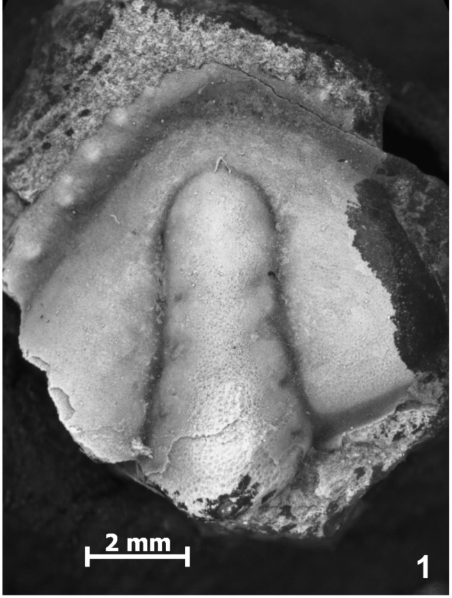
40°
55°
75°
40°
30°
20°
70°
Ak-Kaya section
Mid Cambrian Ust'-Sema Formation
Lower Cambrian Shashkunar Formation
Lower Cambrian Cheposh Formation
Lower Cambrian Manzherok Formation
Vendian-Lower Cambrian Eskongo Formation
Faults

Thèse de Lauren Pouille, Lille 1, 2012

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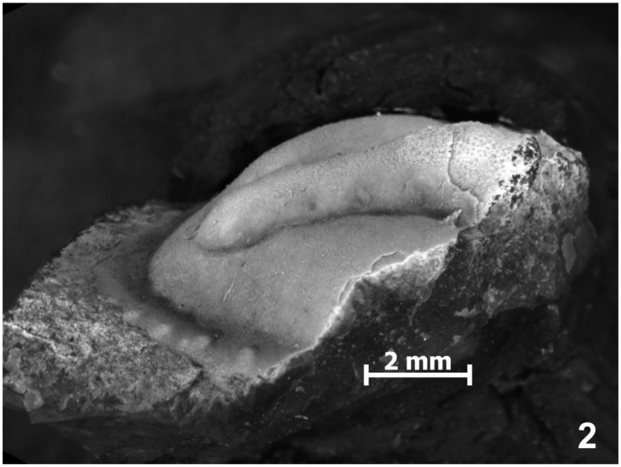
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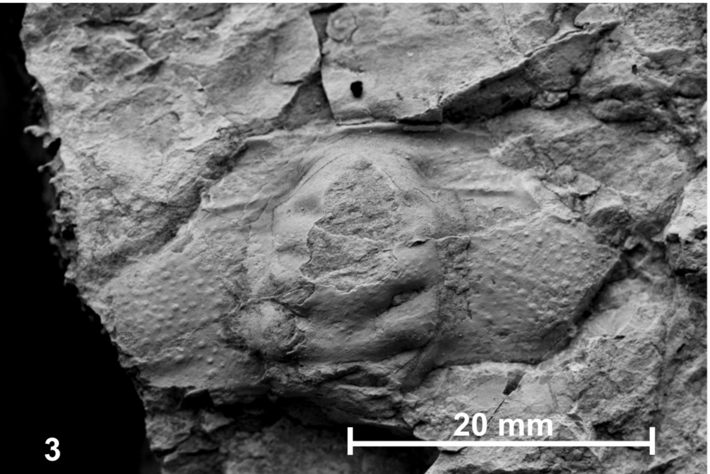
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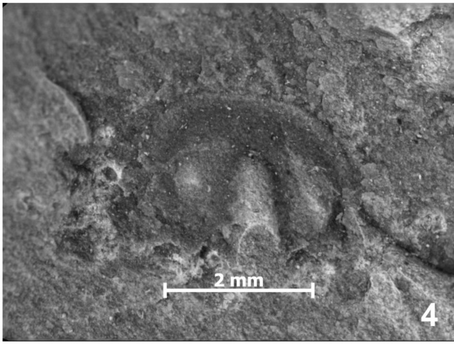
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Palaeogeographic distribution of Ordovician Radiolarian occurrences: patterns, significance and limitations

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Abbreviated title (< 40 characters) : Ordovician Radiolarian distribution

Abstract: Over the past 15 years, significant progress has been achieved in our understanding of Lower Palaeozoic radiolarian faunas. However, description of biogeographic patterns of Ordovician Radiolaria is hampered by the paucity of known occurrences as well as possible taphonomic influences. The distribution of all known assemblages is analysed in time and space. Lower Ordovician (especially Tremadocian) Radiolaria are known from two distinct tropical localities of Laurentia. Geographic coverage is much better for the Middle Ordovician (Darriwilian). However, data are concentrated in tropical palaeolatitudes (between 30°N and 30°S). The absence of data from mid/high latitude localities limits any biogeographic insights. In addition to this there are taphonomic and taxonomic biases. Data are also sparse for the Upper Ordovician. However, comparison between Australian and Nevadan material of Katian age shows strong similarities suggesting the presence of a coherent tropical radiolarian bioprovince, as in the modern ocean.

