The Downtonian and Devonian vertebrates of Spitsbergen. XV*. New Heterostracans from the Lower Devonian Red Bay Group, northern Spitsbergen

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A new vertebrate fauna consisting of two new species of heterostracans (jawless vertebrates), *Anglaspis gjelsviki* (Cyathaspididae) and *Protopteraspis micra* (Pteraspididae), is described from the Wulffberget Member of the Red Bay Conglomerate Formation, northern Spitsbergen. This is the oldest known vertebrate fauna of typical Early Devonian age on Spitsbergen. The discovery of this vertebrate fauna improves the distribution and diversity of early vertebrates in the Red Bay Group.

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Introduction

The Lower Devonian Red Bay Group is the lowermost vertebrate-bearing unit of the Devonian "Old Red Sandstone" deposits of Spitsbergen. The Red Bay Group overlies the older Siktefjellet Group with an angular unconformity and is divided into four formations: the Red Bay Conglomerate Formation, the Andréebreen Formation, the Frænkelryggen Formation, and the Ben Nevis Formation (Fig. 1). The Red Bay Conglomerate Formation is further separated into three members, (from bottom to top) the Wulffberget Member, the Rabotdalen Member, and the Princesse Alicefjellet Member.

Thirty vertebrate-bearing horizons have previously been recognised in the Red Bay Group (Blieck & Heintz 1979), with the oldest being the "*Psammosteus*" horizon. In the original interpretation by Kiær & Heintz (1935), this horizon is located at the base of the Frænkelryggen Formation. However, based on a re-examination of the data, Gjelsvik & Ilyes (1991) suggested that the "*Psammosteus*" horizon is actually located in the yellow-green sandstones of the upper part of the Andréebreen Formation. Gjelsvik & Ilyes did not investigate the actual locality but re-interpreted the original field observations in relation to Gee's 1966 map.

The oldest vertebrates from the "Old Red" deposits of Spitsbergen prior to this study were reported by Gjelsvik & Ilyes (1991), who regarded most of their vertebrate localities to belong to the Andréebreen Formation. Some scattered fragments of primitive spore plants and ostracods have been found in the Rabotdalen Member (Murašov & Mokin 1979), but no vertebrates have been reported from below the Andréebreen Formation until now. The new occurrence of heterostracans, both cyathaspidids and pteraspidids, in the Wulffberget Member of the Red Bay Conglomerate is therefore significant. The description of two new heterostracans increases their diversity and stratigraphical distribution in the Red Bay Group.

One of the authors (Y. O.) recently also found vertebrates in a limestone conglomerate assigned to Red Bay Conglomerate Formation in the western end of Richardvatnet, Spitsbergen. No further studies have, however, been carried out on the material.

* *Correction*. There has been an error in the numbering of the previous paper in the series "The Downtonian and Devonian vertebrates of Spitsbergen". Blieck A. & N. Heintz's "The Cyathaspids of the Red Bay Group (Lower Devonian) of Spitsbergen" (*Polar Res. 1 n.s.*, 1983, pp. 49–74) should have been XIV of the series and not XIII. N. Heintz's "The theolodont *Sigurdia lata* n.g., n.sp. from the Lower Devonian at Sigurdfjellet, Spitsbergen" (*Norsk Polarinst. Årbok 1970*, pp. 112–116) was number XIII. The current paper is therefore number XV in the series (a complete list of the previous publications in the series is found on pages 41–42).

GROUP	Formation	Member	Lithology
RED BAY	Ben Nevis 900 m		grey, micaceous sandstone
	Frænkelryggen 600 m		alternating red and green sand/siltstone
	Andréebreen >200 m		grey-green, yellow-grey sand/siltstone, basal grit
	Red Bay Conglomerate 700 m	Princesse Alicefjellet 300 m	matrix supported, quartz chip conglomerate
		Rabotdalen 200 m	grey-green, in lower part multicoloured sandstone
		Wulffberget 200 m	coarse, massive marble conglomerate
	Unconformity		
SIKTE-FJELLET	Siktefjellet Sandstone 350 m		grey-green sand/siltstone
	Lilljeborgfjellet Conglomerate 400 m		massive, polymict conglomerate

Fig. 1. Stratigraphy and lithology of the Red Bay Group and the Siktefjellet Group in northern Spitsbergen (from Gjelsvik & Ilyes 1991).

