The Downtonian and Devonian vertebrates of Spitsbergen. XIII

The Cyathaspids of the Red Bay Group (Lower Devonian) of Spitsbergen

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Description and validation of the cyathaspids (Vertebrata, Heterostraci) from the Red Bay Group of Spitsbergen, previously introduced and/or described by Kiær (1930, 1932) and Kiær & A. Heinz (1935). The following species are defined: Dinaspidella robusta; Irregularaspis hoeli, I. mirabilis n. sp.; Poraspis polaris, P. brevis, P. rostrata; Homalaspidella nitida; Anglaspis insignis, A. heintzi n. sp., A. elongata n. sp.; Ctenaspis dentata and C. cancellata. The biostratigraphy of these taxa is briefly reviewed. The Spitsbergen cyathaspids are mainly compared with the Canadian Arctic forms, for one of which the new name Dinaspidella elizabethae is introduced. □ Spitsbergen, Lower Devonian, Cyathaspidiformes (Agnatha), systematic revision, new taxa.

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Since the preliminary reports of Kiær (1930, 1932), the Cyathaspidiformes from the Red Bay Group of Spitsbergen have been studied in one monograph by Kiær & Heintz (1935). More recent works by Denison (1964) and Dineley & Loeffler (1976) have shown the necessity of precise definitions of the yet undescribed species. Not to throng the nomenclature with useless names, we propose to validate several of the species names introduced by Kiær (1932) and to give a review of the representatives of the family Poraspididae.

All the present material comes from the Devonian outcrops east of Raudfjorden in northwest Spitsbergen and thus belongs to the Upper Red Bay Group (i.e. from Frænkelryggen and/or Ben Nevis; for localities see Kiær & A. Heintz 1935:11–13; Blieck & N. Heintz 1979, fig. 4). Among the heterostracan assemblages from these localities, the cyathaspids represent the majority both of the individuals and the species. For example, in the Vogti horizon of the Ben Nevis Formation, we find six species of cyathaspids of a total of 13 species of heterostracans (Goujet & Blieck 1977) and about half of all individuals are cyathaspids.

Measurements and indexes used on the dorsal and ventral shields are presented in Fig. 1.

Abbreviations

BMNH – British Museum (Natural History), London
FMNH – Field Museum of Natural History, Chicago

ICZN – International Code of Zoological Nomenclature (Stoll et al. 1964)
MNHN – Muséum National d'Histoire Naturelle, Paris
NHRK – Naturhistoriska Riksmuseet, Stockholm
NMC – National Museums of Canada, Ottawa
PMO – Paleontologisk museum, Oslo
SMC – Sedgwick Museum, Cambridge

Abbreviations used on the figures and in the tables

B, Branchial plate
br, break
br.n, branchial notch
ci, cloaca
D, dorsal shield
D(r), dorsal shield (rostal part)
laO, orbital width of D
laT, total width of D
laV, total length of V
lc, lateral canal of trunk (external pores)
lc.c, lateral dorsal canal (external pores)
LOB, branchial length of D
LoO, orbital length of D
LoP, pineal length of D
LoT, total length of D
LoV, total length of V
LpB, postbranchial length of D
md.c, medial dorsal canal (external pores)
Or, oral cover
orb, orbit
orb.n, orbital notch
Or(m), median oral platlet
Or(1–4), lateral oral platlets
Systematics

Order Cyathaspidiformes Berg (1940: Cyathaspididae).

Definition. – See Denison, 1964: 350–351 (‘Cyathaspididae’).

Superfamily Poraspidoidea Kier (1932: tribe Poraspidae = Poraspidoidei Berg, 1940)

Definition. – See Kjær, 1932: 8 and 12.

Family Irregulareaspididae Kjær & A. Heintz (1935: Irregularaspidae)

Definition. – See Denison, 1964: 396 (‘Irregular-aspidinae’).

Type genus. – Irregulareaspis Zych, 1931.

Genus Dinaspidella Strand, 1934

Definition. – See Denison, 1964: 399.

Type species – Dinaspis robusta Kjær, 1932.

Other material referred to Dinaspidella. – cf. Dinaspidella sp. Denison (1964: 400–401, see also Dineley 1965); Dinaspidella sp. indet. Dineley & Loeffler (1976: 84–92) here named D. elizabethae nom. nov.

Dinaspidella robusta (Kjær, 1932)

(Fig. 2)

□ 1932. Dinaspis robusta n.gen. & sp. – Kjær, figs. 7–8, pl. IV, 2-3. □ 1964. Dinaspidella robusta – Denison, figs. 97C, and 136A–B. □ 1976. Dinaspidella – Dineley & Loeffler, fig. 40B.

Fig. 1. The measurements (in mm) used on the dorsal shields of cyathaspids. A. After Kjær & A. Heintz (1935: 48). B. After Denison (1964: 317). C. After the present authors (for abbreviations, see pp. 49–50).
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Measurements (in mm) and indexes of the type specimen PMO D 454.

| laO | LoO | laT | LoT | LoP | LpB | laO | laT | LoO | LoT |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 15  | 7   | 17.5| 31  | 9   | 12  | 2.14| 0.56| 0.22| 0.29|
| 0.39| 12  |

Discussion. — Denison (1964:399) and Dineley & Loeffler (1976:91) think that Dinaspida is 'not available nomenclatorially because both specific names, D. robusta and D. parvula, are nomina nuda'; however, they could have given a diagnosis for these two species. Dinaspida Strand (1934), in replacement of Dinaspis Kier (1932), is available because Dinaspis is based on a type species, D. robusta Kier, which is not a nomen nudum as there is a statement and figures (Kier 1932:18, figs. 7–8, pl. IV, 2–3) 'that purport to give characters differentiating the taxon' (ICZN art. 13a-b). However, Dinaspis parvula (Kier 1932:18) remains a nomen nudum.

The only other figured material referred to as Dinaspida is Dinaspida sp. indet. Dineley & Loeffler (1976), whose dorsal shield is longer and wider than that of D. robusta (Fig. 2).

Holotype. — Dorsal shield PMO D 454 (Fig. 2) (Kier 1932, pl. IV, 2–3).

Locus typicus. — Frøneelrøggen, 300 m a.s.l. (locality no. 4).

Stratum typicum. — Frøneelrøggen Formation, Primaeva horizon.

Paratype. — Ventral disc PMO D 3068 (Kier 1932, fig. 7) from Pteraspisfjellet (unknown horizon).

Diagnosis. — A rather small species of Dinaspida with laT = 17.5 mm and LoT = 31 mm.
the indexes of the latter fall within the maximum–minimum deviation of the indexes of the former but both taxa are well separated by their measurements. Thus we believe that *D. sp. indet.* Dineley & Loeffler is a different species, and propose the new name *Dinaspidella elizabethae* nom. nov. whose type specimen is NMC 19580 (Dineley & Loeffler 1976, pl. 11, 6).

**Genus Irregulareaspis** Zych, 1931

**Definition.**—See Denison, 1964: 401–402.

**Type species.**—*Irregulareaspis stensioi* Zych, 1931 here emended as *I. stensioei* Zych [*I. stensioi* emend. Brotzen (1936: 6) and *I. stensioi* emend. Denison (1964: 402) and Obruchev (1964: 58) are ‘unjustified emendations’ of the original spelling of the species name (ICZN art. 32 c(i) and 33)].

**Other species.**—*I. hoeli* (Kiar, 1932), *I. mirabilis* n. sp.

*Irregulareaspis hoeli* (Kiar, 1932))

(Figs. 3B, C. D. 4A, B. C.)

Kiar (1932: *Dictyaspis hoeli* n.gen. & sp. – Kiar, fig. 10, pl. V, 1–2, pl. VI, 2–3. Kiar 1958: *Irregulareaspis hoeli* (Kiar) [sic]–Stensiö, fig. 216D. Denison (1964: *Irregulareaspis hoeli* – Denison, fig. 99E. Kiar 1964: *Irregulareaspis hoeli* (Kiar) – Obruchev, fig. 18b, pl. I, 1–2, pl. II, 6. Kiar 1964. *Irregulareaspis hoeli* (Kiar) [sic]–Stensiö, fig. 121D.

