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

ALAIN BLIECK AND NATASCHA HEINTZ

Blieck, A. & Heintz, N. 1983: The Cyathaspids of the Red Bay Group (Lower Devonian) of Spitsbergen. The Downtonian and Devonian vertebrates of Spitsbergen. XIII. *Polar Research 1 n.s.*, 49–74. Oslo.

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; Irregulareaspis 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.*

Natascha Heintz, Paleontologisk museum, Sars gt. 1, Oslo 5, Norway; Alain Blieck, Muséum National d'Histoire Naturelle, Institut de Paléontologie, L.A. 12 du C.N.R.S., 8 rue de Buffon, F-75005, Paris, France. Present address: Université de Lille, UER Sciences de la Terre, Laboratoire de Paléobotanique, GRECO 130007 du CNRS, Villeneuve d'Ascq, F-59655 Cedex, France. June 1982 (revised September 1982).

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.

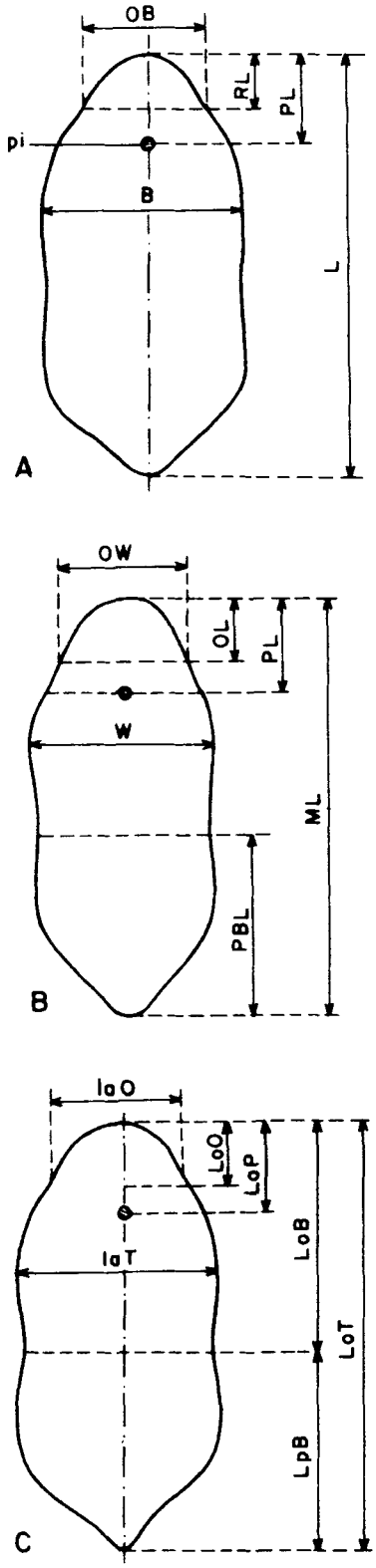
Measurements and indexes used on the dorsal and ventral shields are presented in Fig. 1.

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
cl, cloaca
D, dorsal shield
D(r), dorsal shield (rostal part)
laO, orbital width of D
laT, total width of D
laV, total width of V
lc, lateral canal of trunk (external pores)
ld.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



ov.B, overlap area for the suborbital plate
ov.Or, overlap area for anterior oral plates
ov.V, overlap area for the oral cover
ov.3, overlap area of the third (3) and the fourth (4) oral platlets.
pi, pineal macula
pi.c, pineal canal (external pores)
ppc, prepineal canal (external pores)
ri/mm, number of denting ridges per mm
SO, suborbital plate
V, ventral disc

Systematics

Order Cyathaspidiformes Berg (1940: Cyathaspiformes).
Definition. – See Denison, 1964:350–351 ('Cyathaspididae').

Superfamily PORASPIDOIDEA Kiær (1932: tribe Poraspidei = Poraspidoidei Berg, 1940)
Definition. – See Kiær, 1932:8 and 12.

Family IRREGULAREASPIDIDAE Kiær & A. Heintz (1935: Irregularaspidae)
Definition. – See Denison, 1964:396 ('Irregulareaspidinae').

Type genus. – *Irregulareaspis* Zych, 1931.

Genus *Dinaspidella* Strand, 1934

Definition. – See Denison, 1964:399.

Type species – *Dinaspis robusta* Kiær, 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 (Kiær, 1932)

(Fig. 2)
□ 1932. *Dinaspis robusta* n.gen. & sp. – Kiær, 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 Kiær & A. Heintz (1935: 48). B. After Denison (1964: 317). C. After the present authors (for abbreviations, see pp. 49–50).

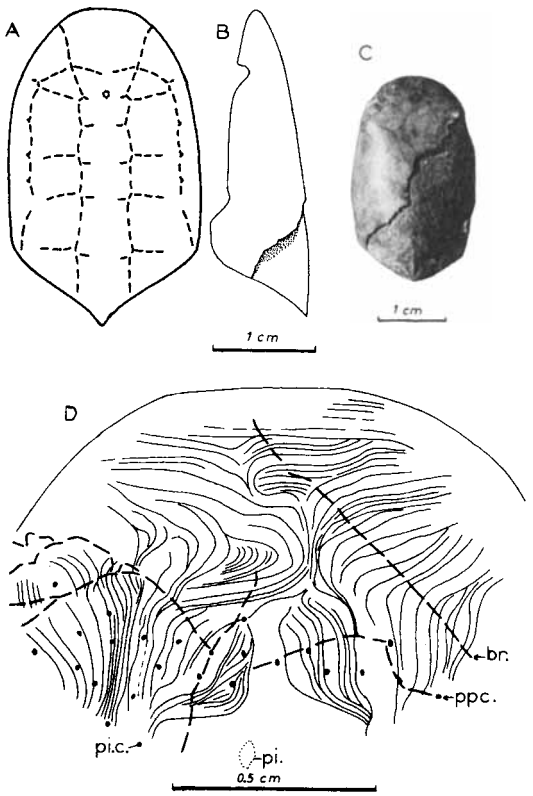


Fig. 2. Dinaspidella robusta, PMO D 454, holotype, dorsal shield. A. Reconstruction of the pattern of the lateral canal system. B. Left lateral view. C. External view of the specimen. D. Detail of the anterior part showing the pattern of some of the dentine ridges, of which there are about 12 ridges pr. mm.

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

Locus typicus. – Frænkelryggen, 300 m a.s.l. (locality no. 4).

Stratum typicum. – Frænkelryggen Formation, *Primaeva* horizon.

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

Diagnosis. – A rather small species of *Dinaspidella* with laT = 17.5 mm and LoT = 31 mm.

Measurements (in mm) and indexes of the type specimen PMO D 454. –

laO	LoO	laT	LoT	LoP	LpB	$\frac{laO}{LoO}$	$\frac{laT}{LoT}$
15	7	17.5	31	9	12	2.14	0.56

$\frac{LoO}{LoT}$	$\frac{LoP}{LoT}$	$\frac{LpB}{LoT}$	$\frac{ri}{mm}$
0.22	0.29	0.39	12

Discussion. – Denison (1964:399) and Dineley & Loeffler (1976:91) think that *Dinaspidella* 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. *Dinaspidella* Strand (1934), in replacement of *Dinaspis* Kiær (1932), is available because *Dinaspis* is based on a type species, *D. robusta* Kiær, which is not a *nomen nudum* as there is a statement and figures (Kiær 1932:18, figs. 7–8, pl. IV, 2–3) 'that purport to give characters differentiating the taxon' (ICZN art. 13a–b). However, *Dinaspis parvula* (Kiær 1932:18) remains a *nomen nudum.*

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

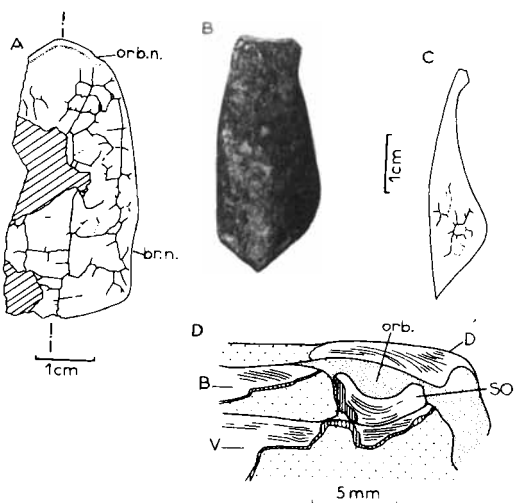


Fig. 3. Irregulareaspis. A. *Irregulareaspis* sp. indet., PMO D 228, visceral face of a dorsal shield with the pattern of the lateral canal system. B–D. *I. hoeli.* B. PMO D 495. Paratype, ventral disc, external view. C. Left lateral view of the same specimen. D. PMO D 474. Holotype, detail of the right orbital region.

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 stensiö'i* Zych, 1931 here emended as *I. stensioei* Zych [*I. stensiöi* 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* (Kiær, 1932), *I. mirabilis* n. sp.

Irregulareaspis hoeli (Kiær, 1932))
(Figs. 3B, C, D, 4A, B. C).
□ 1932. *Dictyaspis hoeli* n.gen. & sp. – Kiær, fig. 10, pl. V, 1–2, pl. VI, 2–3. □ *1958. Irregulariaspis hoeli* (Kiær) [sic] – Stensiö, fig. 216D. □ *1964. Irregulareaspis hoeli* – Denison, fig. 99E. □ 1964. *Irregulareaspis hoeli* (Kiær) – Obruchev, fig. 18b, pl. I, 1–2, pl. II, 6. □ *1964. Irregulariaspis hoeli* (Kiær) [sic] – Stensiö, fig. 121D.