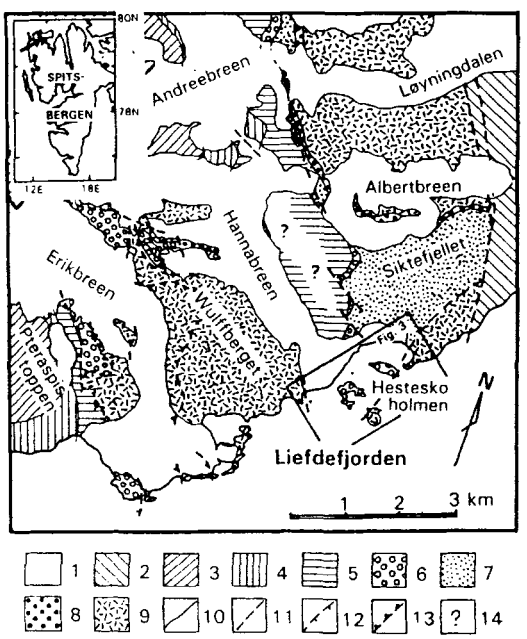

Fig. 2. Map showing the new Early Devonian vertebrate locality on Hesteskoholmen, northern Spitsbergen. Boxed area depicts area shown on Fig. 3. Symbols: 1, glacier and moraine; 2, Wood Bay Fm.; 3, Ben Nevis Fm. (Red Bay Gr.); 4, Frænkelryggen Fm. (Red Bay Gr.); 5, Andréebreen Fm. (Red Bay Gr.); 6, Wulffberget Mbr. (Red Bay Gr.); 7, Siktefjellet Sandstone; 8, Lilljeborgfjellet Conglomerate; 9, phyllite and marble; 10, boundaries; 11, steep faults; 12, fault with dip; 13, thrusts; 14, covered by scree.

Material and methods

The fossil material described here comes from one locality on Hesteskoholmen, a small island located in the northwestern part of Liefdefjorden (Figs. 2 and 3). The material has been collected in situ in the stratigraphic section. The cyathaspidids represent the majority of the vertebrates found at this locality.

The specimens are preserved in a tough micaceous sandstone that can be prepared mechanically. The measurements employed follow those used by Blieck & Heintz (1983) for cyathaspidids (Table 1), and Blieck (1984) for pteraspidids (Table 2). The specimens are deposited in the collections of the Paleontologisk Museum, Oslo, and bear their catalog numbers (prefixed PMO).

Geological setting

The new vertebrate-bearing unit is located in the Wulffberget Member of the Red Bay Conglomerate. It is a red sandstone bed interbedded in a less stratified, coarse, and massive marble-dominated conglomerate (Fig. 4). The conglomerate is of typical Wulffberget Member type, which forms the whole of the western part of the

