

A revised heterostracan-based ichthyostratigraphy of the Wood Bay Formation (Lower Devonian, Spitsbergen), and correlation with Russian Arctic archipelagos

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ABSTRACT

Spitsbergen shows a several kilometers thick, mostly siliciclastic Devonian sequence. In this sequence, the Wood Bay Formation represents a typical Old Red Sandstone megafacies unit of Early Devonian age (Pragian-Emsian). It outcrops in the Andrée Land Block (often wrongly designated as the “main Devonian graben”) in NW Spitsbergen. Its stratigraphy has been mostly established in two areas of this block, that is, in the Woodfjorden area in the north, and in the Dicksonfjorden-Austfjorden area in the south. A revision of the pteraspiform heterostracan vertebrates has been carried out in both areas. Eight different fossil assemblages are defined, five for the Woodfjorden area (WA), and three for the Dicksonfjorden-Austfjorden area (DAA), that enable the correlation of the Sigurdfjellet and Kapp Kjeldsen “faunal divisions” of the lower Wood Bay Formation (in WA) with the Austfjorden Member (in DAA), and the Keltiefjellet “faunal division” of the upper Wood Bay Formation (in WA) with the Dicksonfjorden Member (in DAA). Unfortunately, pteraspids do not help with correlation between the uppermost parts of the Wood Bay Formation in the north and south of the Andrée Land Block. These results are used also for a more precise correlation with the heterostracan-bearing, Early Devonian, Old Red Sandstone series of Novaya Zemlya and Severnaya Zemlya in the Russian Arctic. They also confirm that Spitsbergen and those Russian archipelagos were elements of the Early Devonian, palaeobiogeographic Arctic Province.

KEY WORDS

Old Red Sandstones,
Pragian-Emsian,
Heterostraci,
vertebrates,
Svalbard,
Novaya Zemlya,
Severnaya Zemlya.

RÉSUMÉ

Révision de l'ichtyostratigraphie fondée sur les hétérostracés de la Formation de Wood Bay (Dévonien inférieur du Spitsberg) et corrélations avec les archipels arctiques russes.

Le Spitsberg présente une série sédimentaire dévonienne qui est principalement siliciclastique et épaisse de plusieurs kilomètres. Au sein de celle-ci, la Formation de Wood Bay se présente sous un mégafaciès Vieux Grès Rouges typique d'âge éodévonien (Praguien-Emsien). Elle affleure dans le Bloc d'Andrée Land (souvent désigné sous le nom incorrect de « graben dévonien principal ») du NW du Spitsberg. Sa stratigraphie a été étudiée essentiellement dans deux régions : celle du Woodford dans le nord et celle du Dicksonfjord-Austfjord dans le sud. Nous avons mené une révision des vertébrés hétérostracés ptéraspidiformes dans ces deux régions. Huit assemblages fossiles différents sont définis : cinq pour la région du Woodford (WA) et trois pour celle du Dicksonfjord-Austfjord (DAA). Ceci permet de corréler les « divisions fauniques » de Sigurdfjellet et Kapp Kjeldsen de la partie inférieure de la Formation de Wood Bay (dans WA) avec le Membre de l'Austfjord (dans DAA), ainsi que la « division faunique » de Keltiefjellet de la partie supérieure de la Formation de Wood Bay (dans WA) avec le Membre du Dicksonfjord (dans DAA). Par contre, les ptéraspidés ne sont d'aucune aide pour corréler les parties les plus supérieures de la Formation de Wood Bay entre elles, entre le nord et le sud du Bloc d'Andrée Land. Ces résultats autorisent également des corrélations plus précises avec les Vieux Grès Rouges à hétérostracés d'âge éodévonien de Nouvelle Zemble et de Terre-du-Nord, dans l'Arctique Russe. Ils confirment l'appartenance du Spitsberg et de ces archipels russes à la province paléobiogéographique arctique au Dévonien inférieur.

MOTS CLÉS

Vieux Grès Rouges,
Praguien-Emsien,
Hétérostraci,
vertébrés,
Svalbard,
Nouvelle Zemble,
Terre-du-Nord.

INTRODUCTION

Spitsbergen shows, mainly in its north-western part, a several kilometers thick, mostly siliciclastic sequence of Devonian age which corresponds to the late- and post-orogenic molasse of the late Caledonian (Haakonian-Svalbardian) orogeny in the Svalbard archipelago. In this sequence, the Wood Bay Formation represents a typical Old Red Sandstone megafacies unit of Early Devonian age (Pragian-Emsian). It outcrops in the Andrée Land Block (ALB), in NW Spitsbergen (often wrongly designated as the “main Devonian graben”). Its stratigraphy has been established in two areas of this block, i.e. in the Woodfjorden area in the north, and in the Dicksonfjorden-Austfjorden area in the south, based upon a variety of bio- and litho-stratigraphic informations. This has led to correlation problems between both areas (e.g., Blicek *et al.* 2000). So, a revision of the most significant biological markers in both series has become necessary, in order to propose a more precise correlation between them. Ichthyostratigraphy has been defined by Blicek *et al.* (1995) as an ichthyofauna-based biostratigraphy, and was first applied to the Late Silurian – Early Devonian succession of Artois – Ardenne (N France and S Belgium). The term is here applied to the Early Devonian succession of Spitsbergen. The most recent ichthyostratigraphic results for the Lower and Middle Devonian of Spitsbergen was based upon thelodonts from the Andrée Land Group (Žigaitė *et al.* 2013, 2014). The present work is a new synthesis of the heterostracan biostratigraphy of the Wood Bay Formation. It is based upon the preliminary works of Pernègre (2004c) and Pernègre & Dupret (2004), and is updated by new data recently obtained by the junior author (Pernègre 2004b).

ABBREVIATIONS

CNRS	Centre national de la Recherche scientifique;
MNHN	Muséum national d'Histoire naturelle;
IPEV	Institut Paul-Émile Victor.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The main island of the Norwegian Svalbard archipelago is Spitsbergen. It is located in northern Europe, between 75° and 80° (Fig. 1). The Devonian of Spitsbergen outcrops in three main regions: two are located in the northern part of the island; the third one, located in the southern part (Horn-sund), is smaller (Fig. 1B). There are also other minor areas with remnants of Devonian rocks. The Devonian from the first area in the north-west outcrops in a half graben limited southward by the Raudfjorden Fault Zone and eastward by the pre-Devonian basement in the Friedrichbreen Fault Zone (McCann 2000: fig. 3). The Devonian of the second main area, in the centre-north, outcrops in a wide north-south graben-like structure (Friend & Moody-Stuart 1972). It is limited westward by the Breibogen Fault Zone and eastward by the Billefjorden Fault Zone (Harland 1997: fig. 8.1; Blomeier *et al.* 2003a: fig. 1b).