Holotype. – Articulated specimen PMO D 474 (Fig. 4A, B) (Kiær 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). (Kiær 1932, pl. VI, 2–3) and internal mould of dorsal shield PMO D 497 from Tunge locality (Kiær & 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	LaV	LoV
15	(9)	(19)	(37)	(12)	12	16–18	38–40

$\frac{laO}{LoO}$	$\frac{laT}{LoT}$	$\frac{LoO}{LoT}$	$\frac{LoP}{LoT}$	$\frac{LpB}{LoT}$	$\frac{lav}{LoV}$	$\frac{ri}{mm}$
1.66	(0.51)	(0.24)	(0.32)	0.32	0.42–0.45	8

Discussion. – The ventral discs of *Dictyaspis hoeli* Kiær (1932, fig. 10 and pl. VI, 2–3) have a shape and sensory canals which differentiate the taxon. Thus *D. hoeli* Kiær 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* Kiær (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* Kiær in the genus *Irregulareaspis* Zych (cf. Kiær *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 Kiær and *D. prisca* Kiær are actually *nomina nuda* (Denison 1964: 402) because the type-specimens on which Kiær (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 *Nahanniaspis 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

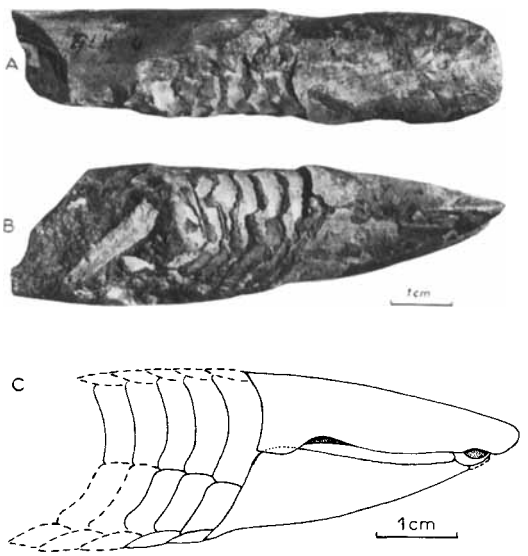


Fig. 4. Irregulareaspis hoeli, PMO D 474, holotype. A. Articulated specimen, dorsal view. B. Right lateral view. C. General reconstruction in right lateral view.

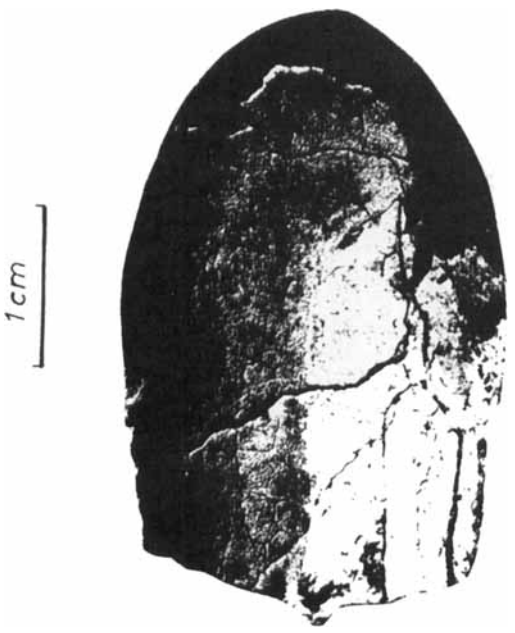


Fig. 5. Irregulareaspis mirabilis nov. sp., PMO D 210. Holotype, visceral face of dorsal shield.

posterolateral corner of the shield (Dineley & Loeffler 1976, fig. 34).

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, *Vogti* 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/LoT	LoP/LoT	LpB/LoT
(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 *Vogti* 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-

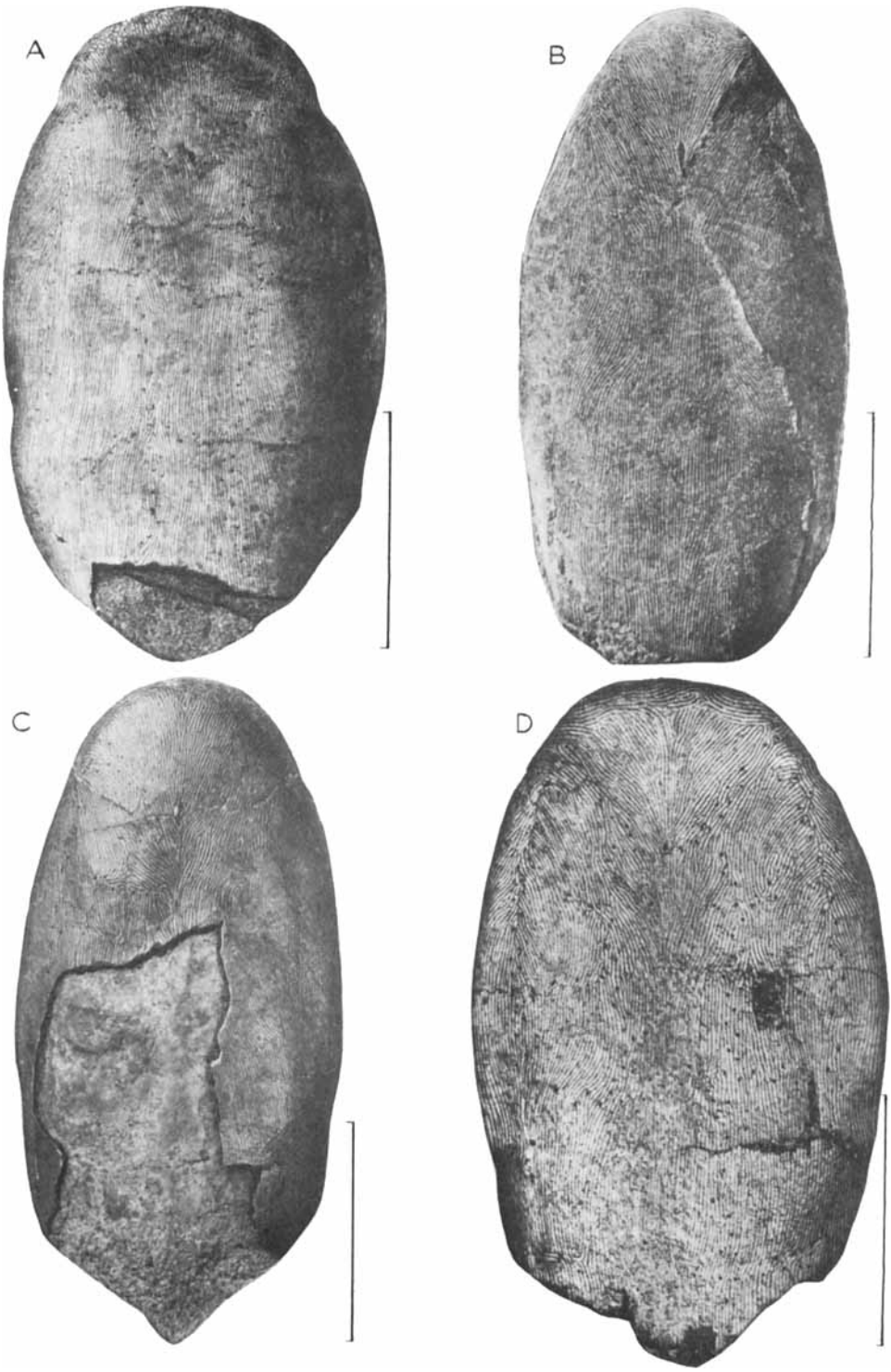


Fig. 6. Poraspis brevis – new definition – dorsal shields. A. PMO D 304, holotype (Kiær & A. Heintz 1935, pl. XIV). B. PMO D 1904, type of '*P. subtilis*' (ibid., pl. XXII). C. PMO D 1308, type of '*P. intermedia*' (ibid., pl. XVI). D. PMO D 293, '*P. intermedia*' (ibid., pl. XVII) (scale 1 cm).

tion, Blieck & N. Heintz 1979: 174), previously referred to as *Dinaspidella* sp., has a lateral canal system closely resembling that of *Irregulareaspis hoeli* 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. hoeli* 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 *Dinaspidella* specimen; thus restricting *Dinaspidella* to the Frænkelryggen Formation and *Irregulareaspis* to the Ben Nevis Formation, as already mentioned by Kiær in 1932.

Family PORASPIDIDAE Kiær (1932; Poraspidae)

Definition. – See Denison 1964: 402 ('Poraspidinae').

Type genus. – *Poraspis* Kiær, 1930.

Genus *Poraspis* Kiær, 1930

Definition. – See Denison 1964: 403.

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

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

Poraspis brevis Kiær, 1932

(Fig. 6)

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

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

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

Stratum typicum. – Frænkelryggen Formation, *Primaeva* horizon.