**Holotype.**—Articulated specimen PMO D 474 (Fig. 4A, B) (Kiar 1932, pl. V, 1–2).

**Locus typicus.**—Ben Nevis, western plateau, 500–550 m a.s.l. (locality no. 12).

**Stratum typicum.**—Ben Nevis Formation, *Benneviaspis* horizon.

**Paratypes.**—Ventral disc PMO D 495 (Fig. 3B, C). (Kiar 1932, pl. VI, 2–3) and internal mould of dorsal shield PMO D 497 from Tunge locality (Kiar & A. Heintz 1935, fig. 1, loc. nr. 13), an equivalent of the *Benneviaspis* horizon.

**Other material.**—Dorsal shield PMO D 476 (Obruchev 1964, pl. I, 1; see also pl. I, 2 and pl. II, 6) from Ben Nevis, *Benneviaspis* horizon.

**Diagnosis.**—The dorsal shield of *I. hoeli* is narrower than that of *I. stensioei*; the pineal macula and the orbits of *I. hoeli* are more posteriorly situated than on *I. stensioei*.

**Measurements (in mm) and indexes of the type specimens PMO D 474 and PMO D 495.**

|       | laO | LoO | laT | LoT | LoP | LpB | Lao | LoV | mm   |
|-------|-----|-----|-----|-----|-----|-----|-----|-----|------|
| 15    | (9) | (19) | (37) | (12) | 12  | 16–18 | 38–40 |

**Discussion.**—The ventral discs of *Dictyaspis hoeli* Kiar (1932, fig. 10 and pl. VI, 2–3) have a shape and sensory canals which differentiate the taxon. Thus *D. hoeli* Kiar is a valid species.

Zych (1931: 83–84) has created the genus *Irregulareaspis* for *I. stensioei* Zych (1931, figs. 46–47 and photo. 5), whose type specimen has not been designated (Denison 1964: 402). The pattern of the sensory canals of *I. stensioei* is unknown (Zych 1931: 84) but the numerous and dispersed external pores of these canals on the whole outer surface of the shield (Zych 1931: 83. See also Obruchev 1964, pl. I: 2 and 5; Stensiö 1964, fig. 77) allow us to conclude that the lateral system of *I. stensioei* is fundamentally the same as that of *Dictyaspis hoeli* Kiar (1932), i.e. it forms a network. This dispersion of the external pores associated with convoluted dentine ridges leads us to include the species of *Dictyaspis* Kiar in the genus *Irregulareaspis* Zych (cf. Kiar in Zych 1931: 83, note 1; Denison 1964; Obruchev 1964; Stensiö 1964; Dineley & Loeffler 1976). Nevertheless the type species of *Irregulareaspis* is poorly known and it needs to be reviewed.

*Dictyaspis complicata* Kiar and *D. prisca* Kiar are actually *nomina nuda* (Denison 1964: 402) because the type-specimens on which Kiar (1932) based these names have not been designated nor found in the collections.

The type specimen of *I. hoeli*, PMO D 474, has a suborbital plate and a trunk-squamation (Figs. 3D and 4) of the same kind as those of *Nahaniaspis mackenziei* Dineley & Loeffler (1976) and *Dinaspidella elizabethae* nom. nov. However on *I. hoeli*, the branchial plate is rather narrow and stops just on the front edge of the postbranchial lobe of the dorsal shield, while this plate on *N. mackenziei* is relatively longer and ends at the
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Irregulareaspis mirabilis n. sp. (Kiær, manuscript) (Fig. 5).

Holotype. – Dorsal shield PMO D 210 (Fig. 5).

Locus typicus. – Ben Nevis, northern plateau, 600 m a.s.l. (locality no. 10).

Stratum typicum. – Ben Nevis Formation, Vogri horizon.

Diagnosis. – Dorsal shield longer and wider than that of I. hoeli; pineal macula more anteriorly situated than in I. hoeli; postbranchial lobes longer than those of I. hoeli.

Measurements (in mm) and indexes of the type specimen PMO D 210. –

| laT | LoT | LoP | LpB | laT | LoP | LpB |
|-----|-----|-----|-----|-----|-----|-----|
| (24) | 40 | (11) | 13 | 0.60 | 0.27 | 0.32 |

Discussion. – This specimen is undoubtedly a representative of the genus Irregulareaspis because of the network of the lateral canal system and the shape of the dorsal shield. But it is longer and wider than I. hoeli and has longer postbranchial lobes. Thus we think it represents a different species from the one which J. Kiær in an unpublished manuscript created as I. mirabilis. However, this new taxon has some characteristics in common with the type species I. stensioei, viz. the location of the pineal macula (LoP/LoT = 0.27 in both species) and a wide dorsal shield (laT/LoT = 0.60 in I. mirabilis and 0.65 in I. stensioei). But we are not sure if these taxa are co-specific because of the few data available concerning I. stensioei.

Furthermore, the ventral discs MNHN, SVD 518a–b, 526–528, 537a–b and 588 from the Vogri horizon (Blieck 1976, fig. 158, pl. X, 4: ‘I. hoeli’) are also wider than those of I. hoeli; so it seems that these specimens have to be included within I. mirabilis n. sp. and correspond to the dorsal shield PMO D 210.

Irregulareaspis sp. indet.

One dorsal shield PMO D 228 (Fig. 3A) from the Ben Nevis Formation (horizon U of Hoel’s sec-

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Fig. 4. Irregulareaspis hoeli, PMO D 474, holotype. A. Articulated specimen, dorsal view. B. Right lateral view. C. General reconstruction in right lateral view.

Fig. 5. Irregulareaspis mirabilis nov. sp., PMO D 210. Holotype, visceral face of dorsal shield.
Fig. 6. *Poraspis brevis* – new definition – dorsal shields. A. PMO D 304, holotype (Kier & A. Heintz 1935, pl. XIV). B. PMO D 1904, type of *P. subtilis* (ibid., pl. XXII). C. PMO D 1308, type of *P. intermedia* (ibid., pl. XVI). D. PMO D 293, *P. intermedia* (ibid., pl. XVII) (scale 1 cm).
tion, Blieck & N. Heintz 1979: 174), previously referred to as Dinaspidea sp., has a lateral canal system closely resembling that of Irregulareaspis hoelii and I. mirabilis n. sp. However, PMO D 228 is the longest representative of Irregulareaspis known at Spitsbergen (LoT = 48 mm), and as we do not have enough specimens to exactly know the individual variations within I. hoelii and I. mirabilis, we cannot say for the time being whether PMO D 228 is a different species or not. But we now think that it is presumably not a Dinaspidea specimen; thus restricting Dinaspidea to the Fränkelryggen Formation and Irregulareaspis to the Ben Nevis Formation, as already mentioned by Kier in 1932.

**Family PORASPIDIDAE** Kier (1932; Poraspidae)

**Definition.** – See Denison 1964: 402 (‘Poraspidae’).

**Type genus.** – *Poraspis* Kier, 1930.

**Genus Poraspis** Kier, 1930

**Definition.** – See Denison 1964: 403.

**Type species.** – *Holaspis sericeus* Lankester, 1873.

**Other species.** – *P. brevis* Kier (1932), *P. polaris* Kier (1930), *P. rostrata* Kier & A. Heintz (1935), *P. barroisi* (Leriche, 1906), *P. simplex* (Brotzen, 1933), *P. sturi* (Alth, 1874), *P. siemiredzki* (Zych, 1931) and *P. pompeckji* (Brotzen, 1933).

*Poraspis brevis* Kier, 1932

*(Fig. 6)*

Kier 1932. *Poraspis brevis* n. sp. – Kier, pl. II. □ 1935. *Poraspis brevis* n. sp. (sic) – Kier & A. Heintz, figs. 20-22, pl. XIV-XV. □ 1935. *Poraspis subtilis* n. sp. – Kier & A. Heintz, fig. 23, pls. XXI, 1 and XXII. □ 1935. *Poraspis intermedia* n. sp. – Kier & A. Heintz, pls. XVI-XVII. □ 1935. *Poraspis elongata*? – Kier & A. Heintz, pl. XXI, 2. □ 1958. *Poraspis polaris f. lata Kier* (sic) – Stensiö, fig. 167A. □ 1964. *Poraspis polaris f. lata Kier* (sic) – Stensiö, fig. 69A.

**Holotype.** – Dorsal shield PMO D 304 (Kier 1932, pl. II; Kier & A. Heintz 1935, pl. XIV).

**Locus typicus.** – Fränkelryggen, 250–350 m a.s.l. (locality no. 4).

**Stratum typicum.** – Fränkelryggen Formation, Primæva horizon.

**Other material.** – From the Ceraspis horizon up to the Anglaspis horizon (see Kier & A. Heintz 1935 for the detailed distribution of the specimens, and Table 1).