The Devonian succession can be understood in a sequence stratigraphic context. Its thickness is estimated at 9000 meters (Blomeier *et al.* 2003a) and it is composed of the following stratigraphical units, from the base to the top: the Siktefjellet Group, the Red Bay Group and the Andrée Land Group (Fig. 2). The base is located at the base of the Siktefjellet Group, and is precisely defined by an angular unconformity above metamorphic, Precambrian basement. The age of the unconformity, however, is not precisely defined. The Siluro-Devonian (S/D) boundary occurs, for some authors, between



FIG. 1. — Geographical and geological setting: **A**, geographical location of Svalbard and Russian Arctic archipelagos: 1, Svalbard; 2, Novaya Zemlya; 3, Severnaya Zemlya; **B**, location of the Devonian outcrops in Spitsbergen, modified from Pernègre (2003, 2004c); **C**, geographical and stratigraphical location of the studied localities from the Woodfjorden area, simplified geological map after Blomeier *et al.* (2003a); **D**, geographical and stratigraphical location of the studied localities from the Dicksonfjorden-Austfjorden area, simplified geological map after Blomeier *et al.* (2003a).

the Lilljeborgfjellet and Albertbreen formations (Murashov & Mokin 1976, 1979; McCann 2000) or into the Lilljeborgfjellet Formation (Harland 1997; Blomeier *et al.* 2003a). There are in fact no precise data for establishing that S/D boundary. The age of the other formations is estimated from

their miospore, plant and vertebrate (fish) contents (Blieck *et al.* 1987; McCann 2000: 570).

The Wood Bay Formation (Holtedahl 1914 cited in Friend 1961; Friend *et al.* 1966) forms the base of the Andrée Land Group (Fig. 2). It overlies the Ben Nevis Formation of the

UPPER DEVONIAN	FRASNIAN	Andrée Land Group	Mimerdalen Formation	
	FAMENNIAN			
MIDDLE DEVONIAN	GIVETIAN		Wijde Bay Formation	
	EIFELIAN		Grey Hoek Formation	
LOWER DEVONIAN	PRAGIAN		?	Wood Bay Formation
	EMSIAN			
	LOCHKOVIAN		Red Bay Group	Ben Nevis Formation
		Fraenkelryggen Formation		
		Andréebreen Formation		
Rivieratoppen Formation				
	Siketfjellet Group	Albertbreen Formation		

FIG. 2. — Stratigraphical section of the Andrée Land Block of northern Spitsbergen, after Harland (1997) and Blomeier *et al.* (2003a). Ages after Blicek *et al.* (2000, 2002) and McCann (2000). Note that: 1) it is common to subdivide the lowermost part of the Red Bay Group into Wulffberget, Rabotdalen (locally present) and Princesse Alicefjellet formations instead of only the Rivieratoppen Formation, according to Murashov & Mokin (1976, 1979) – this subdivision being applicable throughout the Devonian of northern Spitsbergen (Blomeier *et al.* 2003a, b); and 2) the Grey Hoek and Wijde Bay formations are considered as lateral equivalents and Eifelian in age by Schweitzer (1999); however, Schweitzer's idea that the Grey Hoek and Wijde Bay formations are of equal age is certainly not true along Wijdefjorden, where one lies on top of the other with a depositional boundary; upper parts of the Grey Hoek Formation in the Woodfjorden area may be coeval with the Wijde Bay Formation farther east (Blomeier *et al.* 2003a, b; W. Dallmann, pers. comm. 2007).

Red Bay Group (Kiaer 1916 cited in Friend 1961). A continuity of sedimentation between both formations was proposed by Føyn & Heintz (1943) and accepted by Friend (1961), Goujet (1984) and Blicek *et al.* (1987). The age of the boundary between the Ben Nevis and the Wood Bay formations is

still uncertain, and tentatively assigned to the Lochkovian/Pragian boundary (Blicek 1984; Blicek *et al.* 2000). This uncertainty is probably due to the Monacobreen deformation phase that occurred between both formations, based upon the occurrence of a polymictic conglomeratic unit at the base of the Andrée Land Group at Sigurdfjellet (McCann 2000). However, the idea that the Wood Bay Formation overlies the Ben Nevis Formation with a polymictic conglomerate is probably not true. The conglomerate at Sigurdfjellet may be a fault-bound conglomerate of an earlier stage, which occurs at several places along the Breibogen Fault farther north. The boundary between both formations is not exposed. There is still a certain probability of a tectonic phase due to the quite different styles of deformation in the Red Bay and Andrée Land groups (Piepjohn *et al.* 2000) (W. Dallmann pers. comm. 2007). Moreover, the age and correlation of the Wood Bay Formation in the northern and southern parts of the ALB has been a subject of discussions, varying from the Lochkovian/Pragian or "Siegenian" to the Pragian/Emsian or Givetian (Blicek *et al.* 2000: fig. 10). The top of the Devonian sequence is located at the top of the Plantekløfta Member of the Mimerdalen Formation (Fig. 2). Its suggested age is late Famennian, based on the study of its plants and miospore assemblages (Schweitzer 1999; Piepjohn *et al.* 2000). However, the data are very scant, based upon a few specimens of *Retispora lepidophyta* (Kedo, 1957), and thus not very conclusive for dating (J. E. A. Marshall pers. comm. 2007).

During the Devonian, palaeomagnetic data show that Spitsbergen was in an equatorial location, and on the northern edge of Laurentia close to Baltica (Golonka 2000; Friend *et al.* 2000: fig. 6; Scotese 2002; Torsvik & Cocks 2004: fig. 5; Cocks & Torsvik 2011: figs 16, 17). Both palaeocontinents were accreted into the single Old Red Sandstone Continent.

THE WOOD BAY FORMATION

This represents the most important part of the Devonian succession in the centre-north ALB, and is characterized by its dominantly red colour.

Age and composition

The Wood Bay Formation corresponds to the upper part of the Lower Devonian (Fig. 2). It is dated as early Pragian to late Emsian (Blicek 1984; Blicek *et al.* 1987, 2000; Blomeier *et al.* 2003a). This is suggested by its vertebrate and miospore content (Allen 1965, 1967; Blicek *et al.* 1987; Mark-Kurik 1991). However, the age of its upper part is still under debate (Blicek *et al.* 2000); the top of the formation varies from an early Emsian (Stemans *in* Blicek *et al.* 2000) to a late Emsian age (Mark-Kurik 1991). It is considered here that the Wood Bay Formation occupies all of the Pragian and Emsian. Some authors place the base of the Pragian into the Fraenkelryggen Formation of the Red Bay Group (e.g., Harland 1997). This proposal seems strange because the latter author uses palaeontological results which gave a basal Pragian age for the base of the Wood Bay Formation (Blicek *et al.* 1987, 2000). However, we will not discuss this problem here. The Wood Bay Formation is essentially composed of red sandstones (the

Dicksonfjorden Member of Blomeier *et al.* 2003a: fig. 1b) with variations of grain size, from siltstones to conglomerates (Fig. 3). Variations of compaction often occur. In the southern part of the ALB (Dicksonfjorden-Austfjorden area), the oldest sandstones are green-grey with feldspars and carbonate occurrence (the Austfjorden Member of Vogt 1929; also Friend 1961; Friend *et al.* 1966; see Blomeier *et al.* 2003a: fig. 1b; Fig. 3). The thickness of the Wood Bay Formation is about 3000 meters (Blomeier *et al.* 2003a).

Sedimentology

The Wood Bay Formation belongs to the Old Red Sandstone megafacies. The deposits are mostly considered as continental on sedimentological evidence, and as having originated in flood plains, rivers and lakes (Friend 1961; Critelli & Reed 1999; Blomeier *et al.* 2003a, b). On the contrary, the occurrence of fossils such as lingulids (Goujet 1984; Goujet & Emig 1985) and *Cruziana* d'Orbigny, 1842 (Goujet 1984; Harland 1997: 138) leads to the conclusion that the environment was semi-continental in “fjords” or estuaries with dominantly terrigenous material brought by rivers (Goujet 1984; Blicek 1984; Goujet & Emig 1985; Blicek & Janvier 1999). The high level of terrigenous material has been interpreted as the results of a semi-arid climate, with monsoonal periods (Dickins 1993 cited in Blomeier *et al.* 2003a). The Caledonian orogeny (Haakonian phase) is responsible for the siliclastic nature of the sediments.