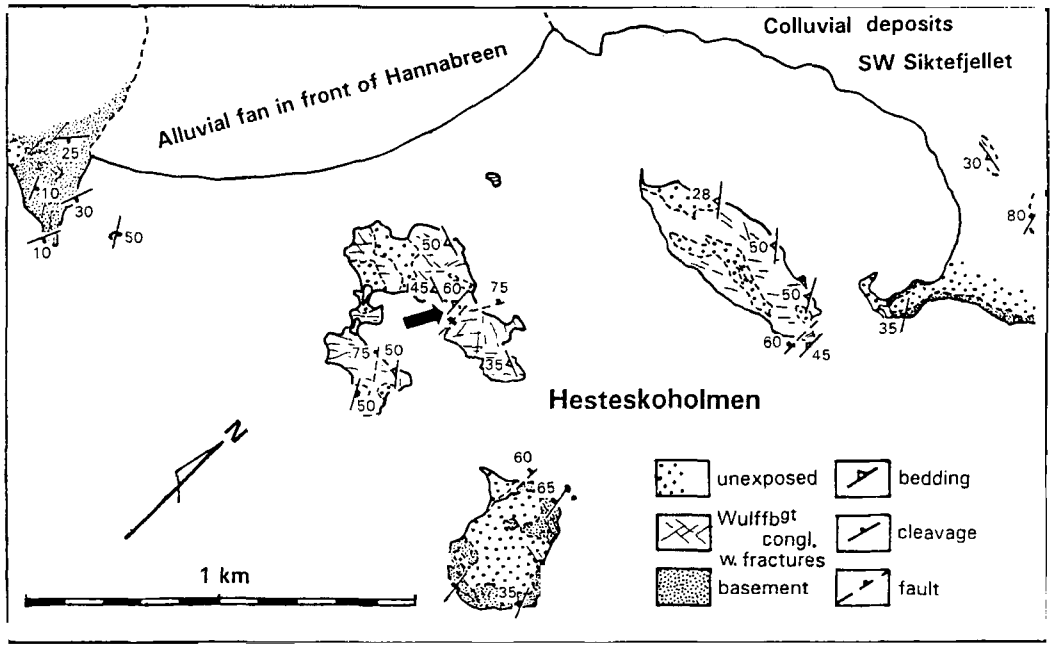

Fig. 3. Local geology of Hesteskoholmen and surrounding areas. Arrow points to the new vertebrate locality

island Hesteskoholmen. The vertebrate-bearing bed is one of two sandstone beds interbedded in the conglomerate in this area, and the only one known to have vertebrates.

The vertebrate-bearing sandstone is approximately 1.5 m thick and at least 8 m in length. To the east the vertebrate-bearing unit is bounded by a local fault, and to the west an approximately 2 m thick conglomerate very rich in marble blocks occurs without a structural break.

Based on the field observations it is suggested that the vertebrate-bearing sandstone bed is a sandstone lens interbedded in the conglomerates of the Wulffberget Member.

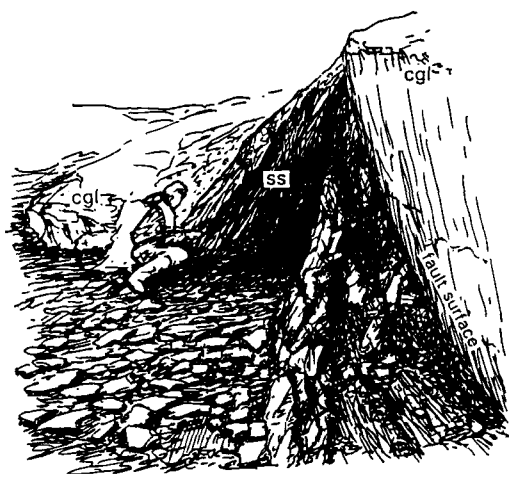

Fig. 4. The geology of the new vertebrate locality in the Wulffberget Member of the Red Bay Conglomerate Formation. Captions: sst, sandstone; cgl, conglomerate.

Systematic paleontology

Order Heterostraci Lankester, 1868
Family Cyathaspididae Kiær, 1932 (Cyathaspidae)
Genus *Anglaspis* Jaekel, 1927

Definition. – See Denison, 1964: 428.

Type species. – *Cyathaspis macculloughi* Woodward, 1891.

Other species. – *A. macculloughi* (Woodward, 1891) type species, *A. insignis* Wills (1936), *A. heintzi* Blieck & Heintz (1983), *A. elongata* Blieck & Heintz (1983), *A. expatriata* Denison (1964).

Anglaspis gjelsviki *n. sp.*

Figs. 5, 6 and 7.