**Diagnosis.** – A very small species of *Poraspis* with LoT < 30 mm, LoP ≈ 6.5 mm and LpB ≈ 11 mm.

**Measurements.** – Table 1 and Fig. 11.

**Discussion.** – This is the smallest of the known species of *Poraspis*, coming from the upper two thirds of the Fränkelryggen Formation. The three taxa *P. brevis*, *P. subtilis* and *P. intermedia* introduced by Kier (1932) and Kier & A. Heintz (1935) must presumably be considered as three populations of a single species here reviewed as *P. brevis* Kier. There are no significant morphological differences between the known specimens of the three species of Kier & A. Heintz and they all give a single ‘cloud’ of points in Fig. 11. This cloud is quite distinct from the clouds found for other species. The supposed sexual dimorphism (forma lata and forma angusta of Kier & A. Heintz) is most likely only individual variations. However, some wider or narrower shields may also be due to tectonic and/or diageneric deformations, as will be illustrated below for *P. polaris* (Fig. 8) (see also Denison 1964: 406 and 415, Dineley & Loeffler 1976: 78).

*Poraspis polaris* Kier, 1930

*(Figs. 7, 8, 9)*

□ 1930. *Poraspis polaris* n. gen. & sp. – Kier, fig. 3a-b. □ 1932. *Poraspis polaris* n. gen. & sp. (sic) – Kier, figs. 1–2, pl. I. □ 1932. *Poraspis cylindrica* n. gen. & sp. – Kier, pl. III, 3. □ 1935. *Poraspis polaris* Kier & A. Heintz, figs. 2, 3, 5, 7–14, pls. 1–VIII, IX, 2, X, 1, XI–XIII, 1, XXV, 1, XXXI, 1, XXXII, 2, XXXIV, 1–5, XXXV–XXXVII, XXXVIII, 1. □ 1935. *Poraspis elongata* n. sp. – Kier & A. Heintz, figs. 24–26, pl. IX, 3, X, 2, XVIII–XX, XXVII, 1. □ 1935. *Poraspis rostrata* n. sp. pro parte – Kier & A. Heintz, pl. XXII, 1. □ 1935. *Poraspis cylindrica* n. sp. pro parte – Kier & A. Heintz, pl. XXVI, 2. □ 1941. *Poraspis polaris* Kier – Søve-Søderbergh, fig. 5. □ 1942. *Poraspis polaris* Kier – Holmgren, fig. 7. □ 1958. *Poraspis cf. polaris* Kier – *A. Heintz, pl. XVI, 2. □ 1964. *Poraspis polaris* Kier – Denison, figs. 98A, 99A, 137 and 102A. □ 1964. *Poraspis cf. polaris* Kier. *Poraspis polaris f. angusta* Kier and *Poraspis cylindrica* Kier – Stensiö, figs. 166B, 167B, 179B and 216A–B. □ 1964. *Poraspis polaris* Kier – Denison, figs. 98A, 99A, 137 and 102A. □ 1964. *Poraspis cf. polaris* Kier. *Poraspis polaris f. angusta* Kier and *Poraspis cylindrica* Kier – Stensiö, figs. 68B, 69B, 81B and 121A–B. □ 1971. *Poraspis* sp. and *Poraspis polaris* – Moy-Thomas & Miles, figs. 3.3 and 3.6A.

**Holotype.** – Dorsal shield PMO D 665 (Fig. 7A). (Kier 1932, pl. I; Kier & A. Heintz 1935, pls. II and XXXIV, 2, Denison 1964, fig. 137).
|          | laO | LoO | laT | LoT | LoP | LpB | laV | LoV |
|----------|-----|-----|-----|-----|-----|-----|-----|-----|
| **P. brevis** (new definition) |
| D 304   | 12  | 4   | 17  | 27  | 6   | 11  | 3   | 0.63|
| D 1259  | 11  | 17  | 26.5| 6.5 | 11  | 2.44| 0.64| 0.17|
| D 368   | 11  | 4.5 | 17  | 26.5| 6.5 | 11  | 2.44| 0.17|
| **P. brevis** (type) |
| D 87    | 15  | 21  |     |     |     |     |     |     |
| D 299   | 15.5| 23  |     |     |     |     |     |     |
| **P. intermedia** |
| D 1308  | 11  | 4   | 15  | 29.5| 6   | 11  | 2.75| 0.51|
| D 293   | 11  | 4   | 16  | 26  | 6.5 | 11  | 2.75| 0.61|
| D 1904  | 8   | 3.5 | 14  | 26  | 5.5 | 10.5| 2.28| 0.54|
| **P. subulis** |
| D 665   | 12  | 6   | 18.5| 40  | 9   | 14  | 2   | 0.46|
| D 241a  | 12  | 5   | 20  | 37  | 9   | 14  | 2.40| 0.54|
| D 241b  | 13  | 4   | 20  | 32  | 8   | 13  | 3.25| 0.62|
| **P. polaris** (new definition) |
| D 241c  | 20  | 28  |     |     |     |     |     |     |
| D 206   | 16  | 26.5|     |     |     |     |     |     |
| D 115   | 13  | 5   | 23  | 34  | 8.5 | 14  | 2.60| 0.68|
| D 113   | 19  | 28  |     |     |     |     |     |     |
| D 001   | 12.5| 6.5 | 18  | 36.5| 9   | 14  | 1.92| 0.49|
| D 38    | 18  | 27.5|     |     |     |     |     |     |
| **P. elongata** |
| D 204a  | 12  | 5.5 | 17  | 36  | 8.5 | 14  | 2.18| 0.47|
| D 204b  | 14  | 7   | 20  | 36.5| 9   | 15  | 2   | 0.55|
| D 002   | 11.5| 5.5 | 19  | 39  | 9   | 14  | 2.09| 0.49|
| **P. rostrata** |
| D 36    |     |     | 16  |     |     |     |     |     |
| D 101   |     |     | 16.5|     |     |     |     |     |
| D 198   | 11  | 5.5 | 16.5| 32  | 7.5 | 14  | 2   | 0.51|
| D 288b  | 11  | 5.5 | 18  | 40  | 8   | ?   | 2   | 0.45|
| D 1161  | 11  | 4   | 19  | 34  | 6.5 | 14  | 2.75| 0.56|
| D 141a  | 12.5| 8   | 19  | 41.5| 10.5|16  | 1.56| 0.46|
| **P. cylindrica** (type) |
| D 141b  |     |     | 16  | 30  |     |     |     |     |
| D 147   |     |     | 9.5 | 15.5| 32  | 9   | 2   | 0.48|
| D 35    |     |     | 13  | 5   | 20  | 37  | 9.5 | 2.60|
| **P. rostrata** (new definition) |
| D 124   | 13.5| 8   | 21  | ?   | 11.5| ?   | 1.69| ?   |
| D 135   |     |     | 18  | 42  |     |     | 1.50| 0.44|
| D 1798  |     |     | 20  | 38  |     |     | 1.50| 0.44|
| **P. cylindrica** |
| D 140   | 15  | 9   | 24  | 53  | 13  | 23  | 1.67| 0.45|
| D 203   | 18  | 11  | 26  | 61  | 15  | 24  | 1.64| 0.43|
| D 200   |     |     | ?   | 25  | 52  | 16  | ?   | 0.48|
| D 138   | 18  | 10  | 25  | ?   | 13  | ?   | 1.80| ?   |
| **P. magna** |
| D 139   |     |     | 23  | ?   |     |     | ?   | ?   |
| D 278   |     |     | 25  | 54  |     |     | 1.50| 0.44|

Table 1. Measurements (in mm) and indexes of the *Poraspis* species from the Red Bay Group (for abbreviations, see p. 49-50; numbers in the right column refer to Fig. 11).
Locus typicus. – Frøkkelryggen, 250 m a.s.l. (locality no. 5).

Stratum typicum. – Frøkkelryggen Formation, Polaris horizon.

Other material. – From the Primæva horizon up to the Benneviaspis horizon (see Kiær & A. Heintz 1935).

Diagnosis. – A medium-sized species of Poraspis with 32 ≤ LoT ≤ 44 mm; 6.5 ≤ LoP ≤ 12 mm and 13 ≤ LpB ≤ 17 mm.