Other material. – From the *Corvaspis* horizon up to the *Anglaspis* horizon (see Kiær & 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 Frænkelryggen Formation. The three taxa *P. brevis, P. subtilis* and *P. intermedia* introduced by Kiær (1932) and Kiær & A. Heintz (1935) must presumably be considered as three populations of a single species here reviewed as *P. brevis* Kiær. There are no significant morphological differences between the known specimens of the three species of Kiær & 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 Kiær & A. Heintz) is most likely only individual variations. However, some wider or narrower shields may also be due to tectonic and/or diagenetic deformations, as will be illustrated below for *P. polaris* (Fig. 8) (see also Denison 1964: 406 and 415, Dineley & Loeffler 1976: 78).

Poraspis polaris Kiær, 1930

(Figs. 7, 8, and 9)

□ 1930. *Poraspis polaris* n. gen. & sp. – Kiær, fig. 3a–b. □ 1932. *Poraspis polaris* n. gen. & sp. (sic) – Kiær, figs. 1–2, pl. I. □ 1932. *Poraspis cylindrica* n. gen. & sp. – Kiær, pl. III, 3. □ 1935. *Poraspis polaris* Kiær – Kiær & A. Heintz, figs. 2, 3, 5, 7–14, pls. I–VIII, IX, 2, X, 1, XI–XIII, 1, XXVI, 1, XXXI, 1, XXXII, 2, XXXIV, 1–5, XXXV–XXXVII, XXXVIII, 1. □ 1935. *Poraspis elongata* n. sp. – Kiær & A. Heintz, figs. 24–26, pls. IX, 3, X, 2, XVIII–XX, XXVII, 1. □ 1935. *Poraspis rostrata* n. sp. *pro parte* – Kiær & A. Heintz, pl. XXIV, 1. □ 1935. *Porapis cylindrica* n. sp. *pro parte* – Kiær & A. Heintz, pl. XXVI, 2. □ *1941. Poraspis polaris* Kiær – Säve-Söderbergh, fig. 5. □ *1942. Poraspis polaris* Kiær – Holmgren, fig. 7. □ *1958. Poraspis* cf. *polaris* Kiær, *Poraspis polaris* f. *angusta* Kiær and *Poraspis cylindrica* Kiær – Stensiö, figs. 166B, 167B, 179B and 216A–B. □ *1964. Poraspis polaris* Kiær – Denison, figs. 98A, 99A, 137 and 102A. □ *1964. Poraspis* cf. *polaris* Kiær, *Poraspis polaris* f. *angusta* Kiær and *Poraspis cylindrica* Kiær – 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). (Kiær 1932, pl. I, Kiær & A. Heintz 1935, pls. II and XXXIV, 2, Denison 1964, fig. 137).

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).

		laO	LoO	laT	LoT	LoP	LpB	laV	LoV	laO/LoO	laT/LoT	LoO/LoT	LoP/LoT	LpB/LoT	laV/LoV	ri mm	n°
P. brevis (new definition)																	
P. brevis (type)	D 304	12	4	17	27	6	11			3	0.63	0.15	0.22	0.41		8	1
	D 1259	10	4	14	24	6	?			2.50	0.58	0.17	0.25	?		7	2
	D 368	11	4.5	17	26.5	6.5	11			2.44	0.64	0.17	0.24	0.41		7	
	D 87							15	21						0.71		
	D 299							15.5	23						0.67	8	
'P. intermedia'	D 1308	11	4	15	29.5	6	11			2.75	0.51	0.13	0.20	0.37		7	4
	D 293	11	4	16	26	6.5	11			2.75	0.61	0.15	0.25	0.42		7	5
'P. subtilis'	D 1904	8	3.5	14	26	5.5	10.5			2.28	0.54	0.13	0.21	0.40		6	6
P. polaris (new definition)																	
P. polaris (type)	D 665	12	6	18.5	40	9	14			2	0.46	0.15	0.22	0.35		9	7
	D 241a	12	5	20	37	7	14			2.40	0.54	0.13	0.19	0.38		?	8
	D 241b	13	4	20	32	8	13			3.25	0.62	0.12	0.25	0.41		?	9
	D 241c							20	28						0.71	?	
	D 206							16	26.5						0.60	5	
	D 115	13	5	23	34	8.5	14			2.60	0.68	0.15	0.25	0.41		5	10
	D 113							19	28						0.68	7	
	D 001	12.5	6.5	18	36.5	9	14			1.92	0.49	0.18	0.25	0.38		8	11
	D 38							18	27.5						0.65	7	
	D 204a	12	5.5	17	36	8.5	14			2.18	0.47	0.15	0.24	0.39		7	12
	D 204b	14	7	20	36.5	9	15			2	0.55	0.19	0.25	0.41		7	13
	D 002	11.5	5.5	19	39	9	14			2.09	0.49	0.14	0.23	0.36		7	14
	D 36							16	?						?	?	
	D 101							16.5	26.5						0.62	?	
	D 198	11	5.5	16.5	32	7.5	14			2	0.51	0.17	0.23	0.44		6	15
	D 28b	11	5.5	18	40	8	?			2	0.45	0.14	0.20	?		8	16
	D 1161	11	4	19	34	6.5	14			2.75	0.56	0.12	0.19	0.41		7	17
'P. elongata'	D 141a	12.5	8	19	41.5	10.5	16			1.56	0.46	0.19	0.25	0.38		9	18
	D 141b							16	30						0.53	6	
	D 147	9	4.5	15.5	32	9	?			2	0.48	0.14	0.28	?		7	19
	D 35							16	30						0.53	6	
	D 84	13	5	20	37	9	13			2.60	0.54	0.13	0.24	0.35		6–7	20
'P. rostrata'	D 128	13.5	8	21	?	11.5	?			1.69	?	?	?	?		7	
'P. cylindrica' (type)	D 205	13.5	8.5	21	44	11.5	17			1.59	0.48	0.19	0.26	0.39		7	21
P. rostrata (new definition)																	
P. rostrata (type)	D 124	15	10	22.5	50.5	13.5	20			1.50	0.44	0.20	0.27	0.40		8	22
	D 135							18	42						0.43	6	
	D 1798							20	38						0.53	?	
'P. cylindrica'	D 140	15	9	24	53	13	23			1.67	0.45	0.17	0.24	0.43		6	23
'P. magna'	D 203	18	11	26	61	15	24			1.64	0.43	0.18	0.24	0.39		6–7	24
	D 200	?	?	25	52	16	?			?	0.48	?	0.31	?		?	25
	D 138	18	10	25	?	13	?			1.80	?	?	?	?		?	
	D 139							23	?						?	?	
	D 278							25	54						0.46	?	

Locus typicus. – Frænkelryggen, 250 m a.s.l. (locality no. 5).

Stratum typicum. – Frænkelryggen Formation, *Polaris* horizon.

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

Diagnosis. – A medium-sized species of *Poraspis* with $32 \leq LoT \leq 44$ mm; $6.5 \leq LoP \leq 12$ mm and $13 \leq LpB \leq 17$ 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 & Loeffler (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, Stensiö 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 Stensiö 1964: 328).

Thus we think that *P. barroisi* (Leriche), *P. sturi* (Alth), *P.* cf. *polaris* Dineley & Loeffler, *'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