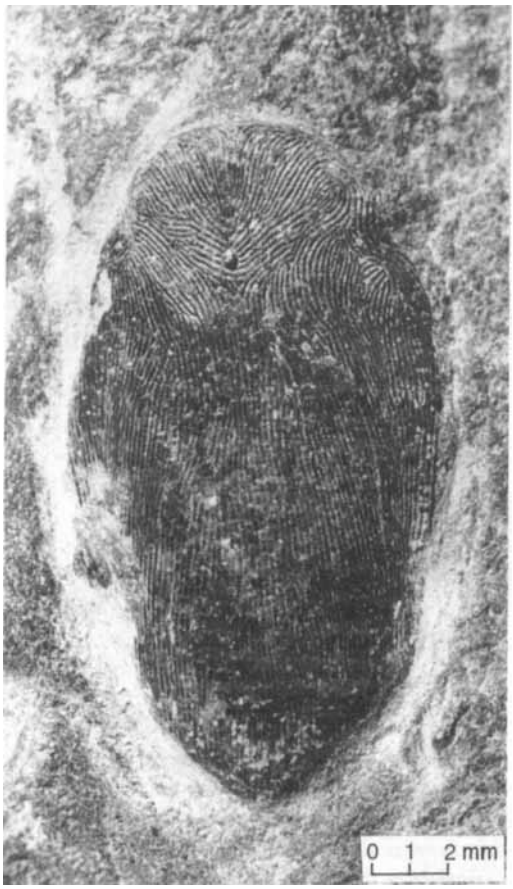

Fig. 5. Anglaspis gjelsviki n. sp. Dorsal view of holotype (dorsal shield), PMO 141.565, 4.5 ×.

Etymology. – Named after Tore Gjelsvik for his work on the Lower Devonian stratigraphy of Spitsbergen.

Holotype. – Dorsal shield PMO 141.565.

Paratypes. – Dorsal shields PMO 141.566–141.575; ventral shields PMO 141.576, PMO 141.577; branchial plate PMO 141.578; scales PMO 141.579–141.582. All from the same locality in the Wulffberget Member of the Red Bay Conglomerate Formation.

Locus typicus and stratum typicum. – Hesteskoholmen; Wulffberget Member of the Red Bay Conglomerate Formation.

Diagnosis. – A species of *Anglaspis* with finer ornamentation (5–6 dentine ridges per mm) than all other species of this genus, and distinctive morphology of the dorsal shield.

Measurements. – Table 1.

Description. – The dorsal shield is narrow and gently domed, with a prominent pineal macula. The lateral epitega form brims; shield constricted at the branchial openings. Branchial plate long with a sharp lateral angulation. Ornamentation of fine dentine ridges, 5–6/mm; sharply crested anteriorly and laterally, round crested on remainder of shield. Lateral-line sensory canal system

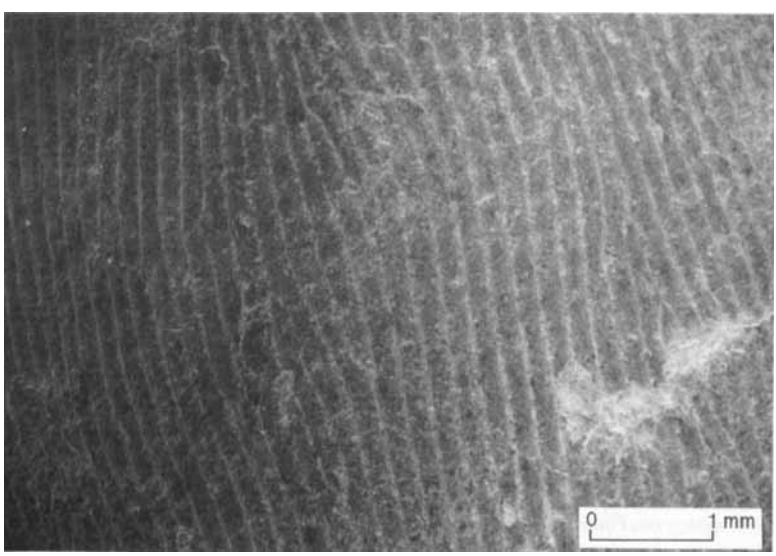

Fig. 6. Anglaspis gjelsviki n. sp. PMO 141.574 SEM micrograph showing detail of ornamentation on mid part of dorsal shield, 15 ×.