Measurements. – Table 1 and Fig. 11.

Discussion. – P. polaris is the best-known species of Poraspis on which Kiær & A. Heintz (1935) based the reconstruction of this genus. It is known from several tens of described and/or figured specimens. There are no significant morphological differences between P. polaris Kiær and P. elongata Kiær & A. Heintz. The biometric study of the whole specimens gives a homogeneous cloud on Fig. 11; the specimens of P. cf. polaris Dineley & Loeffer (1976: 76–78) also fall within this cloud. We believe that these specimens all belong to Poraspis polaris.

The only exceptions are PMO D 128, first described as P. rostrata Kiær & A. Heintz (1935, pl. XXIV, 1, from horizon A in the Ben Nevis Formation), and PMO D 205 the type of P. cylindrica Kiær (1932, pl. III, 3, Kiær & A. Heintz 1935, pl. XXVI, 2, Stensiø 1958, fig. 179B, 1964, fig. 81B from the Benneviaspis horizon). Both specimens have the same shape and size; PMO D 205 might actually be the internal mould of PMO D 128. These specimens are very close to the type specimens of Poraspis barroisi (MNHN, L VI 1–2, Leriche 1906, pl. 1, 2–5) with the same shape, the same size and exactly the same number and pattern of branchial pouches. Furthermore, we did not find any morphological differences between the large specimens of P. cf. polaris Dineley & Loeffler (1976) and some big specimens of P. sturi (for instance NHRM, C 1629, fig. 11, points 29–30). All these specimens (PMO D 128, PMO D 205 and MNHN, L VI 1–2, NHRM, C 1629 and the NMC specimens of P. cf. polaris) look much more like large P. polaris individuals than anything else, and are quite different from the newly defined P. rostrata (see p. 59). The two main differences are:

– the size (LoT of P. rostrata is 1.5 times that of P. polaris)

– the length of the postbranchial part of the dorsal shield which is 49% of LoT in P. rostrata, but only 42% in P. cylindrica (PMO D 205) and in P. barroisi (L VI 1) (see also Stensiø 1964: 328).

Thus we think that P. barroisi (Leriche), P. sturi (Alth), P. cf. polaris Dineley & Loeffer, ‘P. rostrata’ specimen PMO D 128, and the type specimen PMO D 205 of P. cylindrica Kiær are co-specific and synonymous with P. polaris Kiær (1930). And strikingly, P. sturi (Alth 1874) has priority over P. barroisi (Leriche 1906) and P. polaris (Kiær 1930), but as the type specimens of P. sturi have not been reviewed, we provisionally keep the name P. polaris for the Spitsbergen specimens, which are the most numerous representatives of the taxon and give a better idea of its variations.

Lastly, some specimens from the Vogti horizon described by Blieck (1976) as P. rostrata are also much more like P. polaris than the type of P. rostrata Kiær & A. Heintz. These specimens (MNHN, SVD 538, 559, 552, points 38–40, Fig. 11, while having a little longer pineal portion of the dorsal shield, are quite similar to P. cf. polaris Dineley & Loeffler (1976). But the specimen MNHN, SVD 508 (Fig. 11, point 41; Blieck 1976, pl. IX) with its elongate rostrum and longer dorsal shield is really very close to the type of P. rostrata Kiær & A. Heintz (1935, pl. XXIII). Thus we now think that the original material described as P. rostrata from the Vogti horizon (Blieck 1976) in fact corresponds to two different taxa, P. polaris and P. rostrata.

Some deformations in the shields may be due to diagenetic and/or tectonic crushing and stretching. This point of view can best be illustrated on a slab with numerous specimens, like the one that has been figured by Kiær & A. Heintz (1935, pl. I). On this slab the wider specimens are statistically perpendicular to the narrower ones, as interpreted in Fig. 8. However, we cannot at present assess the respective importance of the deformation when compared to the individual biological variations. Nevertheless, it seems that the biometric differences we can observe on P. polaris and on the other Poraspis from Spitsbergen do not come from a sexual dimorphism as previously thought (and we do not presently know how to distinguish both sexes in these jawless
Fig. 7. *Poraspis polaris* - new definition - dorsal shields. A. PMO D 665, holotype (Kier & A. Heintz 1935, pl. II). B. PMO D 198 (ibid., pl. XIII). C. PMO D 84, *P. elongata* (ibid., pl. XXVII, fig. 1). D. PMO D 141a, type of *P. elongata* (ibid., pl. XIX) (scale 1 cm).
vertebrates; see also Blieck 1980). If these variations are particularly clear in the representatives of Poraspis, it is probably because of the thinness of the bone of the shields, which is very fragile and pliant.

We also think that in this particular case the arrangement of the shields in the rock has not been caused by post mortem orientation of the shields by palaeocurrents. We have not seen sedimentary structures on the slab and the whole specimens are not lying in any pronounced direction, as would probably have been the case for oblong shields being moved by a bottom current.

Another interesting point is that we did not find very small individuals in any of the three species of Poraspis discussed here. The maximum–minimum deviation is about 25 to 30% of the medium of each corresponding measurement. Thus the smaller ones might be ‘young adults’ and the bigger ones ‘old adults’, while the youngest stages of development would not be represented. And if the ontogeny of these jawless vertebrates is comparable to that of the extant fishes, it might be assumed that the Poraspis individuals (and the other cyathaspids) acquired their dermal mineralized carapace only after ‘sexual maturity’. However, this mineralization perhaps occurred earlier in the pteraspids, as in Rhinopteraspis, where we know of very small individuals as well as large fully grown ones (Blieck 1980). But the distinctive (diagnostic) characteristics of the shields are also probably acquired rather late during the ontogeny (Denison 1973).

One well-preserved specimen from Frankelryggen, SMC No. F 1315k, shows the left suborbital plate in connection with the dorsal shield and the left branchial plate (Fig. 9A) as on Irregularaspis hoeli (Fig. 4) and Nahanniaspis mackenziei Dineley and Loeffler (1976, figs. 33–34, pl. 13, 9). Another specimen from Arctic Canada, NMC 19860 (ibid., fig. 25, pl. 10, 4) shows the oral cover that consists of a single main plate. We are thus proposing a new reconstruction of the anterior ventral part of the carapace in Poraspis polaris (Fig. 9C) which is complementary to the one of Kier & A. Heintz (1935, fig. 52) who did not know the oral cover nor the suborbital plate. Our reconstruction is also different from the hypothetical one proposed by Denison (1964, fig. 91), which has been further developed by Stensio (1958, fig. 194; 1964, fig. 99; 1968, fig. 13). The anterior rim of the oral cover of specimen NMC 19860 has a transverse area with no dentine ridges; neither has the anterior rim of the ventral disc nor the left branchial plate. On the latter two plates, the anterior rim is where these plates are in contact with the oral cover (Fig. 9B, ou.V) and the left suborbital plate (Fig. 9B, ou.B.). We find it reasonable to assume that the anterior area of the oral cover (ou.Or.) has contact with more anterior plates of this area and that the whole oral cover of P. polaris was made of two rows of plates. (For further discussion see p. 60).

Poraspis rostrata Kier & A. Heintz, 1935 (ex Kier, 1932) (Fig. 10)

- We think that the name P. rostrata introduced by Kier (1932) was a nomen nudum, because it was based on a non-diagnostic ventral shield. But Kier & A. Heintz (1935) validated Holotype. – Dorsal shield PMO D 124 (Fig. 10A; Kier & A. Heintz 1935, pls. XXIII and XXIV, 2).

Locus typicus. – Ben Nevis, westernmost part of the cliff at the northwestern boundary of the western plateau (locality no. 9A) close to Raudfjordbreen.

Stratum typicum. – Ben Nevis Formation, horizon A of Hoel’s section.

Other material. – From the horizon A–I up to the horizon S–U, i.e. the upper three fourths of the Ben Nevis Formation (see Kier & A. Heintz 1935).

Diagnosis. – A rather large species of Poraspis with LoT ≥ 48 mm, LoP ≥ 13 mm and LpB ≥ 20 mm.

Measurements. – Table 1 and Fig. 11.

Discussion. – We think that the name P. rostrata introduced by Kier (1932) was a nomen nudum, because it was based on a non-diagnostic ventral shield.
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Fig. 8. Slab PMO D 241, with numerous shields of *Poraspis polaris* to show the possible biometric variations due to tectonic and/or diagenetic deformations (see Kjaer & A. Heintz 1935, pl. 1). n, narrower shields. w, wider shields. C, crushing. S, stretching.