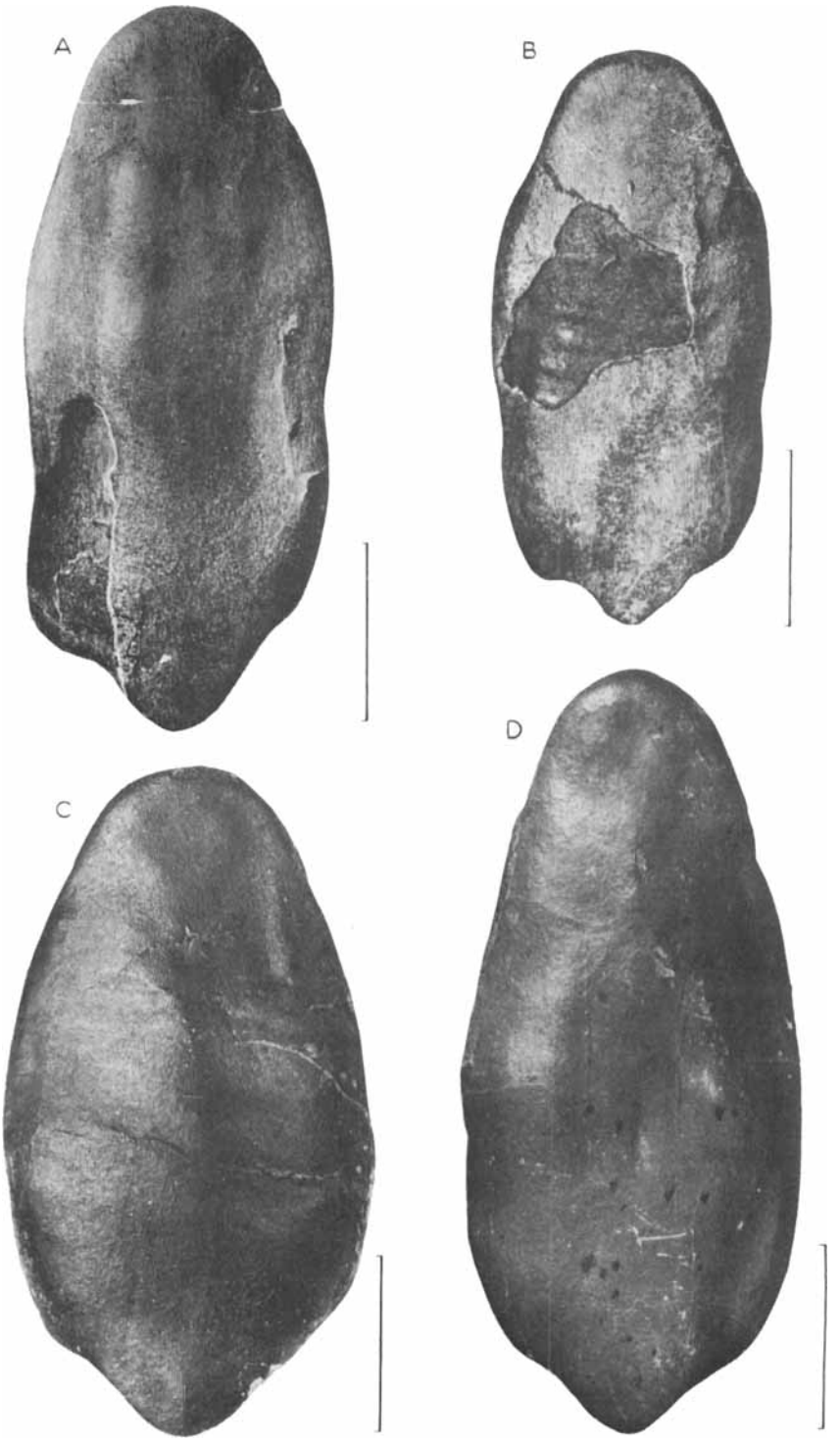


Fig. 7. Poraspis polaris – new definition – dorsal shields. A. PMO D 665, holotype (Kiær & A. Heintz 1935, pl. II). B. PMO D 198 (ibid., pl. XIII). C. PMO D 84, '*P. elongata*' (ibid., pl. XXVII, fig. 1). D. PMO D 141a, type of '*P. elongata*' (ibid., pl. XIX) (scale 1 cm).

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 Frænkelryggen, SMC No. F 1315k, shows the left suborbital plate in connection with the dorsal shield and the left branchial plate (Fig. 9A) as on *Irregulareaspis 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 Kiær & 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 Stensiö (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, *ov.V*) and the left suborbital plate (Fig. 9B, *ov.B.*). We find it reasonable to assume that the anterior area of the oral cover (*ov.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 Kiær & A. Heintz, 1935 (ex Kiær, 1932)

(Fig. 10)

□ 1932. *Poraspis rostrata* n. sp. – Kiær, pl. III, 1–2 (*nomen nudum*). □ 1935. *Poraspis rostrata* n. sp. *pro parte* – Kiær & A. Heintz, figs. 27–28, pls. XXIII–XXV and XXXIX (but not pl. XXIV, 1). □ 1935. *Poraspis cylindrica* n. sp. *pro parte* – Kiær & A. Heintz, figs. 29–30, pls. XXVII, 2 and XXIX, 1 (but not pl. XXVI, 2). □ 1935. *Poraspis magna* n. sp. – Kiær & A. Heintz, figs. 31–32, pls. XXVIII, XXIX, 2, 4, XXXVIII, 2. □ *1941. Poraspis magna* Kiær & A. Heintz – Säve-Söderbergh, fig. 4. □ 1976. *Poraspis rostrata* Kiær & A. Heintz *pro parte* – Blieck, pl IX.

Holotype. – Dorsal shield PMO D 124 (Fig. 10A; Kiær & 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 Kiær & 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 Kiær (1932) was a *nomen nudum*, because it was based on a non-diagnostic ventral shield. But Kiær & A. Heintz (1935) validated

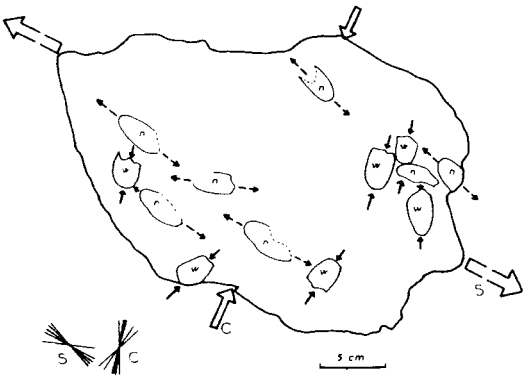


Fig. 8. Slab PMO D 241, with numerous shields of *Poraspis polaris* to show the possible biometric variations due to tectonic and/or diagenetic deformations (see Kiær & A. Heintz 1935, pl. I). *n*, narrower shields. *w*, wider shields. *C*, crushing. *S*, stretching.

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* Kiær & 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 nitider* Kiær, 1932.

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

Homalaspidella nitida (Kiær, 1932)

Before 1964, see Denison 1964: 421.

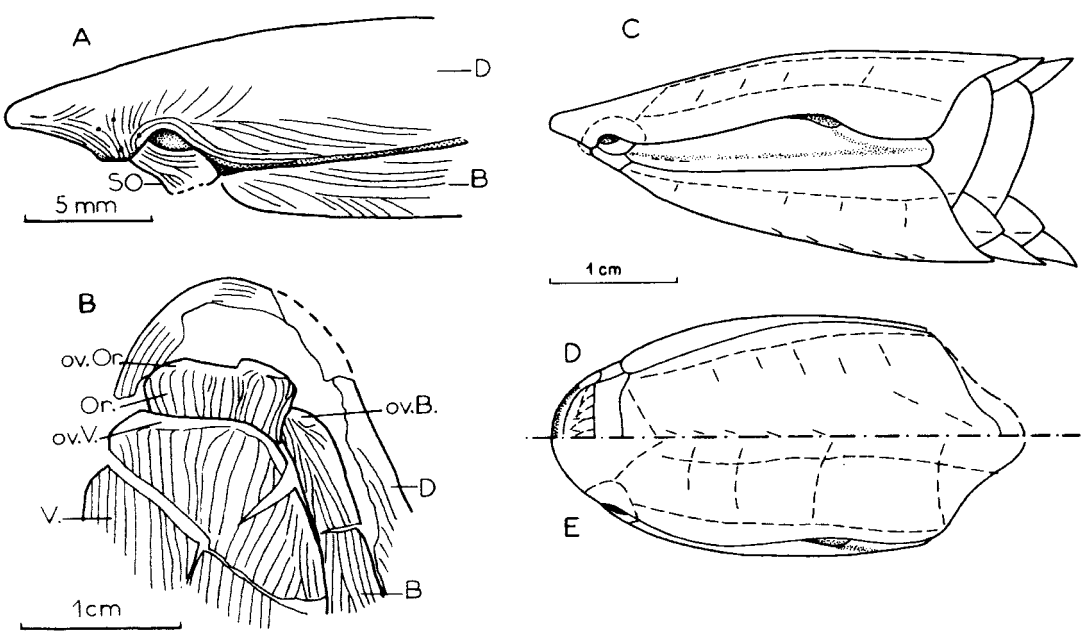


Fig. 9. Poraspis polaris. A. Specimen SMC F 1315k, left lateral view of the dorsal shield. B. Specimen NMC 19860, external view of the ventral shield (after Dineley & Loeffler 1976. fig. 25). C, D, E. General reconstruction. C. In left lateral view. D. In ventral view. E. In dorsal view. (C, D, E after Kiær & A. Heintz 1935, fig. 52, complemented).

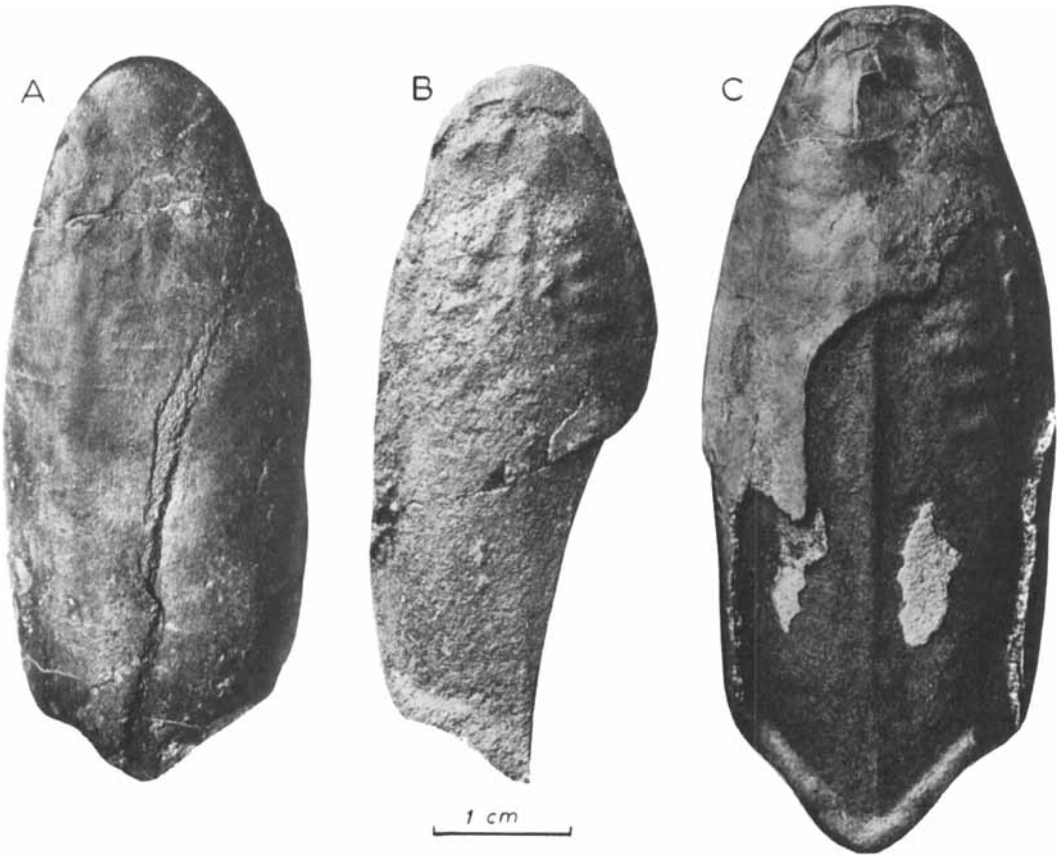


Fig. 10. Poraspis rostrata – new definition – dorsal shields. A. PMO D 124, holotype (Kiær & A. Heintz 1935, pl. XXIII). B. PMO D 140, *'P. cylindrica'* (ibid., pl. XXIX, fig. 1). C. PMO D 203, type of *'P. magna'* (ibid., pl. XXVIII, fig. 1).