Table 1. Measurements (in mm) for *Anglaspis gjelsviki* n. sp. All measurements taken on dorsal shield except for length and width of ventral shield

Orbital width: 7–10 (n = 9)
Orbital length: 3–5 (n = 9)
Total width: 10–13 (n = 9)
Total length: 18–22 (n = 9)
Pineal length: 4–5 (n = 9)
Postbranchial length: 4–6 (n = 9)
Width ventral shield: 10–12 (n = 3)
Length ventral shield: 18–20 (n = 3)
Dentine ridges/mm: 5–6 (n = 9+)

unknown (the preservation of the shields makes it impossible to trace the lateral-line canal system). Ventral shield is gently arched, almost flat, anteriorly and strongly arched posteriorly.

Discussion. – This species is very similar to *Anglaspis insignis* in size. The two forms differ, however, in the overall morphology of the dorsal shield. *Anglaspis gjelsviki* is narrower and the postbranchial length of the dorsal shield is greater than in *A. insignis*. This makes the posterior part of the dorsal shield more pointed in *A. gjelsviki* n sp. than in *A. insignis*. There is also a noticeable difference in the coarseness of the dentine ridges on the central part of the dorsal shield between the two forms, which is a very important taxonomic difference. *Anglaspis insignis* have the coarser ornamentation of the two, with 3–4 ridges per mm compared to 5–6 per mm in this species. Denison (1964) noted, however, that the coarseness of the dentine ridges varies between 3.5 and 5 ridges per mm centrally in *A. insignis*. A study of the type material and other material of *A. insignis* in the collections of the Paleontologisk Museum, Oslo, concludes that the coarseness varies only between 3 and 4 ridges per mm, just as stated by Blieck & Heintz (1983).

The new form shows a very small individual variation in the coarseness of the dentine ridges, as do the other species of the genus *Anglaspis*. The study of the type material suggests that the new form is a valid species, which can be separated from *A. insignis* by its noticeably finer ornamentation and distinctive morphology of the dorsal shield.

Fig. 7. Anglaspis gjelsviki n. sp. Drawing of dorsal view of dorsal shield PMO 141.565, holotype. Scale bar = 5 mm; Abbreviations: orb, orbit; bro, branchial opening.

Family Pteraspididae Claypole, 1885
Subfamily Pteraspidinae Claypole, 1885
Genus *Protopteraspis* Leriche, 1924

Definition. – See Elliot & Dineley, 1983; 478.

Type species. – *Protopteraspis gosseleti* Leriche, 1924.

Other species. – *P. aquilonia* Blieck (1981), *P?. arctica* Elliot & Dineley (1983), *P?. corniga* Elliott & Dineley (1983), *P. leathensis* (White, 1935), *P. primaeva* Kiær (1928), *P. pygmaea* Elliott & Dineley (1983), *P. sartokia* Elliot & Dinely (1983), *P. silikiokia* Elliott & Dineley (1983), *P. vogti* Kiær (1928), *P. whitei* (Denison, 1955).

Protopteraspis micra *n. sp.*

Figs. 8 and 9.

Etymology. – Greek: *μἄκρός, ἀ, ὀν*, small, referring to the very small size of members of this species.

Holotype. – Dorsal shield PMO 141.583–141.584 (part and counterpart).

Paratype. – Dorsal shield PMO 141.585. From the same locality as the holotype.

Locus typicus and stratum typicum. – Hesteskoholmen; Wulffberget Member of the Red Bay Conglomerate Formation.

Fig. 8. Protopteraspis micra n. sp. Dorsal view of holotype (dorsal shield). PMO 141.583. 2.7×.