Polycystine Radiolaria are a Rhizarian group of planktonic heterotrophic protists with a siliceous skeleton and have an exceptionally long fossiliferous and sedimentary record that goes back to the Cambrian (Tolmacheva *et al.* 2001; Pouille *et al.* 2011). Radiolaria are present today in all oceans, inhabit all parts of the water column, and show predictable biogeographic patterns that are dictated largely by latitudinal gradients, water mass structure, productivity and circulation. Modern radiolarian biogeographic provinces are broadly transposed into latitudinal bands, which are also influenced and modified by water mass circulation. In this way tropical, sub-tropical, temperate, subpolar and polar radiolarian bioprovinces are recognized (Casey 1993). Radiolarian bioprovinces have been also recognized for the geological past; few biogeographic studies are available for Mesozoic Radiolaria (i.e. Pessagno & Blome 1986; Matsuoka 1995) and some have successfully linked radiolarian biogeographic patterns with past palaeoceanographic circulation (i.e. Kiessling 1999). The significance of radiolarian palaeobiogeography is much better established for the Cenozoic. Indeed, it is now well established that the entry of the Earth climate to an Icehouse mode since the Middle-Late Eocene enhanced the endemicity of radiolarian faunas and let to the rise of well identified bioprovinces, especially in the high latitudes (Sanfilippo & Caulet 1998; De Wever *et al.* 2001)

During the last few years there has been an increasing interest in documenting the palaeobiogeographic distribution of Ordovician plankton groups (Servais *et al.* 2005) and their potential to elucidate first order questions about past global climatic and oceanographic changes (Vandenbroucke *et al.* 2009, 2010). Given the examples from younger oceanic strata, one would expect a significant potential in the biogeographic record of Ordovician Radiolaria to better understand past climate states. It thus becomes interesting to analyse the existing occurrences in their palaeogeographic framework in order to trace past biogeographic distributions and obtain insights to the Ordovician global climate dynamics. Although papers dealing with Ordovician Radiolaria are much less numerous than for younger periods (i.e. late Palaeozoic), many Ordovician assemblages have been reported from material with relatively good preservation, and as a result Ordovician radiolarian clades and their detailed morphology have become relatively well known (Nazarov & Popov 1980; Nazarov & Ormiston 1984, 1985, 1993; Renz 1990a, b; Wang 1993; Noble & Aitchison 1995, 2000; Danelian & Floyd 2001; Danelian & Popov 2003; Noble & Danelian 2004; Won *et al.* 2005, 2007; Won & Iams 2011; Maletz & Bruton 2005, 2007, 2008; Noble & Webby 2009).

Regrettably, in spite of the relatively large number of descriptive papers published the last fifteen years, the known record of Ordovician Radiolaria remains yet fragmentary, both in terms of its stratigraphic and palaeogeographic coverage, especially in the mid and high latitudes. The objective of this contribution is to state, as clearly as possible, what the current known record is in terms of its temporal and geographic distribution. This update will serve to direct future efforts in new, still unexplored geographic areas.

Comments on the distribution of Ordovician radiolarian assemblages

All currently known Ordovician radiolarian assemblages are listed in Table 1 according to their palaeogeographic location. In addition to the chronostratigraphic assignment provided in the latest International Time Scale (Gradstein *et al.* 2004; Wang *et al.* 2009) we also provide the Ordovician time slices as defined in Webby *et al.* (2004).

Lower Ordovician assemblages

Tremadocian assemblages are known exclusively from Laurentia (Fig. 1). They are essentially composed of spicular forms, some of which often display a sphaerical and internally hollow skeleton formed by numerous irregularly arranged bars (i.e. Fig. 2.d and 2.j). The lowermost Tremadocian radiolarian fauna described by Kozur *et al.* (1996) from Nevada is characterized by a low diversity; the fauna is composed essentially of echidninid-type archaeospicularian Radiolaria. Our best understanding of Tremadocian radiolarian diversity, community structure and evolutionary trends comes mostly from western Newfoundland, where Won *et al.* (2005, 2007) documented exquisitely preserved assemblages of early and middle Tremadocian age, which were dated by co-occurring conodonts. The lower Tremadocian assemblages of Newfoundland, which were living at the time in tropical waters, contain most of the species described by Kozur *et al.* (1996) from the then equatorial site in Nevada, as well as nearly twenty more species belonging to the archaeospicularian and entactinarian Radiolaria. The middle Tremadocian assemblages described by Won *et al.* (2007) from the Cow Head Group of western Newfoundland are characterised by a similar level of diversity as the earlier Tremadocian assemblages; they are dominated by abundant and diverse taxa that belong to the family Aspiculidae and they contain some newly evolved taxa, especially of the family Proventocitiidae (Fig. 2.l).

Laurentia also holds the currently best known record of Floian Radiolaria, including the earliest record of the order Spumellaria (characterised by sphaerical shells with a distinct internal microsphere). The recently described radiolarian fauna from lower Floian (lowermost Arenig) strata of western Newfoundland (Won & Iams 2011) partly completes a substantial gap in knowledge of Lower Ordovician radiolarian assemblages. A substantial faunal change occurs between Arenigian and Tremadocian assemblages (Kozur *et al.* 1996) and this work helps to clarify the timing of this transition. The early Floian radiolarian fauna from Newfoundland is characterized by the origination of new families such as beothukids (Fig. 2.i), antygoporids (Fig. 2.g) and inaniguttids (Fig. 2.a, c, e-f). Late Floian Radiolaria are known from Spitsbergen and belong to the *Beothuka terranova* and *Antygopora bella* assemblages (Maletz & Bruton 2005, 2007).

The early-mid Floian fauna described by Danelian & Popov (2003) from Kazakhstan has a very different composition from the early Floian fauna described from Newfoundland; it is of low diversity and it is dominated by representatives of the family Inaniguttidae. However, it is not clear at this stage whether this reflects biogeographic/palaeoecological differences or whether it should be assigned to a younger time interval (i.e. late Floian; Maletz 2011).