□ *1964. Homalspidella nitida* (Kiær) – Denison, figs. 98D, 99C and 144. □ *1964. Homalaspidella nitida* (Kiær) – Stensiö, figs. 82B and 108B.

Holotype. – Dorsal shield PMO D 156 (Kiær 1932, pl. IV, 1, Kiær & 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 (Kiær & 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 (Kiær & 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, Kiær & 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., Kiær & A. Heintz 1935: 128 and pl. XXXII: 1, Blieck & N. Heintz 1979: 175), specimens MNHN, SVD 504/I, 566, 597 (Ben Nevis, northern ridge, *Vogti* horizon, Blieck 1976, fig. 21, pls. X: 1 and XIX:

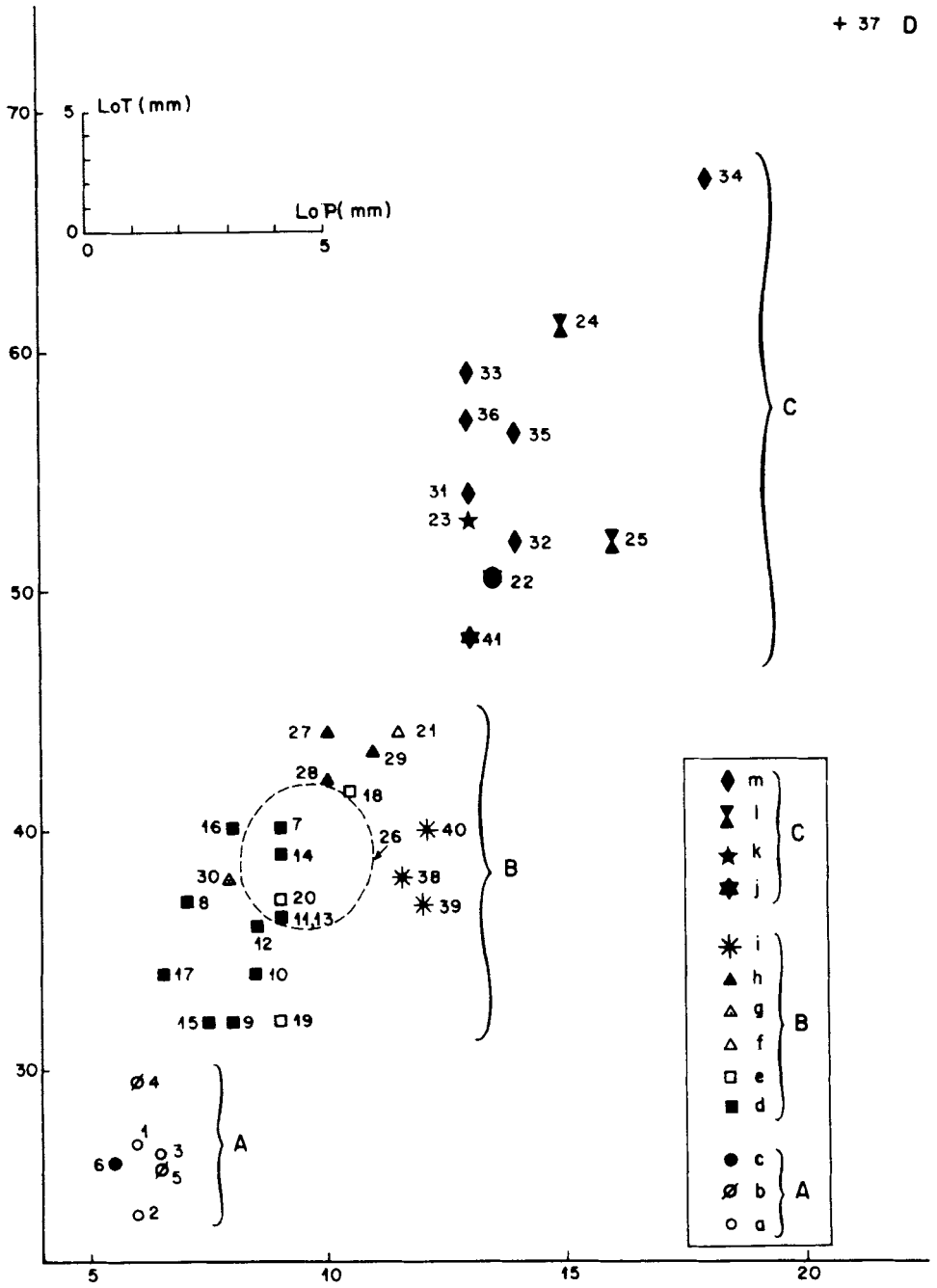


Fig. 11. Diagram of LoP/LoT for various specimens of *Poraspis*. A. *Poraspis brevis* (new definition), a, *P. brevis*; b, *'P. intermedia'*; c, *'P. subtilis'*. B. *Poraspis polaris* (new definition) – *P. sturi* – *P. barroisi*; d, *P. polaris*; e, *'P. elongata'*; f, type of *'P. cylindrica'*; g, *P. sturi*; h, *P. barroisi*; i, *'P. rostrata' in* Blieck (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 & Loeffler (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, 1598e); 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 (Blieck 1976, pl. IX).

4) and ?SVD 611 (Frænkelryggen, *Anglaspis* horizon, Blieck 1976, pl. III, 2).

Diagnosis. – See Denison 1964: 421–422.

Comparison of LoT and LoO/LoT of the species of Homalaspidella. – (After Kiær & A. Heintz 1935, Blieck 1976, Denison 1963, Dineley & Loeffler 1976, Loeffler & Jones 1976).

Discussion. – The specimen PMO D 264 from Ben Nevis (northern plateau, *Vogti* horizon, Kiær & A. Heintz 1935: 132), the holotype of '*Homalaspis nitida* var. *robusta*' Kiær (1932: 14) is only a big individual of *H. nitida* (cf. Denison 1964: 422).

The different species of *Homalaspidella* presently known are badly distinguished on the basis of their measurements and indexes. The main differences are the following morphological ones:

– *H. borealis* has longitudinal sensory canals divided into short lengths, while they are continuous on *H. nitida*

– The rostral part with transverse dentine ridges is long on *H. borealis* and *H.* cf. *borealis*, but short on *H. nitida.*

– The dorsal and ventral shields of *H. borealis* have a distinct external zone with concentric ridges that we do not clearly see on *H. nitida.* But they all have a distinct pineal macula (Dineley & Loeffler 1976: 82) in contrast to the statement by Denison (1964: 424).

Homalaspidella? sp. indet.

The very small ventral disc PMO D 207 from the debris below the south plateau of Ben Nevis, lower part of the Ben Nevis Formation (Kiær & A. Heintz 1935, pl. XXVI, 3), is really not typical and should perhaps not be considered as a *Homalaspidella.*

Specimen PMO D 1769–1770 from Frænkelryggen (300 m a.s.l., *Primaeva* horizon, Blieck & N. Heintz 1979: 171), if really belonging to *Homalaspidella* 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 Kiær, 1932)

(Figs. 12 and 13A–F)

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

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

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

Paratypes. – Dorsal shields PMO D 186a (Fig. 12D). (Kiær 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* Dineley & Loeffler	*H.* cf. *borealis* Loeffler & Jones
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* Kiær (1932) by comparison with the valid type species *A. macculloughi* (ICZN art. 13, Denison 1964: 431). *A. insignis* has been mentioned by Denison (1964: 431) from the *Primaeva* 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* Kiær (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 (Kiær & 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 Kiær, 1932)

(Figs. 15, 16)

□ 1932. *Anglaspis heintzi* n.g. & sp. Kiær, fig. 11 (*nomen nudum*).