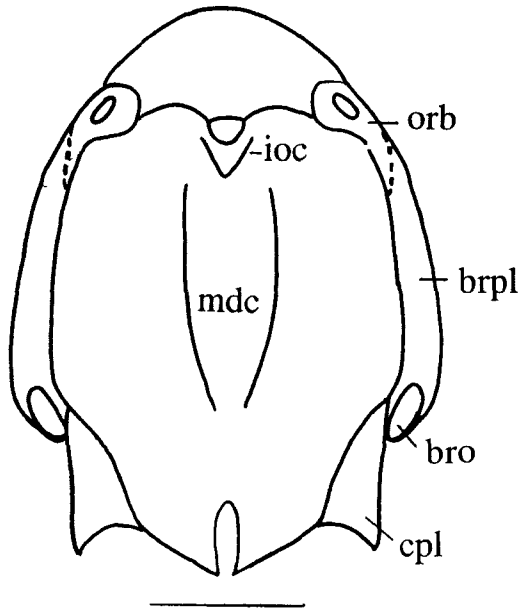

Fig. 9. Reconstruction of *Protopteraspis micra* n. sp. Dorsal view of dorsal shield. Scale bar = 7 mm; Abbreviations: orb, orbital plate; bro, branchial opening; brpl, branchial plate; cpl, cornual plate; ioc, inter-orbital canal; mdc, median dorsal canal.

Diagnosis. – Small protopteraspid with short, broad, and moderately arched dorsal shield and bluntly rounded rostral plate. Orbital plate small, and widely separated from small pineal plate. Branchial plate long and curved, expanding posteriorly to branchial opening. Branchial duct opening dorsally well in advance of postero-lateral corner of dorsal shield. Cornual plate small and subtriangular with blunt postero-lateral point. Ornamentation of fine, sharply crested, dentine ridges with crenulated lateral margins, 8–9/mm.

Measurements. – See Table 2.

Description. – The dorsal disc is oval and gently domed. Rostral plate broad, short, and bluntly rounded; subrostral area not preserved. Orbital plate small; posterior extension unknown. Orbital plates extend only a short distance medially towards the pineal plate. Pineal plate small and subrounded. Branchial plate long, and forming much of the lateral margin of the dorsal shield; it is narrow anteriorly, but expands slightly posteriorly and reaches its maximum width at the posteriorly situated branchial opening. The branchial duct opens dorsally well in advance of the postero-lateral corner of the dorsal shield. Cor-

Table 2. Measurements (in mm) for *Protopteraspis micra* n. sp. ( ) indicates estimated values. All measurements taken on dorsal shield. n = measured specimens.

Length dorsal shield: 25–28 (n = 2)
Width dorsal shield: 18–21 (n = 2)
Length dorsal disc: 19–23 (n = 2)
Width dorsal disc: 15–(18) (n = 2)
Length rostral plate: 5–6 (n = 2)
Width rostral plate: 9–12 (n = 2)
Length branchial plate: 12 (n = 1)
Length cornual plate: 5 (n = 1)
Width cornual plate: 2 (n = 1)
Length pineal plate: 1.02 (n = 1)
Width pineal plate: 1 (n = 1)
Length orbital plate: ?
Length dorsal spine: ?
Height dorsal spine: ?
Dentine ridges/mm: 8–9 (n = 2)

nual plate small and subtriangular, with blunt postero-lateral point. Dorsal spine poorly preserved, but appears to be stout, and laterally compressed.

The lateral-line sensory canal system is incompletely known. The medial dorsal canals diverge and terminate before reaching the inter-orbital canal. The inter-orbital canal forms a "V" shaped loop on the dorsal disc. Ornamentation of fine, sharply crested, dentine ridges with crenulated lateral margins, 8–9/mm. We have decided not to make SEM micrographs of the ornamentation as it would mean the destruction of one of the two existing specimens of this species.

No specimen of the ventral shield of this species is known.

Discussion. – The important taxonomic characters preserved on the dorsal shield indicate that this new form is undoubtedly a representative of the genus *Protopteraspis*. The morphology of the pineal-orbital area and the lateral-line sensory canal system show typical protopteraspid pattern. The pineal plate is widely separated from the orbital plates, and the medial dorsal canals diverge and do not connect with the inter-orbital canal. The inter-orbital canal forms the "V" shaped loop on the dorsal disc typical for the protopteraspids (Elliott & Dineley 1983).