History of the subdivisions of the Wood Bay Formation

For palaeontologists, the Wood Bay Formation is commonly divided into four “faunal divisions”, that is, from base to top: the Sigurdfjellet, Kapp Kjeldsen, Keltiefjellet (“Lykta fauna”) and Stjørdalen faunal divisions (Fig. 3). The three latter were originally proposed by Føyn & Heintz (1943) and revised by Goujet (1984) who introduced the Sigurdfjellet division. Føyn & Heintz (1943) gave the first stratigraphical description of the Wood Bay Formation. They divided it into three divisions called “Series”: “Each of these three divisions is characterised by a group of guide-fossils [...]. With our present knowledge of the stratification and of the fossils, it is therefore impossible to draw distinct limits between the various divisions”, and “In appearance all three divisions have certain (geological) characteristics making possible to distinguish them more or less accurately at a distance” (Føyn & Heintz 1943: 13). This first stratigraphy was faunally and lithologically characterized, but this remained quite vague. Friend (1961) confirmed Føyn & Heintz’ divisions in the Woodfjorden area (north-west of the ALB). However, he quoted: “many of the vertebrates are only represented in collections by isolated fragments and have not yet been adequately described” (Friend 1961: 81). He proposed new lithological characteristics such as colour, composition, grain size and bedding as the fundamental lithostratigraphic basis for mapping. At the same time, he proposed another scheme for the Dicksonfjorden-Austfjorden area (south-east of the ALB), where the sandstones present colour variations. He described two lithostratigraphic units: the “Austfjorden

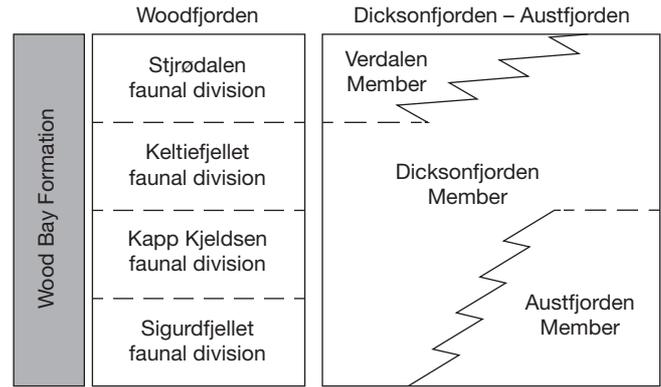


FIG. 3. — Biostratigraphic scale (faunal divisions) of the Wood Bay Formation in the Woodfjorden area, after Goujet (1984), Harland (1997) and Blicek *et al.* (2000), and lithostratigraphic section of the Wood Bay Formation in the Dicksonfjorden-Austfjorden area, after Blomeier *et al.* (2003a).

Sandstone” and the “Dicksonfjorden Sandstone” (Friend 1961: 90-92). Later on, Friend *et al.* (1966) returned to the original concept of “faunal divisions”, based on some publications of the Pteraspidoformes from the formation (Heintz 1960, 1962; Blicek & Heintz 1979), and they characterized each division after some guide-fossils: the genus *Gigantaspis* Heintz, 1962 characterizes the Kapp Kjeldsen faunal division, and the genus *Doryaspis* White, 1935 (with *Doryaspis nathorsti* (Lankester, 1884)) characterizes the Lykta one (later renamed Keltiefjellet). The same authors renamed the two lithostratigraphical units of the Dicksonfjorden-Austfjorden area into “Members” (Friend *et al.* 1966: 61). They described a third unit, i.e. the Verdal Member, for the top of the formation; the latter is mainly composed of calcareous sediments and located principally in the north, with restricted extensions in the southern area. They suggested lateral correlations between the Woodfjorden and the Dicksonfjorden-Austfjorden areas, based on sedimentology, but without faunal considerations. Goujet (1984) is the most recent author to have added a subdivision in to the formation, viz., the Sigurdfjellet division at the base of the succession in the Woodfjorden area. It is supposed to be in conformity with the underlying Ben Nevis Formation, and characterized by a rich and distinctive, but still incompletely published fauna (However, see discussion here above in the “geographical and geological setting” section. This Sigurdfjellet division is characterized by abundant and well-preserved vertebrate fossils, including heterostracans, osteostracans, placoderms and thelodonts that are mostly published; the acanthodian microremains have not yet been described, only some macroremains from the Woodfjorddalen region have been published: Gagnier & Goujet 1997).

Present lithostratigraphic scheme

The Norsk Polarinstittutt geological map describes three members for the Wood Bay Formation, viz., from base to top: the Austfjorden, Dicksonfjorden and Verdal members (Dallmann *et al.* 2002; Blomeier *et al.* 2003a). Green-grey well-cemented sandstones compose the Austfjorden Member, which is only

TABLE 1. — Macrovertebrate content of the different localities of the Wood Bay Formation in the Woodfjorden area, and their attribution to Assemblages 1 to 5. Pteraspidiforms after Pernègre (2002, 2003, 2004a, c, 2005, 2006), Pernègre & Dupret (2004); placoderms after Goujet (1973, 1984, and pers. comm.); osteostracans after Janvier (1985). For locality abbreviations, see text.

	Localities	Pteraspidiforms	Placoderms	Osteostracans
Assemblage 1	B _{IV}	<i>Doryaspis arctica</i> Pernègre, 2002 <i>Gigantaspis minima</i> Pernègre & Goujet, 2007 <i>Xylaspis prima</i> (Pernègre, 2003) <i>Woodfjordaspis felixi</i> Pernègre, 2006	<i>Sigaspis lepidophora</i> Goujet, 1973 <i>Arctaspis</i> sp.	<i>Boreaspis rostrata</i> Stensiö, 1927 <i>Boreaspis intermedia</i> Wängsjö, 1952 <i>Boreaspis ceratops</i> Wängsjö, 1952 <i>Boreaspis ginsburgi</i> Janvier, 1977 <i>Cephalaspis curta</i> Wängsjö, 1952 <i>Norselaspis glacialis</i> Janvier, 1981 <i>Axinaspis whitei</i> Wängsjö, 1952
	B _{II}	<i>Doryaspis arctica</i> <i>Gigantaspis minima</i> <i>Xylaspis prima</i>	<i>Arctaspis</i> sp. <i>Sigaspis lepidophora</i>	
	B _I	<i>Doryaspis arctica</i> <i>Gigantaspis minima</i>		<i>Diademaspis</i> sp.
	B _J	<i>Gigantaspis minima</i>		
	A ₁₁	<i>Xylaspis prima</i>		
	B _{I'}	<i>Doryaspis arctica</i> <i>Gigantaspis minima</i>		
Assemblage 2	B _I	<i>Doryaspis arctica</i> <i>Gigantaspis isachseni</i> Heintz, 1962		
	A ₁₋₄	<i>Doryaspis arctica</i> <i>Gigantaspis isachseni</i> <i>Gigantaspis bocki</i> Heintz, 1962		
	B _L	<i>Doryaspis arctica</i> <i>Gigantaspis isachseni</i> <i>Gigantaspis bocki</i>		
	B _O	<i>Doryaspis arctica</i> <i>Gigantaspis isachseni</i>	<i>Arctaspis</i> sp.	<i>Diademaspis poplinae</i> Janvier, 1985 <i>Parameteoraspis moythomasi</i> (Wängsjö, 1952)
Assemblage 3	H ₁₋₃	<i>Gigantaspis isachseni</i> <i>Doryaspis nathorsti</i> (Lankester, 1884)	<i>Heintzosteus</i> sp.	
	B _G	<i>Gigantaspis isachseni</i> <i>Doryaspis lyktensis</i> (Heintz, 1960)	<i>Arctolepis</i> sp.	
	B _C	<i>Doryaspis nathorsti</i> <i>Gigantaspis isachseni</i>	<i>Arctaspis</i> sp.	
Assemblage 4	B _E	<i>Doryaspis nathorsti</i> <i>Doryaspis</i> sp. 1	<i>Arctolepis decipiens</i> (Woodward, 1891) <i>Arctaspis maxima</i> Heintz, 1929	
	C ₄	<i>Doryaspis nathorsti</i> <i>Doryaspis</i> sp. 1	<i>Arctolepis decipiens</i>	<i>Parameteoraspis lanternaria</i> (Wängsjö, 1952)
	B _d	<i>Doryaspis nathorsti</i> <i>Doryaspis</i> sp. 1	<i>Arctaspis maxima</i> <i>Arctolepis</i> sp.	
Assemblage 5	B _H	<i>Doryaspis nathorsti</i>	<i>Arctolepis decipiens</i>	
	A ₁₆	<i>Doryaspis nathorsti</i>	<i>Arctaspis</i> sp.	<i>Parameteoraspis oblongata</i> (Stensiö, 1927) <i>Parameteoraspis</i> sp.