*P. rostrata* on the description of well-preserved dorsal and ventral shields. *P. cylindrica pro parte* and *P. magna* are considered here as synonyms of *P. rostrata*, as shown from the biometric study of the whole collection in Oslo (Fig. 11). Specimen MNHN, SVD 508 from the Vogti horizon is also a typical *P. rostrata*. Several well-preserved specimens of *P. pompeckji* from Podolia (Fig. 11, points 31–36) are also very close to *P. magna* Kjaer & A. Heintz, and may be considered as synonyms of *P. rostrata* as newly defined. Specimen NHRM, C 1680 (Fig. 11, point 34) is the biggest *P. pompeckji* observed in the Stockholm collections and might be considered here as a particularly large individual of *P. rostrata* or perhaps as belonging to a different species. Nevertheless, we think it is most probably related to *P. rostrata*, being in any case shorter than the type of *P. sericea* (Lankester) from Great Britain (Fig. 11, point 37) which is the biggest *Poraspis* specimen ever collected (see Denison 1964: 409).

Genus *Homalaspidella* Strand, 1934

**Definition.** – See Denison 1964: 421.

**Type species.** – *Homalaspis nitida* Kjaer, 1932.

*Other species.* – *H. borealis* Denison (1963), *H. cf. borealis* Dineley & Loeffler (1976), *H. cf. borealis* Loeffler & Jones (1976).

*Homalaspidella nitida* (Kjaer, 1932)

Before 1964, see Denison 1964: 421.

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Fig. 9. *Poraspis polaris*. A. Specimen SMC F 1315k, left lateral view of the dorsal shield. B. Specimen NMC 19860, external view of the ventral shield (after Dineley & Loeffler 1976: fig. 25). C, D, E. General reconstruction. C. In left lateral view. D. In ventral view. E. In dorsal view. (C, D, E after Kjaer & A. Heintz 1935, fig. 52, complemented).
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Fig. 10. Poraspis rostrata – new definition – dorsal shields. A. PMO D 124, holotype (Kier & A. Heintz 1935, pl. XXIII). B. PMO D 140, ‘P. cylindrica’ (ibid., pl. XXIX, fig. 1). C. PMO D 203, type of ‘P. magna’ (ibid., pl. XXVIII, fig. 1).

\[1964. Homalaspella nitida\] (Kier) – Denison, figs. 98D, 99C and 144. \[1964. Homalaspella nitida\] (Kier) – Stensjö, figs. 82B and 108B.

Holotype. – Dorsal shield PMO D 156 (Kier 1932, pl. IV, 1, Kier & A. Heintz 1935, pls. XXX, 2 and XXXIV, 6).

Locus typicus. – Ben Nevis, cliff on the northern boundary of the western plateau near Raudfjord-breen (locality no. 9).

Stratum typicum. – Ben Nevis Formation, horizon A of Hoel’s section.

Paratypes. – Ventral disc with part of a lateral plate and a scale PMO D 148 (Kier & A. Heintz 1935, Pl. XXX, 1 and XXXIII, 1) from Ben Nevis, southwestern slope, horizon L of Hoel’s section (=Ctenaspis horizon). Internal mould of dorsal shield PMO D 175 (Kier & A. Heintz 1935, pl. XXX, 3) from Ben Nevis, cliff of the western plateau, horizon A of Hoel’s section.

Other material. – Specimens PMO D 183 (Ben Nevis, cliff, horizon A, Kier & A. Heintz 1935, pl. XXXI, 2). PMO D 1929 (horizon A), PMO D 3034–3035 (horizon D), PMO D 1923 (horizon E–F), PMO D 245 (Vogti horizon), PMO D 1930 (horizon J), PMO D 145 and PMO D 170–171 (horizon L), PMO D 1473 (Ctenaspis horizon = horizons J–L), PMO 1500 (Tunge locality), PMO D 176 (SE side of Sigurdfjellet, 200 m a.s.l., Kier & A. Heintz 1935: 128 and pl. XXXII: 1, Blieck & N. Heintz 1979: 175), specimens MNHN, SVD 504/l, 566, 597 (Ben Nevis, northern ridge, Vogti horizon, Blieck 1976, fig. 21, pls. X: 1 and XIX:...
Fig. 11. Diagram of LoP/LoT for various specimens of Poraspis. A. Poraspis brevis (new definition), a, P. brevis; b, 'P. intermedia'; c, 'P. subtilis'. B. Poraspis polaris (new definition) - P. sturi - P. barroisi; d, P. polaris; e, 'P. elongata'; f, type of 'P. cylindrica'; g, P. sturi; h, P. barroisi; i, 'P. rostrata' in Bieck (1976). C. Poraspis rostrata (new definition) - P. pompeckji; j, P. rostrata; k, 'P. cylindrica'; l, 'P. magna'; m, P. pompeckji; D. Poraspis sericea. For numbers 1-25, see Table 1; 26, P. cf. polaris Dineley & Loeffer (1976: 76); 27, P. barroisi (Leriche 1906, pl. I: 2; MNHN, L VI 1, lectotype); 28, P. barroisi (Leriche 1906, pl. I: 3; MNHN, L VI 2); 29, P. sturi (NHTM, C 1629); 30, P. sturi (NHRM, C 1628); 31, P. pompeckji (NHTM C, 1598c); 32, P. pompeckji (NHRM, C 1609); 33, P. pompeckji (NHRM, C 1605); 34, P. pompeckji (NHRM, C 1680); 35, P. pompeckji (NHRM, C 1613); 36, P. pompeckji (NHRM, C 1697a); 37, P. sericea (Lankester 1873, pl. X; BMNH, P 4117, holotype); 38, MNHN, SVD 538; 39, MNHN, SVD 559; 40, MNHN, SVD 552; 41, MNHN, SVD 508 (Bieck 1976, pl. IX).
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Fraenkelryggen (300 m a.s.l., Primæva horizon, Blieck & N. Heintz 1979: 171), if really belonging to Homalaspida would be the earliest representative of this genus in the Red Bay Group in Spitsbergen.

Genus Anglaspis Jaekel, 1927

Definition. – See Denison 1964: 428.

Type species. – Cyathaspis macculloughi Woodward, 1891.

Other species. – A. insignis Wills (1936), A. heintzi n. sp., A. elongata n. sp., A. expatriata Denison (1964).

Anglaspis insignis Wills, 1936 (ex Kïær, 1932) (Figs. 12 and 13A-F)

Before 1964, see Denison 1964: 430 (but not ‘Anglaspis insignis var. brevis’), Kïær (1932, pl. VI, 1), ‘Fraenkelaspis (=Anglaspis) insignis var. brevis (Kïær)’, Stensiö (1958, fig. 180A), ‘Fraenkelaspis brevis (Kïær)’, Stensiö (1958, fig. 205B).

1964. Anglaspis insignis Wills – Denison, figs. 99B and 150A-B. 1964. Fraenkelaspis insignis (=A. insignis Kïær) – Stensiö, fig. 70C-D.

Holotype. – Ventral disc PMO D 186 (Fig. 12C). (Kïær 1932, pl. VII, 1).

Paratypes. – Dorsal shields PMO D 186a (Fig. 12D). (Kïær 1932, pl. VII, 2) and PMO D 186b; Ventral discs PMO D 186c–d (all on the same slab as PMO D 186).

Locus typicus. – Frænkelryggen, 150–200 m a.s.l. (locality no. 6).

Stratum typicum. – Frænkelryggen Formation, Anglaspis horizon.

Other material. – Table 2, all from the Anglaspis horizon.

|                | H. nitida | H. borealis | H. cf. borealis | H. cf. borealis |
|----------------|-----------|-------------|-----------------|-----------------|
| LoT(mm)        | 20–26     | 28–30       | 32              | 26              |
| LoO/LoT        | 0.14      | 0.10–0.12   | 0.13            | 0.15            |
Diagnosis. – See Denison 1964: 421.

Measurements. – Table 2 and Fig. 17.