Middle Ordovician assemblages

To date, there is only a single radiolarian locality from the lower part of the Middle Ordovician (Dapingian), which comes from Laurentia (W. Newfoundland; Maletz 2007b). Geographic coverage is much better for the upper part of the Middle Ordovician, the Darriwilian (Fig. 3). However, data are concentrated to tropical palaeolatitudes (between 30°N and 30°S). The absence of data from mid/high latitude Darriwillian localities hampers any biogeographic insights. In addition to this there are taphonomic and taxonomic biases. One case that is worth discussing is the time interval covered by the *Proventocitum procerulum – Haplentactinia armillata* assemblage, described initially by Nazarov & Popov (1980) from Kazakhstan (sample 19). The assemblage was also found in Spitsbergen (Fortey & Holdsworth 1971; Maletz & Bruton 2008) and, more importantly, in a similar type of lithofacies (pelagic limestones), making comparisons between localities useful from a biogeographic standpoint. Maletz & Bruton (2008), in comparing the faunal composition between the Spitsbergen and Kazakhstan localities (Nazarov 1975), noted that individuals of the index species, established first in the Kazakhstan material, are rather rare in the Spitsbergen material. Interestingly, the genus *Sphaeroentactinia* (Fig. 2.h) is very common in the Spitsbergen material, although it is seemingly absent in the assemblages from Western Newfoundland and Kazakhstan. Maletz & Bruton (2008) also compared their assemblage to the fauna found by Aitchison (1998) from the Ballantrae complex in Scotland. However, comparison of the faunal composition in this case is difficult because of the moderate–poor preservation of the Scottish material that was extracted from radiolarian chert, a more oceanic lithofacies.

From a slightly younger Darriwilian time slice (subinterval 4c) comes a high diversity fauna from Kazakhstan (sample 553-A; Nazarov & Popov 1980), which is dominated by the inaniguttid genera *Inanigutta* (Fig. 2.f), *Inanibigutta* (Fig. 2.c) and *Oriundogutta* (Fig. 2.e). The fauna described by Danelian & Clarkson (1998), Danelian (1999) and Danelian & Floyd (2001) from the Southern Uplands of Scotland is recorded (at least partly) from the same time slice, in which genera *Inanibigutta* and *Protoceratoikiscum* (Fig. 5.h) are rather common. Although the Scottish assemblage shares some common taxa with the coeval fauna from Kazakhstan, comparison is hampered by the different lithofacies (chert *vs.* limestone) from which the two fauna were extracted. In addition, the age of the radiolarian bearing strata is not known with accuracy, although conodonts of the *Pygodus anserinus* conodont zone have been reported in the literature. Faunal comparisons are also delicate between the Kazakhstan assemblage and an inaniguttid-dominated fauna described from chert collected in West Junggar, Xinjiang province of China (Buckman & Aitchison 2001). The Junggar samples are well-dated with co-occurring conodonts (subinterval 4c) and, interestingly, also contain numerous specimens of the easily recognizable species *Protoceratoikiscum clarksoni*, first described from the Scottish cherts.

It is not uncommon that Ordovician chert yields moderately well-preserved radiolarian faunas, as is the case of the high diversity fauna extracted from the Qilian mountains of China (Li 1995). This fauna contains pylomate inaniguttid *Kalimnasphaera* (syn. *Cessipylorum* Nazarov), secuicollactines, palaeoscenidiids, and *Protoceratoikiscum*, as well as other enigmatic elements (i.e. *Etymalbaillella yennienni*) that are reported from younger Ordovician materials elsewhere (Noble & Webby 2009).

The problem in evaluating the Qilian mountains assemblage lies in the lack of precise age constraints on the material, which could be late Darriwilian or younger (Late Ordovician).

Upper Ordovician assemblages

The radiolarian data existing for the Upper Ordovician are equally few and with a very incomplete stratigraphic coverage. Their palaeogeographic distribution on a Hirnantian map (Fig. 4) shows that all of the currently known data come from tropical palaeolatitudes (between 30° N and 30°S).

The oligospecific fauna described by Wang (1993) from China is well preserved, containing pylomate and multi-shelled inaniguttids, but it is difficult to compare with the assemblages documented from Scotland or Australia (Iwata *et al.* 1995), because of their different state of preservation and uncertainties about their age.

The recent study by Noble & Webby (2009) has a particular significance because the radiolarian assemblage studied from the Middle Katian Malongulli Formation of the Cliefen Caves area, in the Lachlan fold belt of eastern Australia (time slices 5c-6a), is fairly diverse (Fig. 5) and was compared with a more or less coeval fauna from the Hanson Creek Limestone in Nevada, USA (time slice 6a). The similarity of the Katian radiolarian assemblage from SE Australia with the one from Nevada was noticed long time ago based on preliminary observations (Renz 1990a, b; Webby & Blom 1986). The two faunas are found to share seven species and are dominated by *Kalimnasphaera maculosa*, *Borisella subulata*, *Palaeoephippium octaramosum* and Haplotaeniatum spp. In addition, species of *Protoceratoikiscum* and secuicollactines are present (Fig. 5). The comparison is facilitated by the similarity in taphonomic conditions, both fauna having been extracted from carbonates occurring in graptolitic calcareous shales.

The Malongulli fauna contains many taxa in common with Katian material from a deeper calcareous mudstone lithofacies at Four Mile Creek and siliceous lithofacies near Taralga in the Lachlan Fold belt (Goto *et al.* 1992), but poorer preservation in the material from deeper facies limits comparison. A poorly preserved assemblage constrained by conodonts to the Upper Ordovician (likely Sandbian-lower Katian) has also been reported from basinal siliceous mudstone facies from the Ballast Quarry in the Lachlan Fold belt of eastern Australia (Iwata *et al.* 1995). The Ballast Quarry material is not well preserved but has yielded secuicollactines and inaniguttids that compare favourably to taxa in the Hanson Creek and Malongulli Formation. It should be noted that the material described by Li (1995) from the Quilan Mountains in China bears closer resemblance to the Katian age materials from the Lachlan Fold belt than to Middle Ordovician assemblages, and suggests a younger age for this material.

From a biogeographic standpoint, the various arc terranes from the Lachlan fold belt and Quilan Mountains of China are all considered to have originated from a low-latitude peri-Gondwanan setting, and the Nevada material represents a low latitude Laurentian continental margin setting. The faunal similarity between geographically separated low latitudinal localities, and between marginal and deeper oceanic facies, suggests the presence of a tropical radiolarian bioprovince, comparable to the modern ocean.