present in the south-eastern part of the ALB (Fig. 3). The red sandstones are grouped into the Dicksonfjorden Member, which is diachronous within the basin (Fig. 3). It comprises the main part of the sediments in the north, and overlies the Austfjorden Member in the south-east (Blomeier *et al.* 2003a: fig. 2). The Verdalen Member is discontinuous and outcrops mainly in the north (Fig. 3). It has been shown to be ichthyostratigraphically equivalent to both the lower Grey Hoek Formation in the north, and uppermost Wood Bay Formation in the south (Blicek *et al.* 1987: fig. 8).

The Norsk Polarinstitut maps use a purely lithostratigraphic subdivision, with lateral (highly diachronous) boundaries between the Austfjorden and Dicksonfjorden members. The reason is that many years of mapping in Andrée Land have shown that it is impossible to assign the faunal divisions (see above) to certain lithological characteristics. Although there are differences in places, there is no critical parameter that can be used to subdivide the strata in accordance with its faunal divisions throughout the Devonian outcrop area. Thus, most of the Wood Bay Formation (except for the Verdalen Mem-

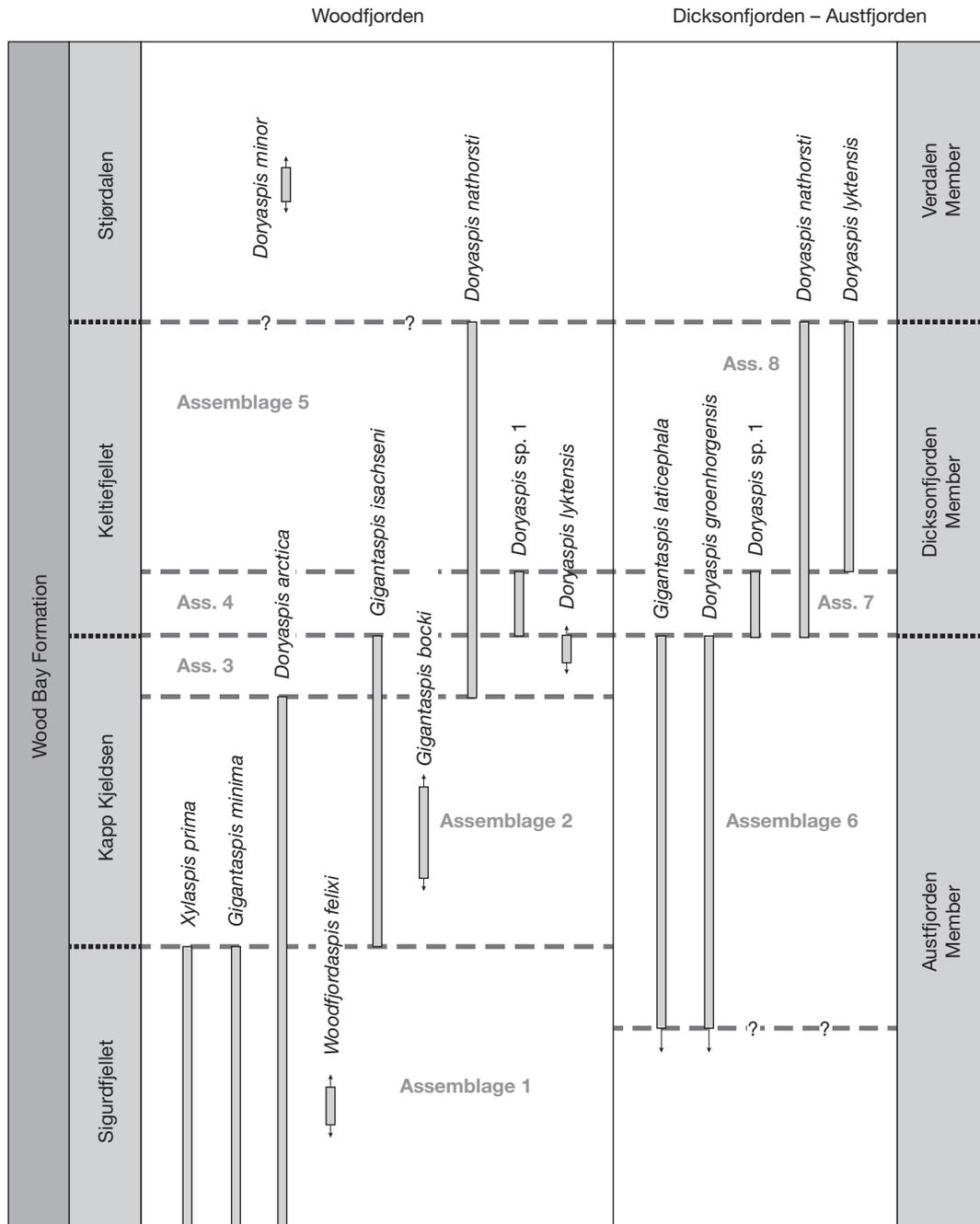


FIG. 4. — New stratigraphic distribution of the pteraspidiiform species and assemblages in the Wood Bay Formation, both in the Woodfjorden and the Dicksonfjorden-Austfjorden areas.

ber) in northern and northwestern André Land belongs to the Dicksonfjorden Member with red to greenish coloured, mostly calcite-free, fine-grained sand- and silt-stones. The Austfjorden Member occurs only in the southeastern part of the area, is coarser grained, with yellow to greenish and calcite-rich sandstones and gritstones. Chronostratigraphically it corresponds to the lower part of the Dicksonfjorden Member in the north and west, and interfingers with it in relatively narrow zones across a stratigraphic interval of several hundred meters (see Blomeier *et al.* 2003a, b; and W. Dallmann pers. comm. 2007).