Discussion. – It was Wills (1936: 429) who validated the name *Anglaspis insignis* Kjaer (1932) by comparison with the valid type species *A. maccullooughi* (ICZN art. 13, Denison 1964: 431). *A. insignis* has been mentioned by Denison (1964: 431) from the Primaeua horizon up to the Red horizon, but it is only well-known in its stratum typicum, i.e. the *Anglaspis* horizon from numerous specimens in the collection of Paleontologisk museum, Oslo. The rostral part of the dorsal shield is anteriorly more or less blunt with dentine ridges radiating from a very distinct pineal macula (Fig. 13A–F).

One specimen, PMO D 1115, previously chosen as the type specimen of *A. platostriata* Kjaer (1932: 20, *nomen nudum*. See Denison 1964: 431) may be considered as a big specimen of *A. insignis*, according to the pineal length and the total length of the dorsal shield (Table 2; Figs. 13G, 14A, 17, point 8). But this specimen comes from the moraine of the Second Glacier, northwest of Ben Nevis (Kjaer & A. Heintz 1935: 11–13) and may have been extracted from the Vogti horizon. Thus *A. insignis* would also be present in the middle of the Ben Nevis Formation.

*Anglaspis heintzi* n. sp. (ex Kjaer, 1932) (Figs. 15, 16) □ 1932. *Anglaspis heintzi* n.g. & sp. Kjaer, fig. 11 (*nomen nudum*).

Holotype. – Dorsal shield PMO D 387 (Figs. 15A, 16A).

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*Fig. 12. Anglaspis insignis*. A. Reconstruction of the dorsal shield with the lateral canal system. B. Reconstruction of the ventral disc with the lateral canal system. C. PMO D 186, holotype, ventral disc. D. PMO D 186a, paratype, dorsal shield. E. PMO D 355, dorsal shield. F. PMO D 367, dorsal shield (C–F same scale).
Table 2. Measurements (in mm) and indexes of the *Anglaspis* species from the Red Bay Group (for abbreviations, see p. 49; numbers in the right column refer to Fig. 17).

| Species       |  |  |  |  |  |  |  |  |  |  |  |  |
|---------------|---|---|---|---|---|---|---|---|---|---|---|---|
| *A. insignis* |  |  |  |  |  |  |  |  |  |  |  |  |
| holotype      |  |  |  |  |  |  |  |  |  |  |  |  |
| D 186         | 12| 19|  |  |  |  |  |  |  |  |  | 0.63|
| D 186a        | 9 | 4 | 13|21.5| 5 | 3 | 2.25| 0.60| 0.19| 0.23| 0.14| 3  |
| D 186b        | 9.5|3.5|12|20| 5 | 2 | 2.71| 0.60| 0.17| 0.25| 0.10| 3  |
| D 186c        |  |  |  |  |  |  |  |  |  |  |  | 0.60|
| D 186d        |  |  |  |  |  |  |  |  |  |  |  | 0.60|
| D 189         | 8 | 3.5|12| ? | 5 | ? | 2.28| ? | ? | ? | ? | 3-4|
| D 356         | 9 | ? | 13| ? | 3 | ? | ? | ? | ? | ? | ? | 4  |
| D 188         | 10| 4| 14|22| 5.5| 3 | 2.50| 0.64| 0.18| 0.25| 0.14| 3  |
| D 364         | 9 | 3 | 13|19| 4.5| 3.5|3 | 0.68| 0.16| 0.24| 0.18| 3  |
| D 365         |  | ? | 12.5| ? | ? | ? | ? | ? | ? | ? | ? | 4  |
| D 366         |  |  |  |  |  |  |  |  |  |  |  | 0.55|
| D 420         | 7.5|3 | ? | 19| 4 | ? | 2.50| ? | 0.16| 0.21| ? | ? |
| D 367         | 10| 4| 14.5|23| 6 | 3 | 2.50| 0.63| 0.17| 0.26| 0.13| 3  |
| D 355         | 10| 3.5|14|21| 5 | 2.5|2.86| 0.67| 0.17| 0.24| 0.12| 3  |
| D 344         |  |  |  |  |  |  |  |  |  |  |  | 0.69|
| D 354         | 9 | 3.5|13|21.5| 5 | 3 | 2.57| 0.60| 0.16| 0.23| 0.14| 4  |
| D 191         |  |  |  |  |  |  |  |  |  |  |  | 0.57|
| 'A. platostriata' |  |  |  |  |  |  |  |  |  |  |  |  |
| D 1115        | 10| 5| 14|25| 6.5| 4 | 2 | 0.56| 0.20| 0.26| 0.16| 3  |

| Species       |  |  |  |  |  |  |  |  |  |  |  |  |
|---------------|---|---|---|---|---|---|---|---|---|---|---|---|
| *A. heintzi*  |  |  |  |  |  |  |  |  |  |  |  |  |
| holotype      |  |  |  |  |  |  |  |  |  |  |  |  |
| D 387         | 11| 6| 16|29| 8 | 6 | 1.83| 0.55| 0.21| 0.27| 0.21| 3  |
| D 384         |  |  |  |  |  |  |  |  |  |  |  | 0.59|
| D 193         | 9 | ? | 14| ? | ? | ? | ? | ? | ? | ? | ? | 3  |
| D 382b        | ? | ? | 13| ? | ? | ? | ? | ? | ? | ? | ? | 3  |
| D 385         | 10| 5| 13|25| 6.5| 5 | 2 | 0.52| 0.20| 0.26| 0.20| 3  |

| Species       |  |  |  |  |  |  |  |  |  |  |  |  |
|---------------|---|---|---|---|---|---|---|---|---|---|---|---|
| *A. elongata* |  |  |  |  |  |  |  |  |  |  |  |  |
| holotype      |  |  |  |  |  |  |  |  |  |  |  |  |
| D 1485        | 7 | 4| 10|20| 5 | ? | 1.75| 0.50| 0.20| 0.25| ? | 4  |
| D 1479        |  |  |  |  |  |  |  |  |  |  |  | 0.53|
| SVD 582       | 11| 22|  |  |  |  |  |  |  |  |  | 0.50|

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Note: For abbreviations, see p. 49; numbers in the right column refer to Fig. 17.
Fig. 13. Variation of the pattern of the dentine ridges on the rostral part of the dorsal shield of *Anglaspis* with the external pores of the lateral canal system. A–F. *A. insignis*. A. PMO D 367, B. PMO D 355, C. PMO D 188, D. PMO D 968, E. PMO D 186a, paratype, F. PMO D 186b, paratype, G. PMO D 1115, 'A. platostriata', H. PMO D 1485, *A. elongata* nov. sp., holotype. (Scale 5 mm).
Locus typicus and stratum typicum. – Frænkelryggen, isolated block 200 m a.s.l. coming from the Primaeuva horizon.

Paratypes. – Ventral shield with oral plates PMO D 384 (Figs. 15C, 16B–C) (A. Heintz 1962, fig. 7; Denison 1964, fig. 94A). Dorsal shield PMO D 385 (Fig. 15B). Dorsal shield PMO D 193 mostly an internal cast, first named 'Anglaspis insignis var. brevis' (Kiaer 1932, pl. VI, 1, Stensio 1958, figs. 180A and 205B, 1964, figs. 82A and 110B); all from the Primaeuva horizon. Articulated specimens PMO D 382a–b from an unknown horizon on Frænkelryggen (Figs. 15E and 16D).

Diagnosis. – A species of Anglaspis with a dorsal shield longer and wider than that of A. insignis, but less wide than that of A. macculloughi. Rostral part triangular and longer than that of A. insignis; posterior part with a short median crest.

Measurements. – Table 2 and Fig. 17.

Discussion. – The type specimens of A. heintzi have never been designated nor figured (Denison 1964: 431). In our opinion, A. Heintz's figure (1962, fig. 7) does not give 'characters differentiating the taxon'. Thus A. heintzi is a nomen nudum that we validate here. (Denison (1964: 431) contradicts himself by saying: ‘the known characters are not sufficient to differentiate this species', and, three lines below: ‘the recent description and figure of the mouth parts by Heintz... may be considered as giving characters differentiating the taxon!’) Kiaer (1932, fig. 11) gave a reconstruction which has become classical (A. Heintz 1933, fig. 4; Moy-Thomas 1939, fig. 2A; Stensio 1958, fig. 166A, 1964, fig. 68A; Tarlo 1962, fig. 3; Denison 1964, fig. 90; Obruchev 1964, fig. 19; Moy-Thomson & Miles 1971, figs. 3. 2). However, we believe that this reconstruction has to be regarded with some caution because:

- The rostral part of the specimen PMO D 382a–b is not preserved.