The late Katian radiolarian assemblage described by Nazarov & Popov (1980) from Kazakhstan was extracted from calciturbidites accumulated above graptolitic shales. The extracted fauna is composed of a small number of taxa with *Inanibigutta excurrens* being the dominant species. The reason (ecological *vs.* preservational) for this oligospecific fauna is currently unclear, and further work is needed to properly assess the Katian radiolarian assemblages from Kazakhstan and compare with other Katian localities.

Finally, two interesting radiolarian assemblages are reported from glacial erratic boulders from Scandinavia. They are reported by Nazarov & Nõlvak (1983) from Estonia and by Gorka (1994) from Poland (micritic limestones dated by graptolites; time slices 5c-5d). However, they are not positioned on Fig. 4, because they were transported for quite a distance, probably for hundreds of kilometres.

Remarks on the quality of current data

Meaningful palaeobiogeographic reconstructions rely on a large number of high quality data from a large number of widely dispersed localities. Below we discuss and emphasize the various types of drawbacks/problems associated to the existing Ordovician radiolarian data in order to account for the lack of progress in palaeobiogeographic analysis for Ordovician Radiolaria.

Stratigraphic accuracy

One of the problems often encountered is the poorly known age of the radiolarian-bearing strata. Radiolarian faunas have frequently been described from intervals without further biostratigraphic control. The *Beothuka terranova* assemblage from western Newfoundland was, for example, dated only indirectly through the radiometric date of the Little Port Ophiolite Complex (Aitchison *et al.* 1998). Further examples include the Upper Ordovician assemblages described from Australia by Goto *et al.* (1992), China by Li (1995) and the Lower (?) Ordovician radiolarian assemblage from Kyrgyzstan described recently by Danelian *et al.* (2011). Still descriptions of these faunas are very important because it allows for improved understanding of biodiversity within a more general time frame, and recognition of new species. As radiolarians are poorly known from many intervals, each new description, even one without a precise stratigraphic framework, may eventually provide valuable information for future biostratigraphic and biogeographic interpretations.

It is important to understand radiolarian faunas in context to other fossil groups in order to establish a precise and useful radiolarian biostratigraphy. Investigation of faunas from well-dated successions will be fundamental in the future. The example of the radiolarians in the Laurentian (Newfoundland) Cow Head Group (see Won *et al.* 2005, 2007; Won & Iams 2011) may provide a guide for future research. Diverse and common radiolarian faunas have been secured from these successions precisely dated by graptolite and conodont faunas and establish a robust and potentially useful biostratigraphy.

Possible palaeoenvironmental influence on the faunal composition

Ordovician radiolarian assemblages occur in marine sedimentary environments, which range from interior seaways, carbonate platforms, marginal basins, flanks of volcanic arcs, to deeper water facies such as radiolarian chert, and graptolitic shales accumulated in ocean basin environments. Evidence from Western Newfoundland (Maletz & Bruton 2008) suggests that faunal composition may be substantially influenced by favourable or stressful palaeoenvironmental conditions. Some assemblages, although well preserved, may be mono- or oligospecific. Based on modern distributions, such assemblages may relate to marginal marine conditions where ocean circulation is restricted, and/or where deeper water mass structures are attenuated. In these marginal environments, radiolarians, when present, are in many cases very well preserved in either carbonate beds. As these exceptionally preserved assemblages are examined, it is important to keep the environmental setting in mind when assessing biodiversity.

Taphonomic biases

Ordovician radiolarian assemblages occur mainly in marine sedimentary environments which range from the upper slope parts of carbonate platforms to deep sea cherts accumulated on oceanic crust. They have also been found in sedimentary rocks that accumulated on shelf environments, such as the Viola Limestone of Oklahoma (Maletz 2007a).

Many preservational biases may be present when comparing radiolarian assemblages recovered from different lithologies. Usually Radiolaria are much better preserved in pelagic carbonates (i.e. Middle Ordovician of Kazakhstan, Lower Ordovician of Newfoundland). Exceptionally preserved material has also been recovered from phosphatic and calcareous concretions. In contrast, radiolarians recovered from chert show a range of preservation from very poor to moderately well-preserved. Although Ordovician radiolarian chert is a common lithology in orogenic belts, it is usually the rare chert sample that yields well-preserved radiolarians, caused in part by the destructive process employing hydrofluoric acid to release the fossils, and in part to the effects of diagenesis and recrystalization on the fossils.

Other biases may be formed through the diagenetic history of the surrounding rocks and resulting modifications of the radiolarian skeletons. Maletz (2007b) described the variation of the biostratigraphically important *Beothuka terranova*, based on diagenetic replacement of the original silica with pyrite in the Cow Head Group of western Newfoundland. The pyritic specimens do not show the fragile skeletons with a microsphere and irregularly placed bars of the original, unmodified specimens preserved in silica. Both preservational aspects might easily be interpreted as different radiolarian species. If the original material of *Beothuka terranova* from the Little Port Complex of wetsren Newfoundland (Aitchison 1998) preserved in silica and resembling more the pyritic specimens from the Cow Head Group, belongs to the same taxon, a complex history of diagenetic modification may have to be expected in fossil radiolarians.

Taxonomic matters

Understanding the test’s internal structure is very important for radiolarian taxonomy. However, structures are not well known for a number of radiolarian taxa described from rather moderately to poorly preserved material, particularly from chert. Numerous morphotypes of Ordovician Radiolaria are composed of sphaerical forms with several shells and often unknown internal structures. Discrimination amongst all these morphotypes is very difficult (especially in poorly preserved material). This is an obstacle to in-depth understanding of the diversity of known assemblages and therefore it hampers detailed comparison between faunas found in various distant localities.