Present palaeontological context

Since the stratigraphic work of Føyn & Heintz (1943), the Pteraspidiiformes have been used as references for the faunal divisions, due to abundant *in situ* material and richness of the resulting collections. These Pteraspidiiformes are easily identifiable at the generic level (Heintz 1962, 1968; Pernègre 2002, 2003). However, the other elements of the fauna are of less value for biostratigraphical correlations, except thelodonts. The osteostracans are quite rare both in the collections and *in situ*, which is a restricting factor for their stratigraphical potential: species are often known from a single specimen only (Janvier

TABLE 2. — Macrovertebrate content of the different localities of the Wood Bay Formation in the Dicksonfjorden-Austfjorden area, and their attribution to Assemblages 6 to 8. Pteraspidiiforms after Pernègre (2002, 2003, 2004a, c, 2005, 2006), Pernègre & Dupret (2004); placoderms after Goujet (1973, 1984, and pers. comm.); osteostracans after Janvier (1985).

	Localities	Pteraspidiiforms	Placoderms	Osteostracans
Assemblage 6	BD & BD'	<i>Doryaspis groenhorgensis</i> Pernègre, 2005 <i>Gigantaspis laticephala</i> (Blicek & Goujet, 1983)	<i>Dicksonosteus arcticus</i> Goujet, 1975 <i>Heintzosteus brevis</i> (Heintz, 1929) <i>Lehmanosteus hyperboreus</i> Goujet, 1984	
	B _S	<i>Doryaspis groenhorgensis</i> <i>Gigantaspis laticephala</i> ?		<i>Nectaspis areolata</i> Wängsjö, 1952 <i>Hildenaspis</i> sp.
Assemblage 7	142	<i>Doryaspis</i> sp. 1		
	BR ₁₋₃	<i>Doryaspis nathorsti</i> (Lankester, 1884) <i>Doryaspis</i> sp. 1	<i>Arctaspis maxima</i> Heintz, 1929 <i>Dicksonosteus</i> sp.	<i>Parameteoraspis lanternaria</i> (Wängsjö, 1952)
Assemblage 8	C ₁₇	<i>Doryaspis nathorsti</i> <i>Doryaspis lyktensis</i> (Heintz, 1960)		
	B _T	<i>Doryaspis nathorsti</i> <i>Doryaspis lyktensis</i>		
	C ₁₈	<i>Doryaspis nathorsti</i> <i>Doryaspis lyktensis</i>		<i>Diademaspis poplinae</i> Janvier, 1985
	C ₁₉	<i>Doryaspis nathorsti</i> <i>Doryaspis lyktensis</i>	<i>Arctaspis maxima</i>	
	B _Y	<i>Doryaspis nathorsti</i> <i>Doryaspis lyktensis</i>	<i>Arctolepis decipiens</i> (Woodward, 1891)	<i>Nectaspis peltata</i> Wängsjö, 1952
	132	<i>Doryaspis nathorsti</i>		

1985), so that their stratigraphic and geographic distributions are poorly known. This also applies to the placoderms. Although their specimens are abundant *in situ* (Heintz 1929; Goujet 1973, 1984), many forms remain undescribed and those named by Heintz (1929) now require revision. Hence, placoderms could probably be used for biostratigraphy, but not at the present state of knowledge. So, the new ichthyostratigraphy of the Wood Bay Formation is mainly based on the distribution of the pteraspidiiform heterostracans. Other data are used here when they are available, after publications by Janvier (1981, 1985) and Goujet (1973, 1984).

DEFINITION OF NEW PTERASPIDIFORM ASSEMBLAGES AND INDEX-TAXA

Localities

The 37 studied localities were collected during various French expeditions, initially during the 1964 and 1969 CNRS-MNHN expeditions lead by Prof. J.-P. Lehman, and subsequently during the 2002-2003 IPEV expeditions lead by Prof. D. Goujet. These localities can be easily plotted on the geological map of Blomeier *et al.* (2003a). They belong to both the Woodfjorden and the Dicksonfjorden-Austfjorden areas (Fig. 1 C-D). The localities have been coded during the field expeditions for quick marking of the specimens. These codes are still used in collection. For the 1964-1969 expeditions, different teams were constituted (A, B, C...) and each one harvested different localities, so called A, B, C... Each team selected its own labelling of the

localities (a, b, c; I, II, III; 1, 2, 3... plotted after the letter of the team). This explains the diversity of codes found in collections (e.g., B_{IV}, B_L, C₄). During the 2002-2003 expeditions a single number was given to each locality where fossils were found (e.g., '142').

In the Woodfjorden area, all localities belong to the Dicksonfjorden Member (red sandstones; Figs 1C and 3). This area was investigated only in 1969. The vertebrate content of the localities is given in Table 1. B_{iv} is the richest locality, where the specimens are only represented by isolated elements. Specimens in articulation are known in the B_i, B_j, and B_l localities, where isolated elements are also known (Fig. 1C). A single specimen comes from the A₁₁ locality. Only isolated elements have been found in the B_T, A₁₋₄, B_L, B_O, H₁₋₃, B_G, B_C, B_E, C₄, B_D, B_H and A₁₆ localities (Fig. 1C and Table 1).

In the Dicksonfjorden-Austfjorden area, localities were visited in 1964, 1969 and 2002-2003. The vertebrate content of these localities is given in Table 2. The B_Δ, B_{Δ'} and B_S localities are in the Austfjorden Member (grey-green sandstones; Fig. 3). The two first ones are close to each other and belong to the same outcrop level, having been collected in 1964 and 1969 respectively. Rare specimens are anatomically articulated (except in the BD locality with *Gigantaspis laticephala* (Blicek & Goujet, 1983)), isolated elements represent the main material. A badly preserved disc is attributed to *Gigantaspis laticephala* in the B_S locality. The BR₁₋₃ and '142' localities are close to the Austfjorden