- The rear part of the caudal fin of specimen PMO D 382a is not hypobatic, but seems to be trilobated as in other heterostracans (Denison 1971). The
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The notochord passes on into the ventral lobe (Denison 1971).

A. heintzi has a typically triangular rostrum (Fig. 16A) with one median dentine ridge extending from the pineal macula to the anterior border of the dorsal shield. This shield very often bears a small median crest at its posterior end, a character never found in A. insignis beside which all the measurements of A. heintzi are bigger. The oral cover of A. heintzi typically consists of a single row of oral plates (Fig. 16B). So, it seems that the known cyathaspids either have one row of oral plates (Anglaspis) or two rows of oral and postoral plates (Poraspis, pp. 55-58 and Allocryptaspis, see Denison 1960, 1964). And as the pteraspids also show either one or two rows of plates in the oral cover, it might be possible to define the same morphcline in both groups: 1 row → 2 rows (cf. Blieck 1980, 1981).

Anglaspis elongata n. sp. (ex Kijær, 1932) (Figs. 13H and 14B-C)

Holotype. – Dorsal shield PMO D 1485 (Figs. 13H and 14B).

Paratype. – Ventral disc PMO D 1479 (Fig. 14C).

Locus typicus. – Ben Nevis, northern plateau, 600 m a.s.l. (locality no. 10).

Stratum typicum. – Ben Nevis Formation, Vogt horizon.

Diagnosis. – The smallest known species of Anglaspis with a dorsal shield less wide than that of A. insignis; rostral part with typical V-shaped dentine ridges and a blunt anterior border.

Measurements. – Table 2 and Fig. 17.

Discussion. – This species is as short as A. insignis but with narrower dorsal and ventral shields. On the rostral part, the dentine ridges are typically transversally arranged with a V-shaped pattern. Specimens MHNN, SVD 565, 592, 596 (Blieck 1976, pl. X, 3, pl. XX, 1-2, ‘Anglaspis sp.’) from the Vogt horizon, seem to be other representatives of A. elongata, particularly because of the great resemblance between the ventral shields of

Fig. 15. Anglaspis heintzi nov. sp. A. PMO D 387, dorsal shield, holotype. B. PMO D 385, dorsal shield, paratype. C. PMO D 384, ventral shield, paratype. D. General reconstruction in left lateral view (after Kijær 1932, fig. 11, slightly modified). E. Slab PMO D 382a-b, articulated specimens, paratypes. dorsal view (scale 1 cm).

natural boundary of the tail is not preserved on the original specimen (Fig. 16D), but the ventral lobe seems to be a little longer than the other two. As for this problem, we also think a hypocercal tail is not diagnostic of heterostracans because:

– It has never been found on any specimen (not even in Pteraspis rostrata sensu White, 1935).

– We know of numerous heterostracans with isobatic or epibatic tails (Denison 1971; Dineley 1976; Dineley & Loeffler 1976), and even if there is a hypobatic tail, there is no evidence that the
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**Fig. 16. Anglaspis heintzi nov. sp.** A. Specimen PMO D 387, rostral part of the dorsal shield, holotype. B. PMO D 384, anterior part of the ventral shield with the oral plates, external view, paratype. C. The same specimen in left lateral view. D. PMO D 382a, trunk squamation and caudal fin, left lateral view, paratype (scale 5 mm - camera lucida drawings).

PMO D 1479 and MNHN, SVD 582 (same elongated shape, same measurements, cf. Table 2).

This latter species of *Anglaspis* is the smallest one presently known and differs from all the others by its peculiar rostral ridge pattern. *A. macculloughi*, on the other hand, is the biggest species, with a rostral pattern very like that of *A. heintzi* (see Wills 1936, pl. I, 4, 12, pl. II, 1–9). The measurements discriminate rather poorly between the five species of *Anglaspis* (Fig. 17). The morphological differences are also rather meagre (pineal macula, posterolateral corners, posterior median crest). Thus *A. heintzi* seems to be closely related to *A. macculloughi*, and *A. expatriata* does not seem to be very different from *A. insignis*. We think that if all these species had come from the same geographical area, fewer taxa would have been defined. However, as we did not see all the specimens, we prefer to provisionally retain the five names.

*Anglaspis* sp. indet.

Some fragments PMO D 2148 come from the horizon O of Hoël's section (*Benneviaspis* horizon).

Family Ctenaspidae Kiær (1930, Ctenaspidae)

**Definition.** – See Denison 1964: 438-439 ('Ctenaspidae').

**Type genus.** – *Ctenaspis* Kiær, 1930.

Genus *Ctenaspis* Kiær, 1930

**Fig. 17.** Diagram of LaT/LoT for various specimens of *Anglaspis*. a. *A. insignis*. b. 'A. platostrata'. c. *A. heintzi*. d. *A. elongata*. e. *A. expatriata*. f. *A. macculloughi*. For numbers 1–11, see Table 2. 12– specimen NMC 10038 (holotype of *A. expatriata*; Denison 1964, fig. 151A). 13– specimen BMNH P 4797 (holotype of *A. macculloughi*; Woodward 1891, pl. IX, fig. 4). 14–16– after Wills (1936: 430).
Definition. – See for the family.

Type species. – *Ctenaspis dentata* Kjær, 1930.

Other species. – *C. cancellata* Kjær (1930), *C. kiaeri* Zych (1931), *C. obrucheui* Dineley (1976), *C. russelli* Dineley (1976) and *C. ornata* Dineley (1976).

*Ctenaspis dentata* Kjær, 1930

(Fig. 18A-B)

Before 1964, see Denison 1964: 440.

ɔ 1964. *Ctenaspis dentata* Kjær – Denison, figs. 97D, 99F, 101C, 154 and 155 (pro parte cop. Kjær, 1930). □ 1964. *Ctenaspis dentata* Kjær – Stensio, fig. 79A-B.

Holotype. – Dorsal shield PMO D 582 (Kjær 1930, figs. 1a, 4a).

*Locus typicus*. – Southwest side of Ben Nevis, 532 m a.s.l. (locality no. 11).

*Stratum typicum*. – Ben Nevis Formation, *Ctenaspis* horizon (horizon L of Hoel’s section).

Paratype. – Ventral disc PMO D 584 (Kjær 1930, fig. 1b) from *Bennevisaspis* horizon (horizon O of Hoel’s section, 627 m a.s.l., southwest side of Ben Nevis).

Other material. – Specimens NHRM, C 1615 from unknown horizon (Stensio 1958, fig. 177; 1964, fig. 79), FMNH, PF 1088 from unknown horizon (Denison 1964, fig. 155) and ?MNHN, SVD 599b from the *Vogti* horizon (Blieck 1983).

Diagnosis. – See Denison 1964: 440.

Measurements. – Table 3.

Discussion. – *C. dentata* with its typical outer ornamentation of fine tubercles is rather suggestive of the Canadian arctic species described by Dineley (1976). However, the tubercles of *C. dentata* are triangular, and its dorsal length is half that of the Canadian species. But *C. obrucheui* Dineley with its less wide dorsal shield seems to be most closely related to *C. dentata* Kjær.

In Spitsbergen, *C. dentata* is known from the *Ctenaspis* horizon of the Ben Nevis Formation. But if the fragment of shield MNHN, SVD 599b really belongs to *C. dentata*, it indicates that this species also occurs in the *Vogti* horizon, below the *Ctenaspis* horizon.

The different species of *Ctenaspis* have flat dorsal shield, arched ventral disc and an apparently anterodorsal mouth (Dineley 1976). They seem to have been agnathes which swim very near the surface, i.e. they were nectonic animals and not benthonic, as suggested by Dineley (1976). Furthermore, the relative importance of the carapace and the trunk and tail (Dineley 1976, fig. 8) leads one to believe that they were good swimmers. They are known from Arctic Canada, Spitsbergen, Podolia, and perhaps also from England (Wills 1936: 428-429 and pl. I, 1, ‘cf. *Ctenaspis*’).

*Ctenaspis cancellata* Kjær, 1930

(Fig. 18C-F)

See Denison 1964: 440-441.

Holotype. – Dorsal shield PMO D 543a (Fig. 18C-D), (Kjær 1930, fig. 4b).

Paratype. – Dorsal shield PMO D 543b on the same slab (Fig. 18E).

*Locus typicus*. – Ben Nevis, western plateau, 300-400 m a.s.l., (locality no. 10).