Conclusions

Radiolarian occurrence data are still few to draw any meaningful biogeographic conclusions. Regrettably, in spite of the relatively large number of papers published the last fifteen years, the known record of Ordovician Radiolaria still remains fragmentary, both in terms of its stratigraphic and palaeogeographic coverage, especially in the mid and high latitudes, and many well preserved assemblages are known from only a limited geographic area. Given these large limitations, including some taphonomic and taxonomic biases, palaeogeographic plots of currently known Ordovician radiolarian assemblages are interesting in several respects. They emphasize the fact that nearly all known findings are concentrated in tropical palaeolatitudes (between 30°N and 30°S). Our account highlights the urgent need to discover radiolarian fossiliferous sites from higher Ordovician palaeolatitudes.

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Captions

Table 1 : Ordovician radiolarian collections, their age, geographic location and lithofacies of the fossil-bearing rocks.

Fig. 1. Distribution of Lower Ordovician radiolarian occurrences on a Lower Tremadocian (485 Ma) palaeogeographic reconstruction (after Torvsik 2009). Locality numbers correspond to collection numbers in Table 1.

Fig. 2. Scanning electron micrographs of Lower and Middle Ordovician radiolarians from the Shundy Formation of Kazakhstan (specimens a, c, e-f, and k), the Valhallfonna Formation of Spitzbergen (specimens b, g, h, i and l) and the Green Point Formation of Western Newfoundland (specimens d and j). Specimens b, g, h, i and l are also illustrated in Maletz & Bruton 2007 and 2008. Scale bar = 100 µm. a) *Inanihella bakanasensis* (Nazarov 1975); b) *Nyfrieslandia sphaeroidea* Maletz & Bruton 2007; c) *Inanibigutta* sp.; d) *Parechidnina jamesi* Won & Iams 2002.; e) *Oriundogutta miscella miscella* (Nazarov 1980); f) *Inanigutta gansuensis* Wang 1993; g) *Antygopora bella* Maletz & Bruton 2007; h) *Sphaeroentactinia hexaspinosa* Maletz & Bruton 2007; i) *Beothuka terranova* Aitchison *et al*. 1998; j) *Echidnina conexa* Won *et al*. 2005; k) *Haplotaeniatum* sp.; l) *Proventocitum procerulum* (Nazarov) *in* Nazarov & Popov 1980.

Fig. 3. Distribution of Middle Ordovician Radiolarian occurrences on a Dapingian (470 Ma) palaeogeographic reconstruction (after Torvsik 2009). For locality numbers see Table 1.

Fig. 4. Distribution of Upper Ordovician Radiolarian occurrences on an Upper Katian (440 Ma) palaeogeographic reconstruction (after Torvsik 2009). For locality numbers see Table 1.

Fig. 5. Katian Radiolarian assemblage from the Malongulli Formation, Australia (a selection of species illustrated in Noble & Webby 2009). Scale bar = 100 µm for figs. 2-6, 8-12; 50 µm for fig. 1 and 20 µm for fig. 7. a) *Secuicollacta ornata* Goto *et al.* 1992. Closely related to *S. micra* in the Hanson Creek Formation of Nevada but spines are slightly longer; b) *Inanigutta complanata* (Nazarov 1975); c-d) *Borisella subulata* (Webby and Blom 1986). Entactinarian species abundant in both Malongulli and Hanson Creek formations of Nevada; Notice the six-rayed bar centered internal spicule in fig. d, e-g). *Kalimnasphaera maculosa* Webby & Blom

1986. Notice the doubled medullary shell in fig. g and h) *Protoceratoikiscum chinocrystallum* Goto *et al.* 1992; i-j) *Haplotaeniatum spongium* (Renz 1990). The internal structure shows a small microsphere (fig. j) surrounded by a spiraliform spongy labyrinthine shell. k-l) *Palaeoephippium octaramosum* Renz 1990a. Characterized by a 6-rayed spicule with short median bar and variably developed helmet-shaped skirt. Ray position is highly variable. Some have 2 basal and 4 apical spines (fig. k), others have 3 basal and 3 apical spines (fig. l).

Table 1 : *Ordovician radiolarian collections, their age, geographic location and lithofacies of the fossil-bearing rocks.*

Collection/Publication	Time slice	Age	Basis For age	Geographic area	Lithology
1. - Kozur *et al.* (1996)	1a	L. Tremadocian	Conodonts	Windfall Fm (Nevada)	Black shales & silty limestones
2a. - Won *et al.* (2005)	1a-1b	L. Tremadocian	Conodonts	Cow Group (W. Newfoundland)	Lime mudstone
2b. - Won *et al.* (2007)	1b-1c	M. Tremadocian	Conodonts	Cow Group (W. Newfoundland)	Lime mudstone
2c. - Won & Iams (2011)	2a	L. Floian	Conodonts	Cow Group (W. Newfoundland)	Lime mudstone
3. - Aitchison *et al.* (1998)	2a	L. Floian	Radiolaria	New Port Complex (Newfoundland	Radiolarian chert
4. - Danelian & Popov (2003)	2a-2b	Floian	Conodonts	Kazakhstan	Limestones
5a. - Maletz & Bruton (2005)	2c	Late Floian	Graptolites	Spitsbergen	Black limestones & shales
5b. - Maletz & Bruton (2007)	2c-3a	Late Floian- E. Dapingian	Graptolites	Spitsbergen	Black limestones & shales
6. - Aitchison (1998)		Late Floian- E. Dapingian ?		Ballantrae Complex (Scotland)	Radiolarian chert
7. - Maletz (2007b)	3a-3b	Dapingian	Graptolites	Cow Head (W. Newfoundland)	Limestone
8. - Fortey & Holdsworth (1971), Maletz & Bruton (2008)	4a-4b	Darriwilian	Graptolites	Spitsbergen	Limestone
9. – Hinde (1890), Danelian & Clarkson (1998), Danelian (1999), Danelian & Floyd (2001)	4c-5b	L. Darriwilian-E. Sandbian	Conodonts Radiolaria	Southern Uplands (Scotland)	Radiolarian chert
10. - Nazarov & Popov (1980)	4b-4c	L. Darriwilian	Graptolites	Kazakhstan	Limestone
11. - Buckman & Aitchison (2001)	4c	L. Darriwilian	Conodonts	Kekesayi terrane, Xinjian (China)	Radiolarian chert
12. - Maletz *et al.* (2009)	4a-4b	E. Darriwilian	Conodonts	Argentina	Limestone
13. - Wang (1993)	4c-5a	L. Darriwilian – E. Sandbian	Graptolites	China	Limestone
14.- Renz (1990b)	4b-4c	M.-L. Darriwilian	Brachiopods, Conodonts, Graptolites	Newfoundland	Nodular limestone
15. - Li (1995)		Late Darriwilian or younger	Radiolaria	Qilian Mts (China)	Yellow-green cherts in a mélange
16a.- Goto & Ishiga (1991);	5a-6c	Late Ordovician	Radiolaria	Lachlan Fold Belt (SE Australia)	Black siliceous mudstones &