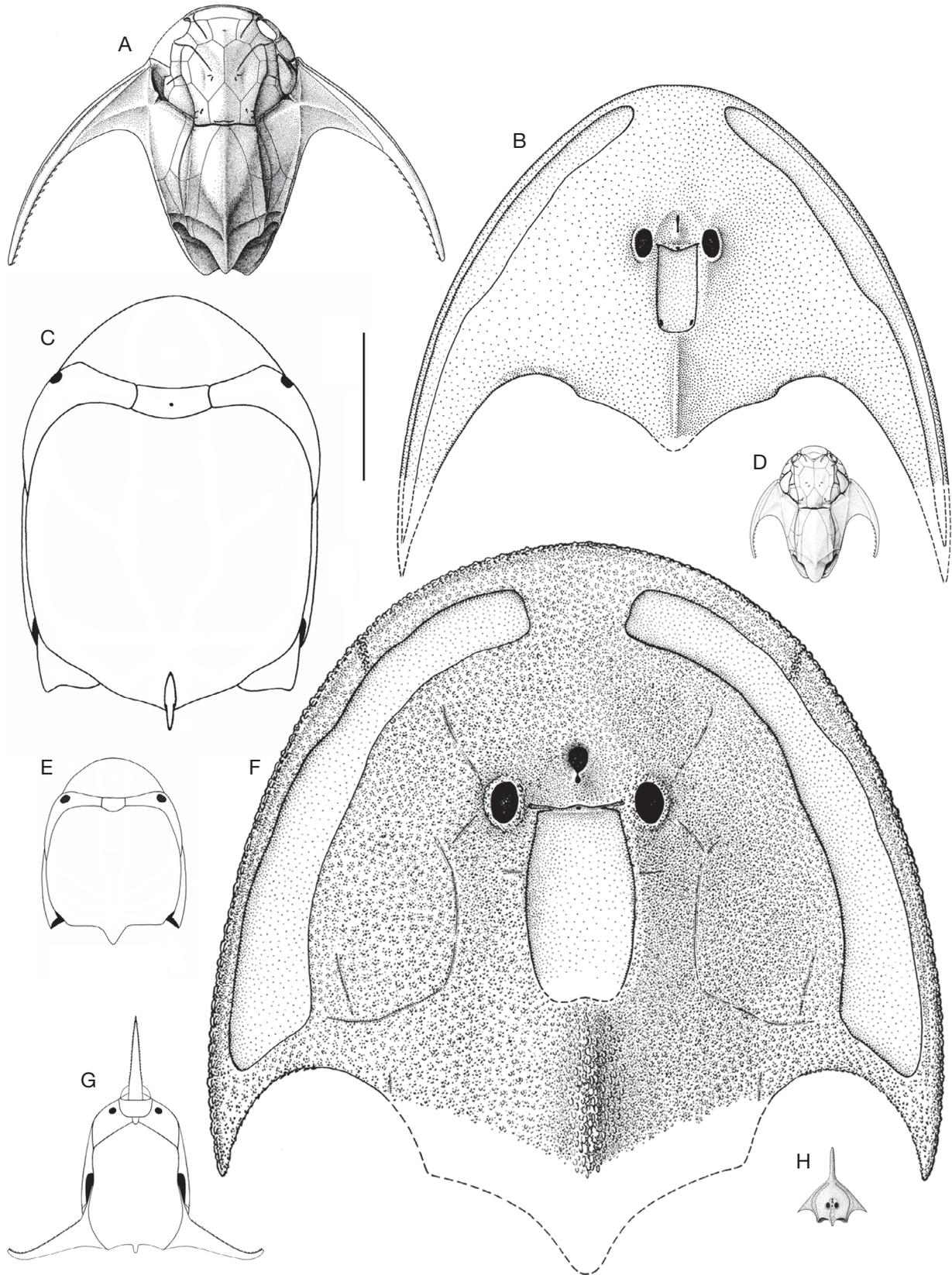


FIG. 5. — Illustrations of some representatives of the main genera of vertebrates in the Wood Bay Formation: **A**, *Arctolepis* Eastman, 1908; **B**, *Parameteoraspis* Blicek, Goujet & Janvier, 1987; **C**, *Gigantaspis* Heintz, 1962; **D**, *Dicksonosteus* Goujet, 1975; **E**, *Xylaspis* Pernègre, 2004; **F**, *Diademaspis* Janvier, 1985; **G**, *Doryaspis* White, 1935; **H**, *Boreaspis* Stensiö, 1927; **A**, **D**, placoderms; **B**, **F**, **H**, osteostracans; **C**, **E**, **G**, heterostracans. Scale bar: 5 cm.

Member – Dicksonfjorden Member boundary (Fig. 1D). They are composed of grey (BR₁; Austfjorden Member) or grey-red sandstones (BR₃ and ‘142’; Dicksonfjorden Member). Only isolated elements are found in the C₁₇₋₁₉, B_Y and ‘132’ localities, whereas subcomplete specimens (e.g., spécimen MNHN.F.SVD870) were collected in the B_T locality (Fig. 1D and Table 2).

New pteraspidiiform assemblages

In the Woodfjorden area, the Wood Bay Formation is mainly represented by red sandstones of the Dicksonfjorden Member (Fig. 3). The faunal divisions, originally described in this area (Føyn & Heintz 1943; Friend *et al.* 1966; Goujet 1984; Fig. 3) were previously based on two Pteraspidiiformes, *Gigantaspis* and *Doryaspis*. *Gigantaspis* was the index-fossil for the Kapp Kjeldsen and Sigurd fjellet divisions (*Gigantaspis* sp. in Blicek *et al.* 1987), whereas *Doryaspis nathorsti* was the index-fossil for the Keltiefjellet and Stjørdalen divisions (Friend *et al.* 1966; Goujet 1984; Blicek *et al.* 1987). However, results from the investigated localities suggest new characteristic assemblages, with new species distributions, and a redefinition of the biostratigraphical subdivision of this region. Assemblage 1 (Table 1) contains *Gigantaspis minima* Pernègre & Goujet, 2007, *Xylaspis prima* (Pernègre, 2003) and *Doryaspis arctica* Pernègre, 2002 in the B_{IV}, B_{II}, B_i, B_J, A₁₁ and B_I localities, as well as *Woodfjordaspis felixi* Pernègre, 2006 in locality B_{IV} (Pernègre 2006). Characteristic of the base of the Wood Bay Formation, it corresponds to the *Gigantaspis*, *Zascinaspis* Stensiö, 1958 and *Doryaspis* assemblage of Blicek *et al.* (1987: 203). It is equivalent to the Sigurd fjellet faunal division (Fig. 4), previously characterized by a distinctive but incompletely published fauna in Goujet (1973; 1984: 26; also Blicek *et al.* 1987; Harland 1997: 295, fig. 16.5; Žigaitė *et al.* 2013, 2014). Assemblage 2 (Table 1) contains *Doryaspis arctica* and *Gigantaspis isachsenseni* Heintz, 1962 in the B_I, A₁₋₄, B_L et B_O localities, plus *G. bocki* Heintz, 1962 in locality A₁₋₄. It corresponds to the *Gigantaspis* and *Doryaspis* sp. assemblage proposed by Blicek *et al.* (1987: 203, 206; Fig. 4 here). Assemblage 3 (Table 1) contains *Gigantaspis isachsenseni* and *Doryaspis nathorsti* in the H₁₋₃ and B_C localities, while *D. nathorsti* is replaced by *D. lyktensis* in the B_G locality. It corresponds to the *Gigantaspis* and *Doryaspis nathorsti* assemblage of Blicek *et al.* (1987: 203, 206; Fig. 4). Assemblages 2 and 3 are considered as equivalent to the Kapp Kjeldsen faunal division, as redefined by Goujet (1984: 26) and Blicek *et al.* (1987: 203, 206). It is based on the occurrence of *Gigantaspis isachsenseni* in both assemblages. Assemblage 2 is correlated to the lower part of the Kapp Kjeldsen division, while Assemblage 3 is equivalent to its upper part (Fig. 4), due to the occurrence of *Doryaspis nathorsti* as proposed by Friend *et al.* (1966), Goujet (1984) and Blicek *et al.* (1987). Assemblage 4 (Table 1) contains *Doryaspis nathorsti* and *Doryaspis* sp. 1 (unpublished) in localities B_E, C₄ and B_D. It is strictly equivalent to the *Doryaspis nathorsti* and the “huge species of *Doryaspis*” assemblage mentioned by

Blicek *et al.* (1987: 206; Fig. 4 here). Assemblage 5 (Table 1) is not a well defined assemblage, it contains a single pteraspidiiform species, *Doryaspis nathorsti*. It is found in the B_H and A₁₆ localities (Fig. 4). Assemblages 4 and 5 equal the Keltiefjellet division as defined by Blicek *et al.* (1987) and Harland (1997). The former one characterizes the lower part of the faunal division by the occurrence of *Doryaspis* sp. 1 (unpublished), while the latter one represents its upper part with only *Doryaspis nathorsti* (Fig. 4). The diversity of the Pteraspidiiformes decreases towards the top of the Wood Bay Formation, as it was presumed by Føyn & Heintz (1943), Friend *et al.* (1966), Goujet (1984), Blicek *et al.* (1987) and Harland (1997).