*Stratum typicum*. – Ben Nevis Formation, equivalent of the *Vogti* horizon.

Other material. – Fragment of dorsal shield MNHN, SVD 599a from Ben Nevis, northern ridge, *Vogti* horizon (Fig. 18F, Blieck 1976, pl. X, 2 and 1983a).

Diagnosis. – See Denison 1964: 441.

Measurements. – Table 3.

Discussion. – The occurrence of MNHN, SVD 599a (with its typical outer surface of reticular ridges and tubercles) (Fig. 18C, F) in the *Vogti* horizon on the northern ridge of Ben Nevis and the occurrence of PMO D 543 on the western plateau of Ben Nevis ‘in a somewhat older layer than the rich *Ctenaspis* horizon’ (Kjær 1930: 7) confirms that the *Vogti* horizon has its equivalent on the cliff of the western plateau just below the *Ctenaspis* horizon (see Kjær & A. Heintz 1935: 14 and Blieck & N. Heintz 1979, fig. 4. locality ‘10?’).
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Fig. 18. Ctenaspis. A-B. C. dentata. A. Reconstruction of the dorsal shield with the lateral canal system. B. Reconstruction of the ventral shield (after Kiaer 1930, fig. 1; Stensiö 1964, fig. 79B). C-F. C. cancellata. C. PMO D 543a, dorsal shield, holotype, detail of the left anterior part. D. The same specimen, general view (same specimen as Kiaer 1930, fig. 4b). E. PMO D 543b, dorsal shield, paratype. F. MNHN SVD 599a, fragment of the right orbital region of a dorsal shield.

| Table 3. Measurements (in mm) and indexes of the *Ctenaspis* species from the Red Bay Group of Spitsbergen and of *C. kiaeri* from Podolia (for abbreviations, see p. 49). |
|-----------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|                | laO   | LoO   | laT   | LoT   | LaP   | laV   | LoO  | laT  | LoT  |
| *C. dentata*   |       |       |       |       |       |       |      |      |      |
| holotype D 582 | 10    | 3     | 17    | 25    | 7     |       | 3.33 | 0.68 | 0.12  | 0.28  |
| D 584          | 15    | 24    |       |       |       |       |      |      |       | 0.62  |
| *C. cancellata*|       |       |       |       |       |       |      |      |      |
| holotype D 543a| 11    | 3     | 24    | ?     | ?     |       | 3.67 | ?     | ?     |
| D 543b         | ?     | 25    | 29    |       |       |       | ?    | 0.86 | ?     |
| *C. kiaeri*    |       |       |       |       |       |       |      |      |      |
| lectotype C 1616| 9     | 3     | 15    | 22    | 6     |       | 3    | 0.68 | 0.14  | 0.27  |
| C 1619         | ?     | 3     | 23    |       |       |       | ?    | 0.78 | 0.13  |
| C 1634         | 11    | 3     | 17    | 23.5  | 6.5   |       | 3.67 | 0.72 | 0.13  | 0.28  |
Føyn & A. Heintz (1943: 42) report the occurrence of *Ctenaspis* in the Frøenkleryggen Formation, a fact which has not been noted (Friend 1961: 111; Denison 1964: 443), but needs to be confirmed (Bliéc & N. Heintz 1979, fig. 5). Denison (1956: 400) also reports 'a form related to *Ctenaspis* in the Psammosteus horizon of the Frøenkleryggen Formation perhaps after the specimen PMO D 500 with 'a *Ctenaspis*-like ornamentation of very fine tubercles' (Bliéc & A. Heintz 1979: 172). However, after comparison with specimens in the Bristol collection, we now think that PMO D 500 is not *Ctenaspis* but would more likely be a representative of another taxon of cyathaspid (see Elliott 1979).

*C. cancellata* is very closely related to *C. kiaeri* Zych (1931) from the Devonian of Podolia (= *Bothriaspis kiaeri* (Zych) in Obruchev 1964, fig. 22), but *C. kiaeri* is shorter and has a more anterior pineal macula (Table 3). The reconstruction of *Ctenaspis kiaeri* Zych by Obruchev (1964) is based on the specimens NHRM, C 1616 [lectotype designated by Denison 1964: 441, figured in Stensio (1958, fig. 176: 'C. kiaeri n. sp.'), 1964, fig. 78: 'C. zychi Stensio')] and in Obruchev (1964, fig. 22: 'Bothriaspis kiaeri'), C 1619 (Stensio 1958, fig. 178B; 1964, fig. 80B) and C 1634. These specimens are at present deposited in Oslo. *Ctenaspis zychi* Stensio (1958: 295) is therefore synonymous with *C. kiaeri* Zych (1931) from the Iwane horizon of Podolia ('passage beds', Obruchev 1964, Denison 1964).

*Fig. 19. Biozonation of the cyathaspidi in the Red Bay Group of Spitsbergen. * - stratum typicum of each species. + - other records.*

Ctenaspis sp. indet.

Some fragments PMO D 830, PMO D 1886, PMO D 4011 and PMO D 3055 have been found in respectively the Benneviaspis, O, *Rotundata* and I horizons of the Ben Nevis Formation.

Biozonation

According to the reviewed vertical distribution of the cyathaspidi in the Red Bay Group (Fig. 19), it is quite obvious that the Frøenkleryggen and Ben Nevis Formations have different faunal assemblages. The Frøenkleryggen Formation is characterized by a *Dinaspidella–Poraspis brevis–Anglaspis insignis–* A. heintzi *assemblage while the Ben Nevis Formation has a typical *Irregulareaspis–Poraspis rostrata–Homalaspida–Anglaspis elongata–* Ctenaspis assemblage. *Poraspis polaris* (new definition), the most abundant species of the whole fauna, occurs from the base up to the top of the sequence; thus the Frøenkleryggen Formation is well defined by the *P. polaris–P. brevis* assemblage and the Ben Nevis Formation by the *P. polaris–P. rostrata* assemblage. However, the representatives of *P. polaris* as newly defined are generally longer in the Ben Nevis Formation than in the Frøenkleryggen Formation.

As for correlations with the Canadian Arctic, we wrote (Bliéc & N. Heintz 1979: 178, Bliéc 1981: 157) that locality GSC 69014 (Dineley & Loeffler 1976: 5-7) might be related either to the Upper Frøenkleryggen Formation or to the Lower Ben Nevis Formation. The occurrence of *Protopteraspis vogti, Poraspis polaris*, and *Lepidaspis* at GSC 69014 is in our opinion an argument for correlating it more closely with the Ben Nevis Formation than with the Frøenkleryggen Formation. The occurrence of *Dinaspidella elizabethae* nom. nov. at GSC 69014 does not favour an argument against this correlation, because *D. elizabethae* is larger than *D. robusta* from the Frøenkleryggen Formation and can well be a later species of *Dinaspidella*. Another argument for correlating GSC 69014 with the Ben Nevis For-
mation is the recent discovery of specimen PMO D 3888–3889 from the Rotundata horizon, at the basis of the Ben Nevis Formation: this specimen is very like Canadapteraspis alacostomata Dineley & Loeffler (1976, pl. 17: 3) whose type locality is GSC 69014 (ibid.: 113).

Conclusions
This revision of the Spitsbergen Lower Devonian cyathaspidas has defined only twelve different species. Some of them give new morphological characters that allow us to propose new reconstructions (Irregularaspis hoelii, Poraspis polaris, Anglaspis heintzi, Ctenaspis dentata). The whole fauna can be well separated into two major assemblages: a lower one in the Frendelbyggen Formation and an upper one in the Ben Nevis Formation. Poraspis polaris, thought to be restricted to the Frendelbyggen Formation, is in fact a faunal component of the whole Red Bay Group, but is associated with different species in the two formations. It also appears that the Canadian Arctic and Spitsbergen Lower Devonian series have numerous common heterostracans (cyathaspidas and pteraspids mainly), due to a geographical proximity in those times. However, different palaeoecological interpretations have been proposed: in Canada the heterostracan-bearing beds are interpreted as lagoonal palaeoenvironments (see for instance Dineley & Loeffler 1976: 5–7), while in Spitsbergen they are thought to have been nearshore marine facies (Goujet & Blieck 1977). This disagreement first of all comes from the different lithologies, but mainly from the supposed palaeobiotopes of the agnathans themselves (freshwater or marine forms). In our opinion, this problem has not been satisfactorily solved and will need further investigation and comparison.

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