Goto *et al.* (1992); Umeda *et al.* (1992)					cherts
16b. - Iwata *et al.* (1995)	5a-5c ?	Sandbian- E. Katian ?	Conodonts	Ballast Fm, Lachlan Fold belt (SE Australia)	Siliceous mudstones
17.- Webby & Blom (1986), Noble & Webby (2009)	5d-6a	Katian	Graptolites, conodonts	New South Wales (Australia)	Limestone Carbonate/graptolitic shale
18.- Dunham & Murphy (1976), Renz (1990a)	6a	Late Katian	Graptolites	Eureka County (Nevada) Hanson Creek Formation	Calcareous concretion in carbonate/graptolitic shale
19.- Nazarov & Popov (1980)	6b	Late Katian	Graptolites	Kazakhstan	Dark-grey micritic limestones

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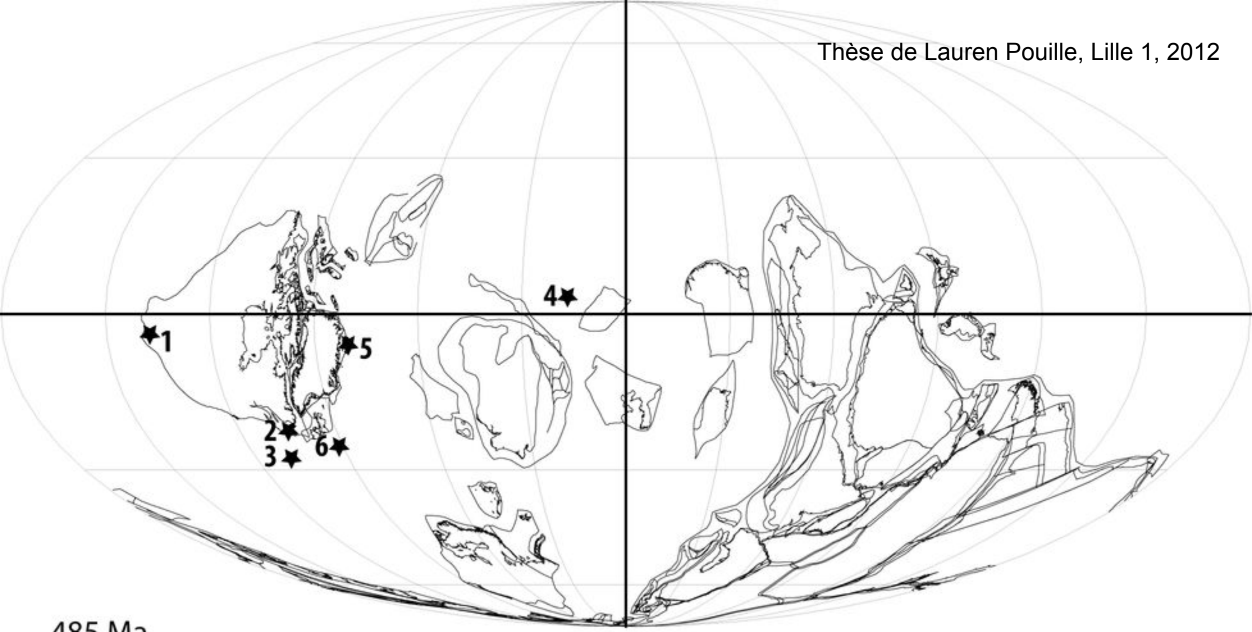
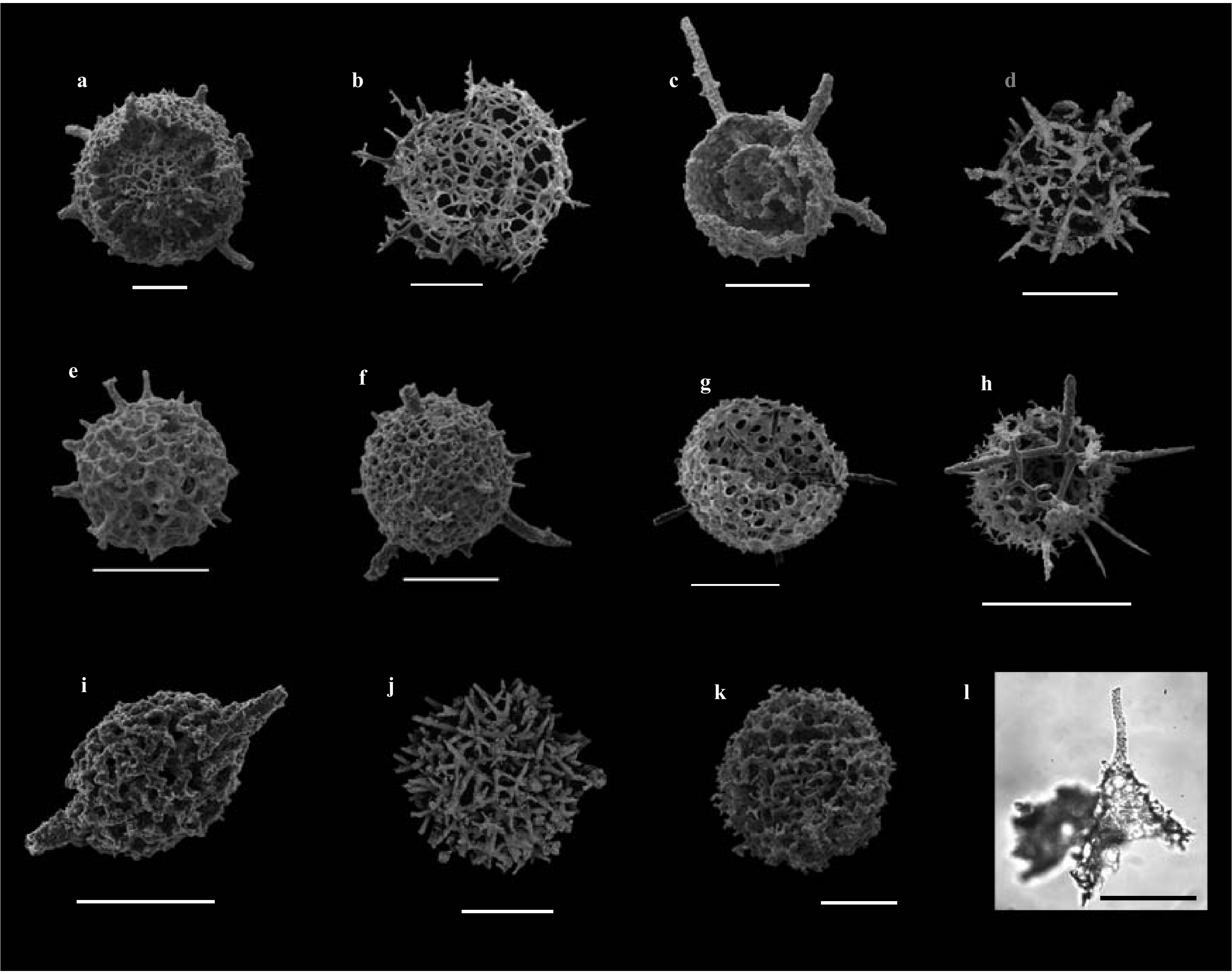