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

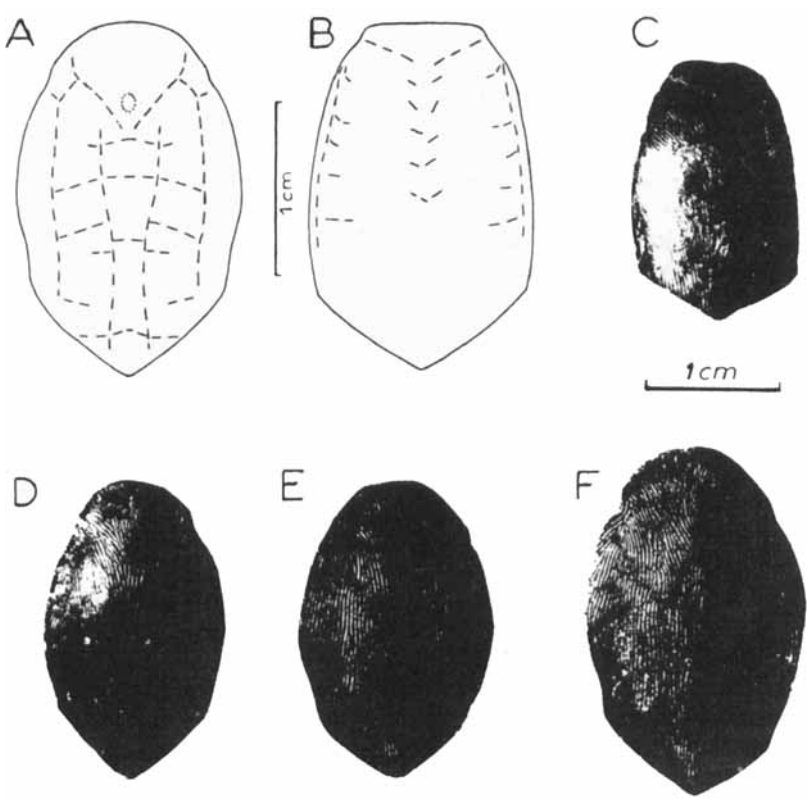


Fig. 12. Anglaspis insignis. A. Reconstruction of the dorsal shield with the lateral canal system. B. Reconstruction of the ventral disc with the lateral canal system. C. PMO D 186, holotype, ventral disc. D. PMO D 186a, paratype, dorsal shield. E. PMO D 355, dorsal shield. F. PMO D 367, dorsal shield (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).

		laO	LoO	laT	LoT	LoP	LpB	LaV	LoV	laO/LoO	laT/LoT	LoO/LoT	LoP/LoT	LpB/LoT	laV/LoV	ri/mm	n°
A. insignis																	
holotype	D 186							12	19						0.63	4	
	D 186a	9	4	13	21.5	5	3			2.25	0.60	0.19	0.23	0.14		3	1
	D 186b	9.5	3.5	12	20	5	2			2.71	0.60	0.17	0.25	0.10		3	2
	D 186c							11.5	19						0.60	3	
	D 186d							11.5	19						0.60	4	
	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	3
	D 364	9	3	13	19	4.5	3.5			3	0.68	0.16	0.24	0.18		3	4
	D 365	?	?	12.5	?	?	?			?	?	?	?	?		4	
	D 366							10	18						0.55	3	
	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	5
	D 355	10	3.5	14	21	5	2.5			2.86	0.67	0.17	0.24	0.12		3	6
	D 344							11	16						0.69	4	
	D 354	9	3.5	13	21.5	5	3			2.57	0.60	0.16	0.23	0.14		4	7
	D 191							12	21						0.57	3	
'A. platostriata'																	
	D 1115	10	5	14	25	6.5	4			2	0.56	0.20	0.26	0.16		3	8
A. heintzi																	
holotype	D 387	11	6	16	29	8	6			1.83	0.55	0.21	0.27	0.21		3	9
	D 384							13	22						0.59	3	
	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	10
A. elongata																	
holotype	D 1485	7	4	10	20	5	?			1.75	0.50	0.20	0.25	?		4	11
	D 1479							10	19						0.53	4	
	SVD 582							11	22						0.50	?	

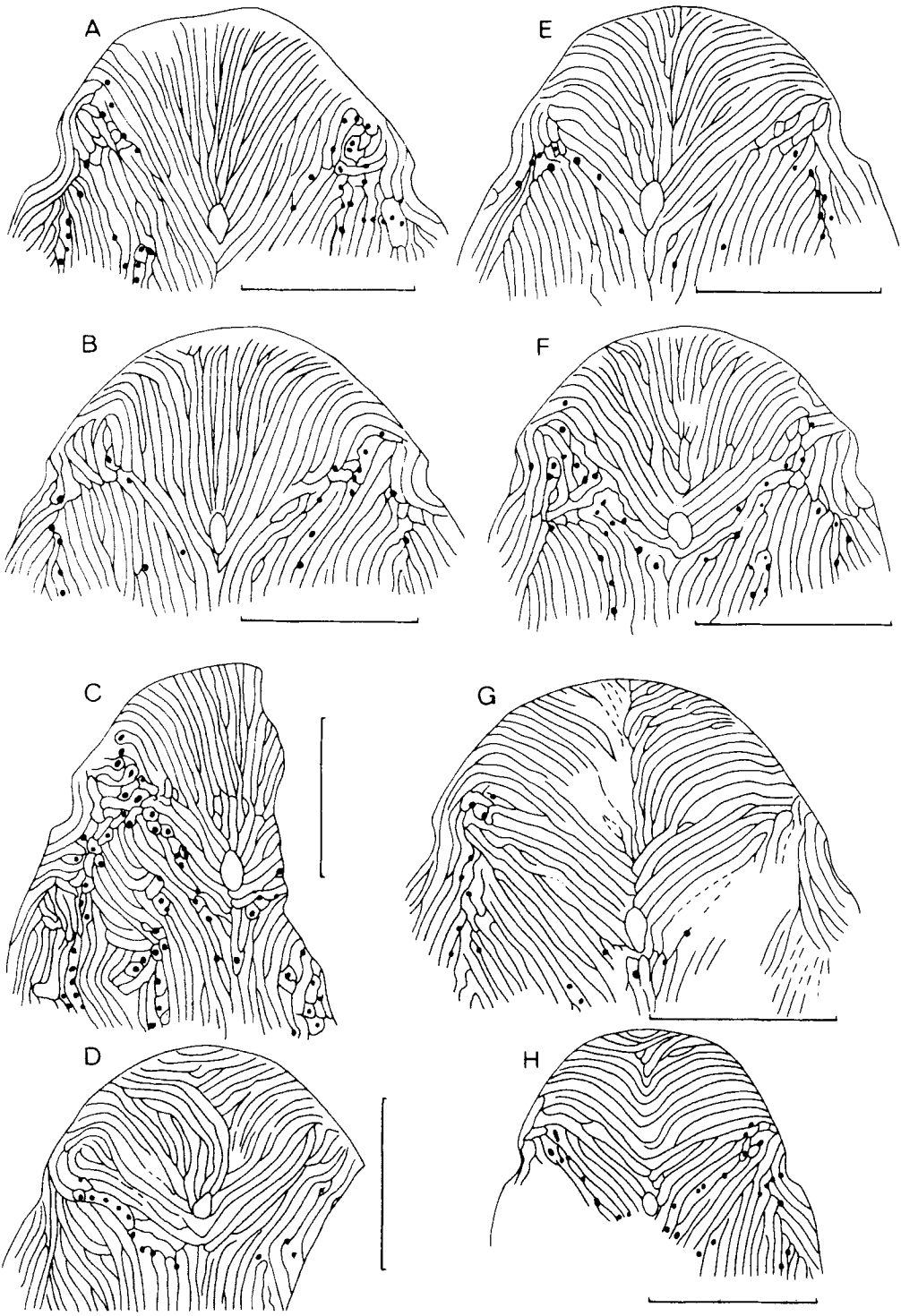


Fig. 13. Variation of the pattern of the dentine ridges on the rostral part of the dorsal shield of *Anglaspis* with the external pores of the lateral canal system. A–F. *A. insignis*. A. PMO D 367, B. PMO D 355, C. PMO D 188, D. PMO D 968, E. PMO D 186a, paratype, F. PMO D 186b, paratype, G. PMO D 1115, '*A platostriata*', H. PMO D 1485, *A. elongata* nov. sp., holotype. (Scale 5 mm).

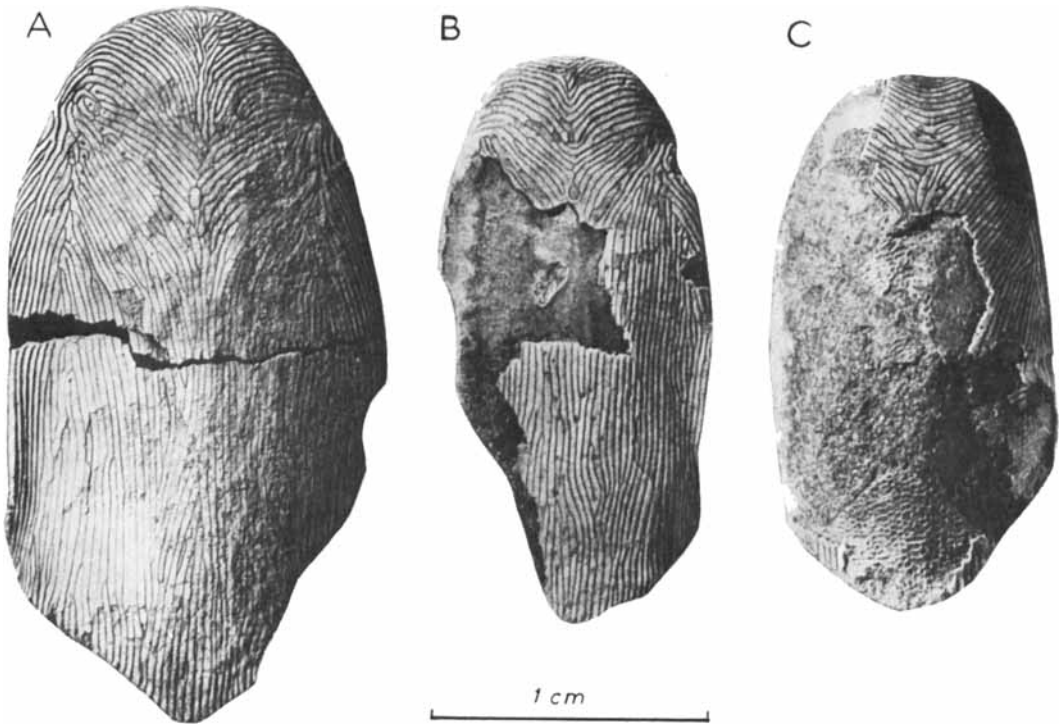


Fig. 14. Anglaspis. A. PMO D 1115, *'A platostriata'*, dorsal shield. B. PMO D 1485, *A. elongata* nov. sp., dorsal shield, holotype. C. PMO D 1479, *A. elongata* nov. sp., ventral disc., paratype.