In the Dicksonfjorden-Austfjorden area, the Wood Bay Formation is divided in two lithological members characterized by different fossil data. Assemblage 6 (Table 2) contains *Doryaspis groenhorgensis* and *Gigantaspis laticephala* in the BD, BD’ and B_S localities which belong to the Austfjorden Member (Fig. 4). It can be correlated with Assemblages 1, 2 and 3 defined in the Woodfjorden area, by the co-occurrence of *Doryaspis* and *Gigantaspis*. Assemblage 7 (Table 2) contains *Doryaspis nathorsti* and *Doryaspis* sp. 1 (unpublished) in the BR₁₋₃ and ‘142’ localities, at the base of the Dicksonfjorden Member. This assemblage is equivalent to Assemblage 4 proposed in the Woodfjorden area. Assemblage 8 (Table 2) contains *Doryaspis nathorsti* and *Doryaspis lyktensis* in the C₁₇₋₁₉, B_T, B_Y and ‘132’ localities, in the Dicksonfjorden Member. A possible equivalent in the Woodfjorden area is the poorly defined Assemblage 5 (Fig. 4).

Index-taxa

Concerning the faunal divisions of the Woodfjorden area, after the pioneer works of Føyn & Heintz (1943) and Friend *et al.* (1966), it is possible to propose new assemblages (Fig. 4) and to define new index-taxa (Fig. 5). The Sigurd fjellet faunal division at the base of the formation does correspond to Assemblage 1 with two guide-fossils, *Xylaspis prima* and *Gigantaspis minima* (Figs 4 and 5E). The Kapp Kjeldsen faunal division, originally characterized by the occurrence of the genus *Gigantaspis* (Føyn & Heintz 1943; Friend *et al.* 1966), in fact equals Assemblages 2 and 3 with *Gigantaspis isachsenseni* as new guide-fossil (Fig. 5C). The Keltiefjellet faunal division, first named “Lykta division” by Føyn & Heintz (1943) and Friend *et al.* (1966), and renamed by Friend (1961; also in Blicek *et al.* 2000; Harland 1997), corresponds to Assemblages 4 and 5. The base of the division is characterized by the occurrence of *Doryaspis* sp. 1 (unpublished). *Doryaspis nathorsti* has also been reported throughout the whole division, but cannot be considered as a guide-fossil due to its presence at the top of the underlying division (Fig. 4). No pteraspidiiform has been recently collected from the Stjørdalen faunal division. The samples collected in 1969 do not contain representatives of this order. The studied samples in the Oslo collections contain only rare fragments of possibly *Doryaspis*. *Doryaspis minor* was mentioned from this division by Heintz (1960) (Fig. 4). However, this species is the most poorly known of the

North-west (Woodfjorden) – south-east (Austfjorden-Dicksonfjorden) correlation

The basal layers of the Wood Bay Formation in both areas show a specific regional problem. It is clear from recent geological studies that the basal part of the Wood Bay Formation does not exist in the Dicksonfjorden-Austfjorden area (Blomeier *et al.* 2003a: 160). It would be interesting to investigate the basal parts of the Wood Bay Formation where it unconformably overlies the Precambrian basement in the area between Dicksonfjorden and Kongsfjorden (W. Dallmann pers. comm. 2007). Furthermore, the lower Wood Bay Formation in the north-west (Woodfjorden area: lower Dicksonfjorden Member, Fig. 3/Sigurdfjellet faunal division) does not show any species in common with the Austfjorden Member in the south-east (Dicksonfjorden-Austfjorden area) (Fig. 4). However, the co-occurrence of the genera *Gigantaspis* and *Doryaspis* suggests that part of the Austfjorden Member (Assemblage 6) is an equivalent of the Sigurdfjellet and Kapp Kjeldsen faunal divisions (Assemblages 1 to 3) (Fig. 4). This correlation is plausible because the genus *Gigantaspis* is restricted to these assemblages in both areas. The first common species, *Doryaspis* sp. 1 (unpublished), is found at the base of the Keltiefjellet faunal division (Woodfjorden) and the Dicksonfjorden Member (Dicksonfjorden-Austfjorden) (Fig. 4). So, both levels can be considered as ichthyostratigraphically equivalent. As already said, the upper part of the Wood Bay Formation remains poorly dated because of a scarcity of pteraspidiiforms, and as discussed here above, a revision is required for the placoderm fauna, which is well known in the upper parts of the Wood Bay Formation in both areas of the ALB.

DISCUSSION

The new palaeontological information, as compared to the lithostratigraphy of the ALB sediments, shows that lithological variations are related to faunal variations. The upper part of the Dicksonfjorden Member may be followed all over the ALB, where the conditions of deposition are homogeneous. The pteraspidiiform fauna present in these levels is the same in both parts of the ALB and composed of *Doryaspis* sp. 1 (unpublished) and *Doryaspis nathorsti*. This may mean that the environment and conditions of life were the same. However, contrary to its upper part, the lower part of the Wood Bay Formation present different lithologies in both areas of the ALB: the Austfjorden Member in the south-east area and the Dicksonfjorden Member in the north-west area. They are both composed of sandstones, but their colour differs and the Austfjorden Member contains feldspars and micas (Friend & Moody-Stuart 1972). So, geological information would suggest that these elements come from two distinct sources: from the far south-east for the Dicksonfjorden-Austfjorden area and from the south-east for the other part of the ALB (Friend & Moody-Stuart 1972; Harland 1997: fig. 16.7D). The pteraspidiiform fauna is composed of the same genera in these layers, but with different species in the

Woodfjorden and the Dicksonfjorden-Austfjorden areas. Finally, the earlier phase of sedimentation in the ALB may be interpreted either as two different basins or as one basin with two areas with differential sedimentation. Additionally, the Austfjorden Member deposits laterally interfinger with the red beds of the lower Dicksonfjorden Member in the north-west (Woodfjorden area, southern André Land), while they lie with a transitional boundary below the Dicksonfjorden Member in the south-east (Dickson Land) (Dallmann *et al.* 2002; Blomeier *et al.* 2003a: 160). This is certainly a major cause for difficulties in the lateral biostratigraphic correlations between both areas.

In a global context for the Arctic region, Blicek (1984) proposed a biostratigraphic scheme with a “lower *Doryaspis* zone with *Gigantaspis* and *Zascinaspis*, only known in Spitsbergen” (biozone 1d of Blicek 1984: 141 and fig. 75), and an “upper *Doryaspis* zone, also only known in Spitsbergen” (Blicek 1984: biozone 1e). Considering our new data, this biozonation can be revised and completed for Spitsbergen. The lower *Doryaspis* biozone corresponds to the distribution of the genus *Gigantaspis*, as it was originally proposed by Blicek (1984). However, the genus *Zascinaspis* is not represented in this biozone because *Z. laticephala* Blicek & Goujet, 1983 has been re-assigned to *Gigantaspis* (Pernègre 2004c; Pernègre & Goujet 2007). The lower *Doryaspis* biozone is equivalent to Assemblages 1, 2 and 3 in the Woodfjorden area (Sigurdfjellet + Kapp Kjeldsen faunal divisions) and to Assemblage 6 in the Dicksonfjorden-Austfjorden area (Austfjorden Member). The base of the upper *Doryaspis* biozone corresponds to the appearance of *Doryaspis* sp. 1 (unpublished). *Doryaspis nathorsti* which appears in the lower *Doryaspis* biozone has its acme in the upper *Doryaspis* biozone. It corresponds to Assemblages 4 and 5 in the Woodfjorden area (Keltiefjellet faunal division) and Assemblages 7 and 8 in the Dicksonfjorden-Austfjorden area (Dicksonfjorden Member) (Fig. 4).