485 Ma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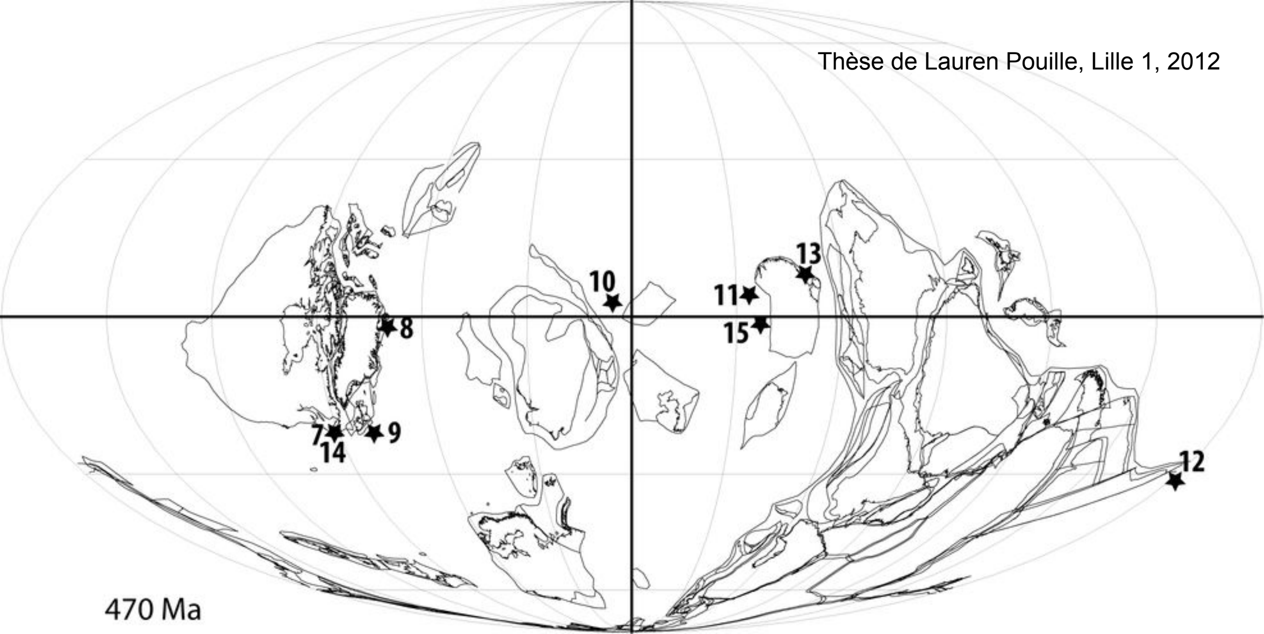

Thèse de Lauren Pouille, Lille 1, 2012
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