Locus typicus and stratum typicum. – Frænkelryggen, isolated block 200 m a.s.l. coming from the *Primaeva* 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'* (Kiær 1932, pl. VI, 1, Stensiö 1958, figs. 180A and 205B, 1964, figs. 82A and 110B); all from the *Primaeva* 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'!) Kiær (1932, fig. 11) gave a reconstruction which has become classical (A. Heintz 1933, fig. 4; Moy-Thomas 1939, fig. 2A; Stensiö 1958, fig. 166A, 1964, fig. 68A; Tarlo 1962, fig. 3; Denison 1964, fig. 90; Obruchev 1964, fig. 19; Moy-Thomas & 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

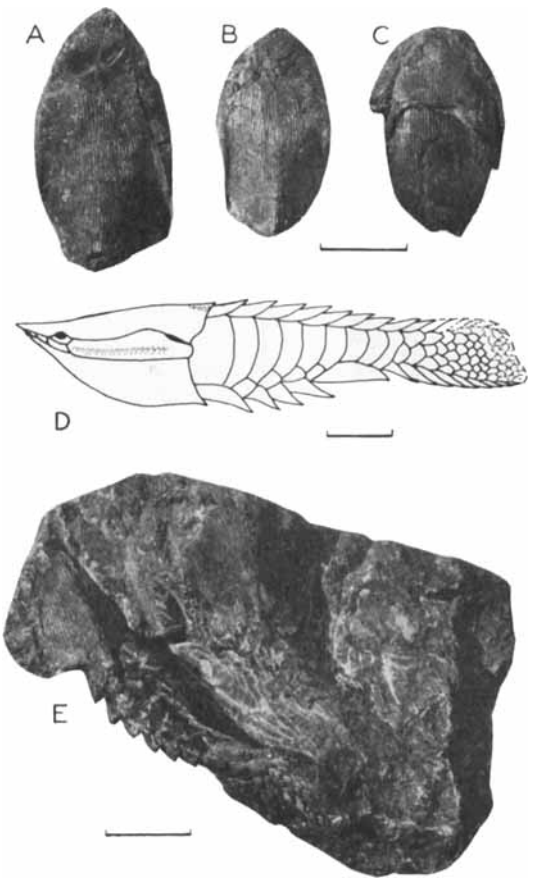


Fig. 15. Anglaspis heintzi nov. sp. A. PMO D 387, dorsal shield, holotype. B. PMO D 385, dorsal shield, paratype. C. PMO D 384, ventral shield, paratype. D. General reconstruction in left lateral view (after Kiær 1932, fig. 11, slightly modified). E. Slab PMO D 382a–b, articulated specimens, paratypes. 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 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 morphocline in both groups: 1 row → 2 rows (cf. Blieck 1980, 1981).

Anglaspis elongata n. sp. (ex Kiær, 1932)

(Figs. 13H and 14B–C)

□ 1932. *Anglaspis elongata* n. sp. – Kiær: 20 (*nomen nudum*).

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, *Vogti* 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 *Vogti* horizon, seem to be other representatives of *A. elongata*, particularly because of the great resemblance between the ventral shields of

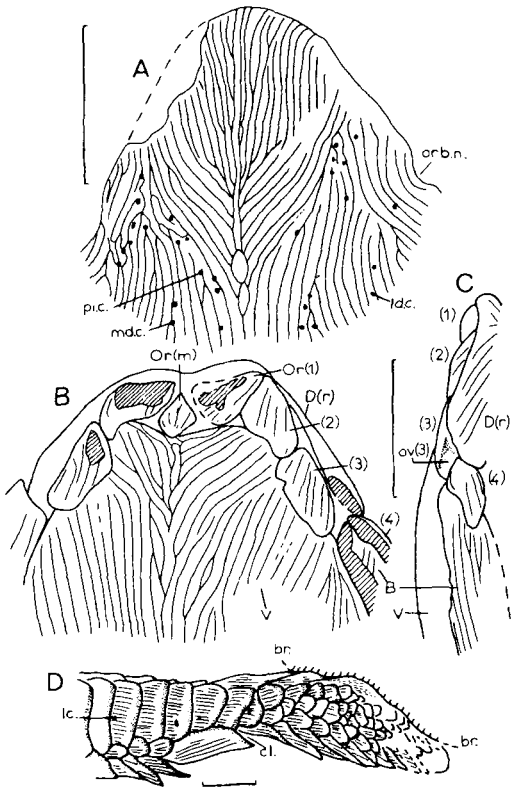


Fig. 16. Anglaspis heintzi nov. sp. A. Specimen PMO D 387, rostral part of the dorsal shield, holotype. B. PMO D 384, anterior part of the ventral shield with the oral plates, external view, paratype. C. The same specimen in left lateral view. D. PMO D 382a, trunk squamation and caudal fin, left lateral 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. heinzi* 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 Hoel's section (*Benneviaspis* horizon).

Family Ctenaspididae Kiær (1930, Ctenaspidae)

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

Type genus. – *Ctenaspis* Kiær, 1930.

Genus *Ctenaspis* Kiær, 1930

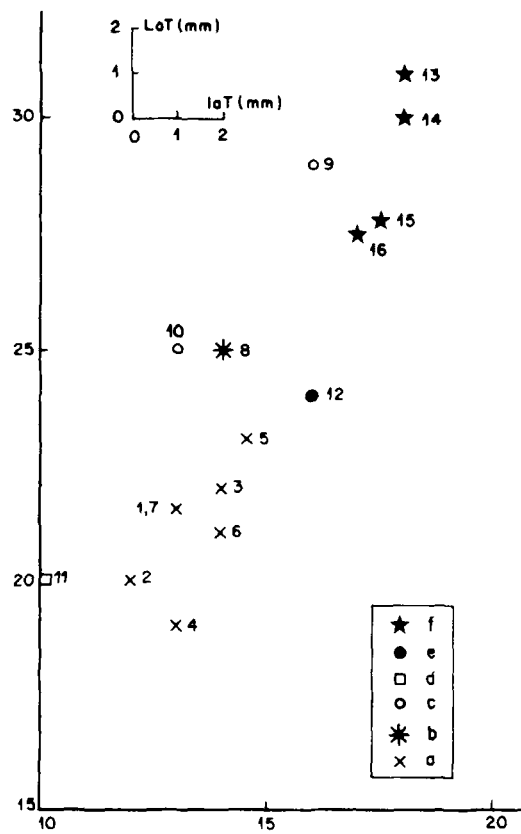


Fig. 17. diagram of laT/LoT for various specimens of *Anglaspis*. a. *A. insignis*. b. *'A. platostriata'*. c. *A. heintzi*. d. *A. elongata*. e. *A. expatriata*. f. *A. macculloughi*. For numbers 1–11, see Table 2. 12 – specimen NMC 10038 (holotype of *A. expatriata*; Denison 1964, fig. 151A). 13 – 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* Kiær, 1930.

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

Ctenaspis dentata Kiær, 1930

(Fig. 18A–B)
Before 1964, see Denison 1964: 440.
□ 1964. *Ctenaspis dentata* Kiær – Denison, figs. 97D, 99F, 101C, 154 and 155 (*pro parte* cop. Kiær, 1930). □ 1964. *Ctenaspis dentata* Kiær – Stensiö, fig. 79A–B.

Holotype. – Dorsal shield PMO D 582 (Kiær 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 (Kiær 1930, fig. 1b) from *Benneviaspis* 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 (Stensiö 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. obruchevi* Dineley with its less wide dorsal shield seems to be most closely related to *C. dentata* Kiær.

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 swam 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 Kiær, 1930

(Fig. 18C–F)
See Denison 1964: 440–441.

Holotype. – Dorsal shield PMO D 543a (Fig. 18C–D), (Kiær 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' (Kiær 1930: 7) confirms that the *Vogti* horizon has its equivalent on the cliff of the western plateau just below the *Ctenaspis* horizon (see Kiær & A. Heintz 1935: 14 and Blieck & N. Heintz 1979, fig. 4. locality '10?').