The previously described protopteraspids from Spitsbergen are shown in Fig. 10. The size and morphology of *Protopteraspis micra* clearly separate it from *P. vogti* and *P. aquilonia*. The overall morphology of the new species is quite similar to Blieck's (1981) reconstruction of *P. primaeva*. A comparison of the new species with the type material of *P. primaeva* shows that the two forms differ in size, *P. micra* being noticeably smaller. There is also a morphological difference between these two species found in the shape of the connection between the rostral plate and the dorsal disc, and in the shape of the branchial plate and branchial opening. Other important morphological differences can be found in the shape of the posterior part of the dorsal disc and cornual plate. The noticeable and important morpho-

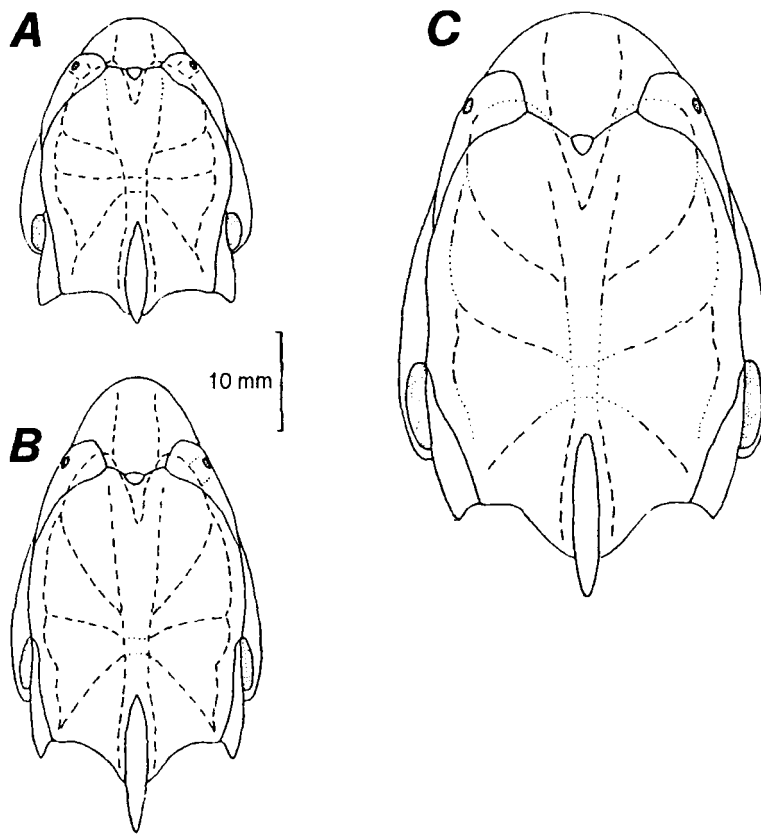

Fig. 10. Previously described protopteraspids from Spitsbergen. All from the Red Bay Group. Scale bar = 10 mm (from Blieck 1984). A = *Protopteraspis primaeva*, B = *P. aquilonia*, C = *P. vogti*.

logical differences between the two forms indicate for us that *P. micra* is a species different from *P. primaeva*. Intraspecific variability is known in the pteraspidids, e.g. *Protopteraspis gosseleti* and *Pteraspis rostrata* (A. Blieck pers. commun.), but we feel that the difference in morphology between *Protopteraspis micra* and *P. primaeva* is too great to indicate intraspecific variability. We feel, however, that the two species are closely related.

Invertebrates and palaeoecology

In addition to the vertebrates, the rock samples contain bivalves (Fig. 11). Their preservation is extremely poor, and the bivalves appear only as molds and casts in the matrix. The largest specimens have a length around 15 mm and width around 11 mm. No important taxonomic features are preserved, making their determination difficult. The external morphology of the bivalves suggests that all the individuals belong to *Modiomorpha?* sp. This genus is common in Upper Silurian, Lower and Middle Devonian sand- and siltstones (C. Babin pers. comm.).