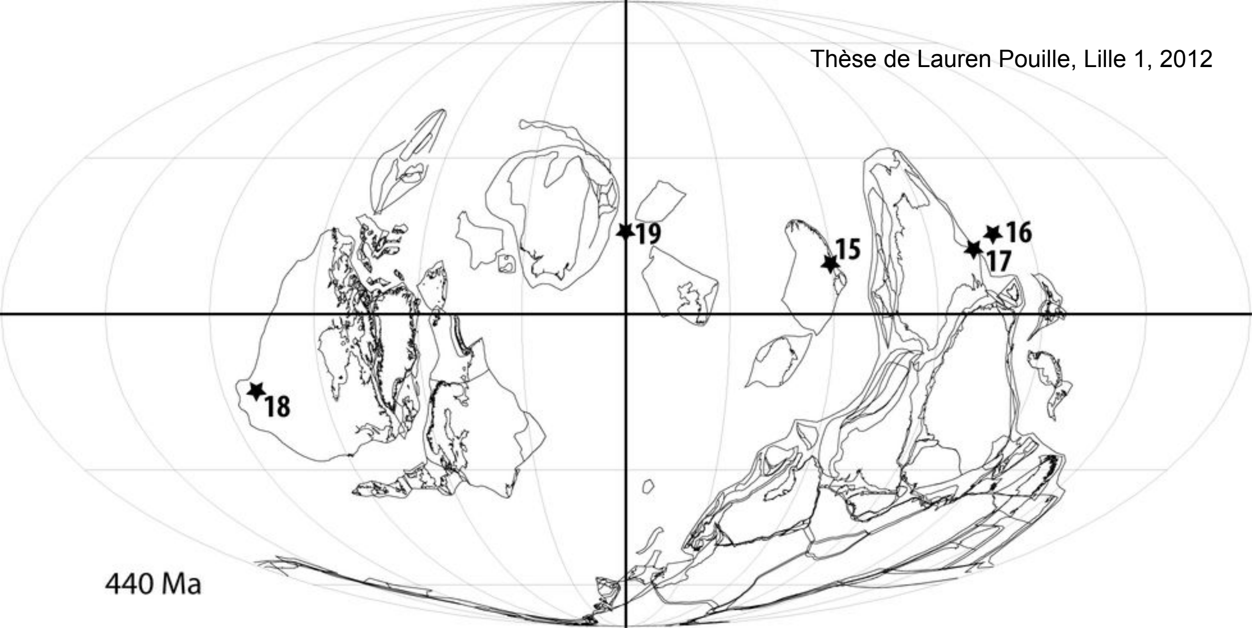
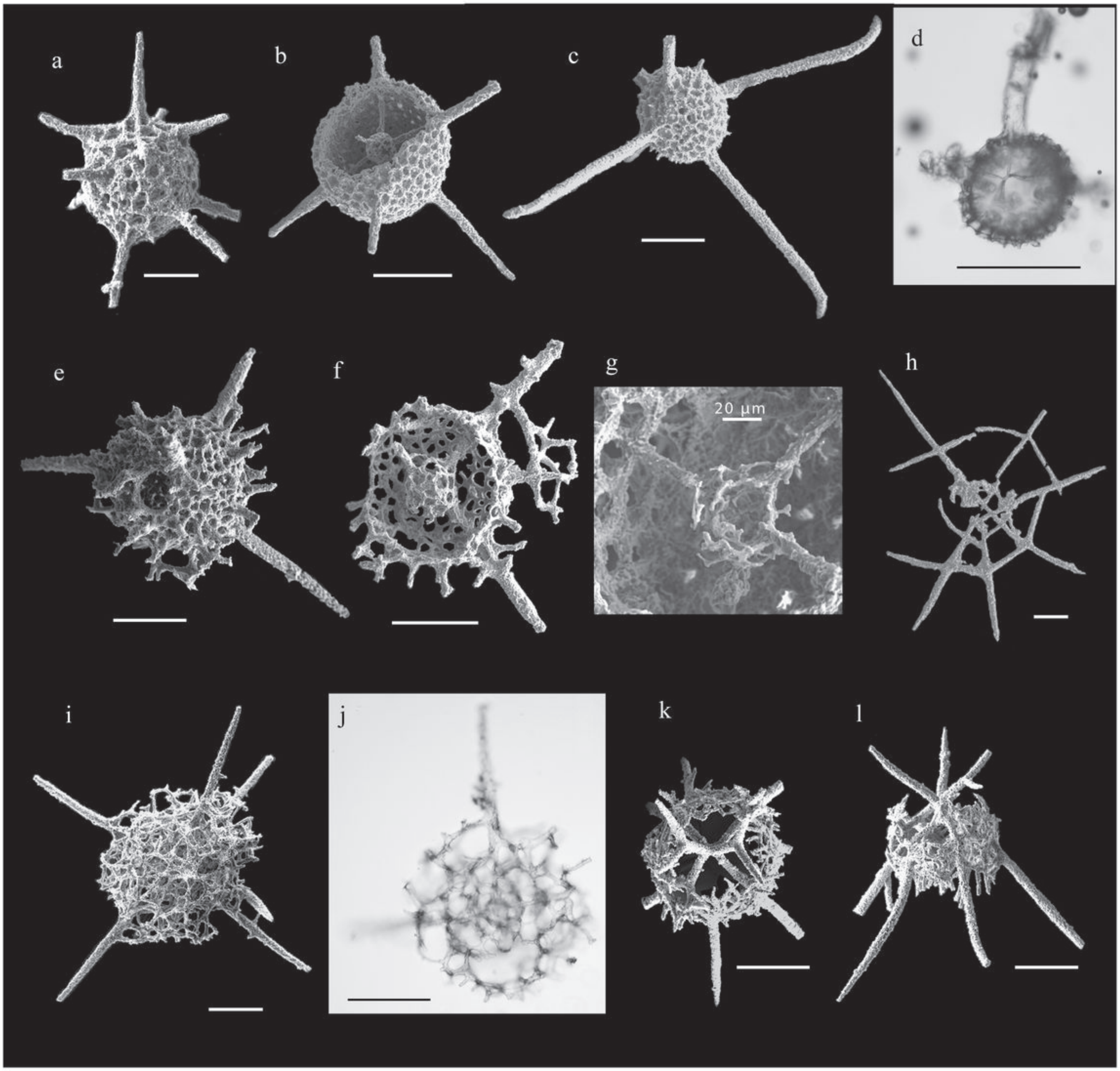


Thèse de Lauren Pouille, Lille 1, 2012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