COMPARISON WITH RUSSIAN ARCTIC ARCHIPELAGOS

The comparisons and correlations are mainly based on the pteraspidiiform fauna, and among the Arctic regions, they are limited to the Russian archipelagos, because these are the only known regions which present a pteraspidiiform fauna similar to the one found in the Pragian-Emsian of Spitsbergen.

Novaya Zemlya

It is the largest archipelago of the Russian Arctic (Fig. 1A), located at the east of the Barents Sea, between 70.5° and 77°, and in continuity with the Ural Mountains. It is composed of two main islands, and the studied interval comes from the northern island. The first Devonian fish remains were found by V. Bondarev in 1973, in the basal Devonian layers of the northern island (the sediments are described as “terrigenous rocks” in Mark-Kurik & Novitskaya 1977). They were found in the Schmidt Peninsula of the Russkaya Gavan Bay. The first work on the fauna (Mark-Kurik & Novitskaya 1977) was restricted to generic comparisons with

Spitsbergen. The authors mention a “large Pteraspidiiforme similar to *Gigantaspis*” and another “similar to the aberrant Pteraspidiiforme from the Lykta and Stjørdalen Formations” [sic], that is, *Doryaspis* (Mark-Kurik & Novitskaya 1977: 149). This preliminary work is taken into account by Novitskaya (1986): “Pteraspidiiformes indet. were discovered in the lower Devonian deposits of the Northern island of Novaya Zemlya. They come from the base of the Devonian section to the East of the Russkaya Gavan Bay. The material consists of central plates, belonging mostly to a small form that resembles *Grumantaspis* Obruchev from the Wood Bay Series, Spitsbergen. Together with the above form exists a large form with characters showing similarity to *Gigantaspis* N. Heintz from the same series of Spitsbergen (Mark-Kurik & Novitskaya 1977)” (translated by E. Mark-Kurik, pers. comm. to VNP) (*Grumantaspis* is a synonym of *Doryaspis*: Blicek 1984: 183; Pernègre 2002). The Pteraspidiiformes are found in the Veselye Mounts Formation which overlies the Kanyon Creek Formation, which in turn is overlaid by the Restovskoe Lake Formation (Cherkesova 1988: 674, fig. 2). Until now, there is no more detailed information on the pteraspidiiform fauna from Novaya Zemlya (note that these pteraspidiiform remains are not taken into consideration by Novitskaya 2004). However, comparisons with Spitsbergen are possible: a *Doryaspis*-*Gigantaspis* assemblage is only found in the lower Wood Bay Formation, so that the Veselye Mounts Formation can be considered as biostratigraphically equivalent to the Austfjorden Member and the Sigurdfjellet-Kapp Kjeldsen divisions. Hence, the Veselye Mounts Formation is considered here as Pragian in age (Fig. 6).

Severnaya Zemlya

This archipelago is located at the east of the Kara Sea, north of the Taimyr Peninsula, between 78° and 81°, and comprises three main islands (Fig. 1A). The most important one is October Revolution Island, which has a good pteraspidiiform fauna. This material is found in the Silurian-Devonian layers sampled along Recent river beds. The fauna has been mentioned by Karatajūtė-Talimaa (1983) who proposed preliminary determinations at the generic level, and identified *Gigantaspis*, *Miltaspis* and *Doryaspis*? in the Spokojnaya Formation. This enables a correlation with the Wood Bay Formation (Karatajūtė-Talimaa 1983: 25). Recently, Blicek *et al.* (2002; preliminary version by Karatajūtė-Talimaa & Blicek 1999), in a review of the Silurian-Devonian heterostracans from Severnaya Zemlya, introduced a revised determination of the genera, i.e. *Gigantaspis*?, *Miltaspis*?, and “... Protopteraspidiidae gen. et sp. 1 with a *Doryaspis*-like ornamentation of tuberculated dentine ridges (previously designated as *Doryaspis* sp. nov) [...]” (Blicek *et al.* 2002: 812 and fig. 4). These authors propose an equivalence between the base of the Wood Bay Formation and the base of the Spokojnaya Formation. The new biostratigraphical data from the Wood Bay Formation leads us to refine this correlation. *Doryaspis* and *Gigantaspis* being only associated in the lower Wood Bay

Formation, it is proposed here to correlate the Spokojnaya Formation with the Austfjorden Member and the Sigurdfjellet-Kapp Kjeldsen divisions (Fig. 6). However, the occurrence of *Miltaspis*? in the Russian archipelago is problematic. This genus was defined by Blicek (1981) in the Ben Nevis Formation of Spitsbergen, below the Wood Bay Formation. Other Protopteraspidiidae [*sensu* Blicek 1984; “Protopteraspidiidae” of Pernègre & Elliott 2008] associated with Cyathaspidiiformes in Severnaya Zemlya do not correspond to the fauna of the Wood Bay Formation, thus giving uncertainty over the correlation of the base of the Spokojnaya Formation with the base of the Wood Bay Formation (Blicek *et al.* 2002: fig. 5). In conclusion, the Spokojnaya Formation can be correlated with the lower Wood Bay Formation, but its base may be older. The discussion is presently limited due to the lack of precisely known vertical distributions of the various genera in Severnaya Zemlya. The Rusanov Formation, above the Spokojnaya Formation, does not contain Pteraspidiiformes, so its possible correlation with the upper part of the Wood Bay Formation is still uncertain (Blicek *et al.* 2002).

CONCLUSION

This revised ichthyostratigraphy of the Wood Bay Formation leads us to propose a new faunal characterization based upon pteraspidiiform assemblages. It helps in revising correlations of lithostratigraphic units throughout the Andrée Land Block. However, the base of the Austfjorden Member in the Dicksonfjorden-Austfjorden area (Dickson Land) still remains undated, as well as the top of the formation which does not contain pteraspidiiforms. Correlation with other circum-Arctic regions are only made with the Russian Arctic archipelagos, which show faunal similarities to Spitsbergen. Other regions of the Old Red Sandstone Continent contain Pragian-Emsian Pteraspidiiformes, but without any taxa in common (Karatajūtė-Talimaa 1989). Some regions such as the Canadian Arctic have been correlated only with older formations in Spitsbergen (e.g., the Red Bay Group: Dineley & Loeffler 1976; Elliott 1984; Blicek *et al.* 1987, 2002). Completion and revision of the Silurian-Devonian fauna from the Russian Arctic would probably lead to refinement of the correlation with Spitsbergen. Moreover a complementary work including revision and biostratigraphy of the placoderm fauna from the Wood Bay Formation would surely lead to enlarge the circum-Arctic biostratigraphic potential of the Early Devonian succession of Spitsbergen. All these results show that, in Pragian-Emsian time, Spitsbergen, Novaya Zemlya and Severnaya Zemlya were elements of what has been called the Arctic Province of the Old Red Sandstone Continent by Blicek & Janvier (1999: fig. 9.14), a conclusion which is also drawn for Spitsbergen, Severnaya Zemlya, Chukotka and the North-West Territories of Canada in Lochkovian time (Mark-Kurik *et al.* 2013).

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