This species appears to be a restricted shelly invertebrate fauna present in the vertebrate-bearing strata. No brackish water indicators or normal marine indicators have been found in the studied samples. However, due to a lack of an accurate sedimentologic log it is not possible to determine the depositional environment at the present time.

All the studied bivalves are disarticulated, and only one of the cyathaspidid specimens has articulated dorsal and ventral shields (PMO 141.575). The studied fossil material shows, however, no signs of abrasion. The composition of the fossil material ranges from minute fragments to complete specimens of variable size, indicating that there has been little or no size sorting of the fossils. The fossil material has no preferred orientation. The data suggest that the origin of the fossil material was in or close to the area of deposition, and that the disarticulation of the material was in situ by current action and biogenic activity.

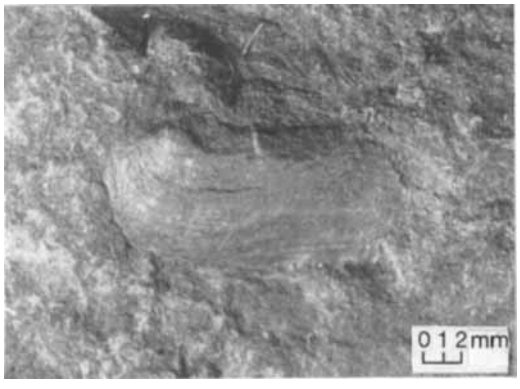

Fig. 11. Unidentified bivalve, PMO 141.586, 4.5×.

Age and significance of the vertebrate fauna

Early Devonian vertebrate faunas of similar overall composition to that found in the Wulffberget Member of the Red Bay Conglomerate have previously been described from the Frænkelryggen and Ben Nevis Formations (Blieck et al. 1987). The Wulffberget Member fauna has, however, no species in common with the other known vertebrate faunas of the Red Bay Group, and their similarity is only at the generic level.

An accurate dating of the Wulffberget Member has been difficult to obtain because the strata contain no characteristic microfossils useful in dating. The occurrence of *Protopteraspis* and *Anglaspis*, two typical Early Devonian genera in Spitsbergen, suggests an Early Devonian age for these strata. An Early Devonian age (Lochkovian) for the lower parts of the Red Bay Group was also suggested by Murašov & Mokin (1979) and Blieck et al. (1987). Murašov & Mokin reported (but did not figure) the occurrence of typical Early Devonian plant fragments from the Rabotdalen Member of the Red Bay Conglomerate. This substantiates the Early Devonian age on the base of this formation suggested by the new vertebrates.

Murašov & Mokin (1979) also reported Early Devonian plants from the base of the type strata of the Siktefjellet Group on the northern side of Liefdefjorden. The new data indicate that the Silurian/Devonian boundary on Spitsbergen is located somewhere below the Red Bay Group, maybe in the Siktefjellet Group. New field evidence suggests however, that the Murašov & Mokin plant locality is actually located in the Wulffberget Conglomerate, making their age dating somewhat dubious.

The correlation of the Devonian of Spitsbergen to the "classic" Anglo-Welsh area has been, and still is, quite problematic. Blieck et al. (1987) correlated the "*Psammosteus*" horizon of Spitsbergen with the Anglo-Welsh *pococki* zone. The

genera *Protopteraspis* and *Anglaspis* occur together in the Anglo-Welsh *symondsi* zone, but *Anglaspis* is not registered in the *pococki* zone (Blieck & Heintz 1979).

Based on this information it is tentatively suggested that the Wulffberget Member at the base of the Red Bay Conglomerate, and then also the base of the Red Bay Group, might also correlate with the Anglo-Welsh *pococki* zone. This indicates that the stratigraphic section between the base of the Red Bay Conglomerate, where the new fauna comes from, and the "*Psammosteus*" horizon is fairly close in time, and that the extensive lithostratigraphic separation of the two faunas is due to a high sedimentation rate.

So far no microvertebrates (thelodonts) or spores have been found in the samples from the Wulffberget Member to support this hypothesis at the present time. Only further collecting can test this hypothesis.

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