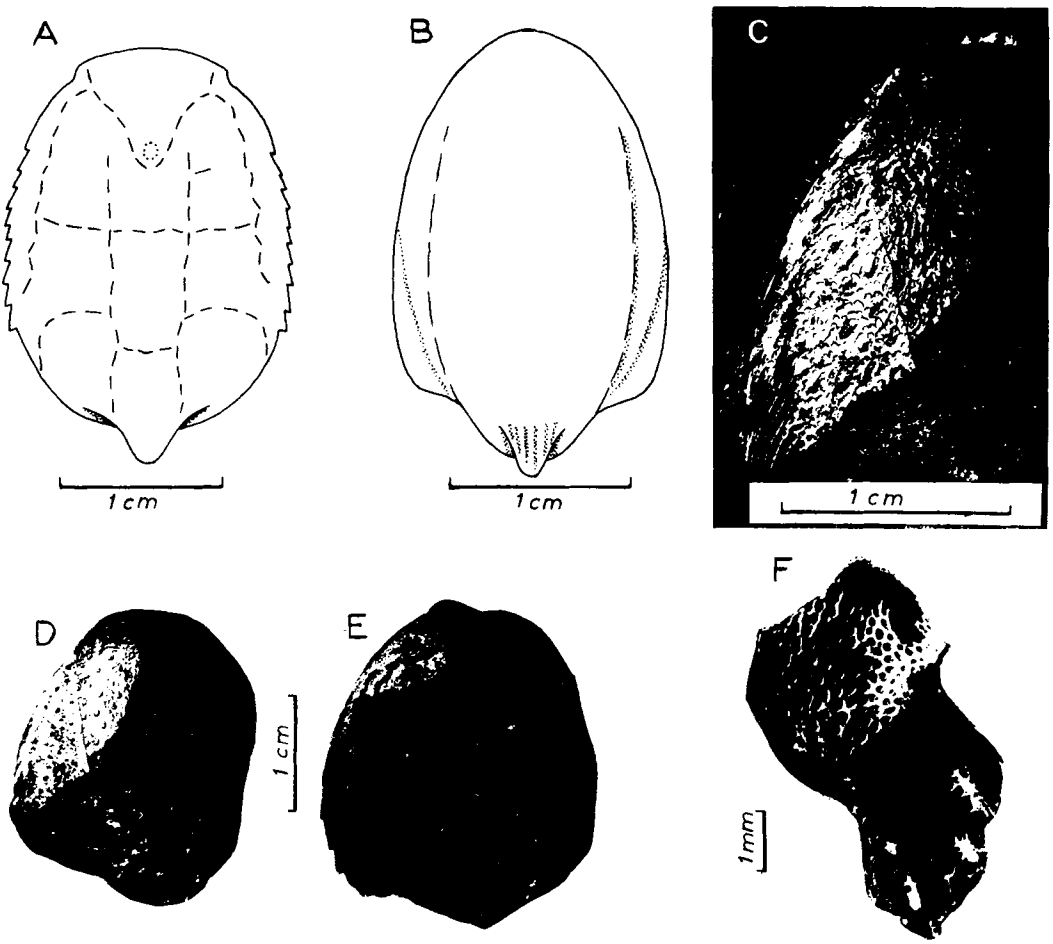


Fig. 18. Ctenaspis. A–B. *C. dentata.* A. Reconstruction of the dorsal shield with the lateral canal system. B. Reconstruction of the ventral shield (after Kiær 1930, fig. 1; Stensiö 1964, fig. 79B). C–F. *C. capcellata.* C. PMO D 543a, dorsal shield, holotype, detail of the left anterior part. D. The same specimen, general view (same specimen as Kiær 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	LoP	laV	LoV	$\frac{laO}{LoO}$	$\frac{laT}{LoT}$	$\frac{LoO}{LoT}$	$\frac{LoP}{LoT}$	$\frac{laV}{LoV}$
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	18	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 Frænkelryggen Formation, a fact which has not been noted (Friend 1961: 111; Denison 1964: 443), but needs to be confirmed (Blieck & N. Heintz 1979, fig. 5). Denison (1956: 400) also reports 'a form related to *Ctenaspis*' in the *Psammosteus* horizon of the Frænkelryggen Formation perhaps after the specimen PMO D 500 with 'a *Ctenaspis*-like ornamentation of very fine tubercles' (Blieck & 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 cyathaspids (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* Stensiö (1958, fig. 176: '*C. kiaeri* n. sp.', 1964, fig. 78: '*C. zychi* Stensiö') and *in* Obruchev (1964, fig. 22: '*Bothriaspis kiaeri)*], C 1619 (Stensiö 1958, fig. 178B; 1964, fig. 80B) and C 1634. These specimens are at present deposited in Oslo. *Ctenaspis zychi* Stensiö (1958: 295) is therefore synonymous with *C. kiaeri* Zych (1931) from the Iwane horizon of Podolia ('passage beds', Obruchev 1964, Denison 1964).

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 cyathaspids in the Red Bay Group (Fig. 19), it is quite obvious that the Frænkelryggen and Ben Nevis Formations have different faunal assemblages. The Frænkelryggen Formation is characterized by a *Dinaspidella–Poraspis brevis –Anglaspis insignis–A. heintzi* assemblage while the Ben Nevis Formation has a typical *Irregulareaspis – Poraspis rostrata – Homalaspidella – Anglaspis elongata – Ctenaspis* assemblage. *Poraspis polaris* (new definition), the most abundant

+ ✱ σ o	FRAENKELRYGGEN FM.						BEN NEVIS FORMATION							
	Psammosteus hor	Corvaspis hor	Plant horizon	Primadeva hor	Polaris hor	Anglaspis hor	Red horizon	Rotundata hor	A–I horizons	Vogti horizon	Ctenaspis hor	M–N horizons	Benneviaspis hor	S–U horizons
Dinaspidella robusta				✱										
Irregulareaspis hoeli													✱	
I. mirabilis n. sp										✱				
I. sp. indet														+
Poraspis brevis		+	+	✱	+	+								
P. polaris				+	✱	+			+	+			+	
P. rostrata									✱	+	+	+	+	+
Homalaspidella nitida									✱	+	+		+	
H. nitida ?						+								
H. ? sp. indet				+						+	+			
Anglaspis insignis						✱								
"A. platostriata"										+				
A. heintzi				✱										
A. elongata										✱				
A. sp. indet					~		~						+	
Ctenaspis dentata											✱		+	
C. dentata ?										+				
C. cancellata										✱				
C. sp. indet								+	+				+	

Fig. 19. Biozonation of the cyathaspids in the Red Bay Group of Spitsbergen. ✱ – stratum typicum of each species. + – other records.

species of the whole fauna, occurs from the base up to the top of the sequence; thus the Frænkelryggen 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 Frænkelryggen Formation.

As for correlations with the Canadian Arctic, we wrote (Blieck & N. Heintz 1979: 178, Blieck 1981: 157) that locality GSC 69014 (Dineley & Loeffler 1976: 5–7) might be related either to the Upper Frænkelryggen 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 Frænkelryggen 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 Frænkelryggen 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 alocostomata* Dineley & Loeffler (1976, pl. 17: 3) whose type locality is GSC 69014 (ibid.: 113).

Conclusions

This revision of the Spitsbergen Lower Devonian cyathaspids has defined only twelve different species. Some of them give new morphological characters that allow us to propose new reconstructions (*Irregulareaspis hoeli, Poraspis polaris, Anglaspis heintzi, Ctenaspis dentata*). The whole fauna can be well separated into two major assemblages: a lower one in the Frænkelryggen Formation and an upper one in the Ben Nevis Formation. *Poraspis polaris*, thought to be restricted to the Frænkelryggen 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 (cyathaspids 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.

Acknowledgements. – A. Blieck thanks the CNRS (Paris) and the University of Oslo for financial support during the work in Oslo and Stockholm. We are indebted to Dr. P. F. Friend (Cambridge), who loaned us a slab from Spitsbergen bearing a well-preserved specimen of *Poraspis*, to Dr. E. J. Loeffler (Bristol) for useful discussions about the morphology of the cyathaspids, to Dr. P. L. Fortey (London) for sending casts of *Poraspis sericea* and *Anglaspis macculloughi*, to Prof. D. L. Dineley and Dr. E. J. Loeffler (Bristol) for casts of Canadian cyathaspids. G. Winter (l'Hay-les.Roses, France) translated the original diagnosis of *Irregulareaspis* by Zych (1931). J. Chalavoux (CNRS, Paris) made the photographs from the original glass plates of J. Kiær and A. Heintz and from some views by A. Blieck, F. Pilard (Paris) made the drawings of Figs. 1, 9, 11, 17 and 19. E. Molin (Paris) and A. M. Sunding (Oslo) typed the manuscript. We express our gratitude to all of them.

References

Alth, A. von 1874: Ueber die palaeozoischen Gebilde Podoliens und deres Versteinerungen. *Abhandl. geol. Reichsanst. Wien, 7(1)*, 1–79.

Berg, L. S. 1940: Classification of fishes, both recent and fossil. *Trav. Inst. Zool. Acad. Sc. URSS, 5(2)*, 1–517.

Blieck, A. 1976: *Contribution a l'étude des Hétérostracés de l'horizon 'Vogti' (Dévonien inférieur du Spitsberg)*. These Doct. 3e cycle Univ. Paris 6, 102 p., 24 fig., 21 pl. (unpublished).

Blieck, A. 1980: Le genre *Rhinopteraspis* Jaekel (Bertébrés, Hétérostracés) du Dévonien inférieur: systématique, morphologie, répartition. *Bull. Mus. nation. Hist. nat.* 4e sér. *2, C(1)*, 25–47.

Blieck, A. 1981: Le genre *Protopteraspis* Leriche (Vertébrés, Hétérostracés) du Devonien inférieur nord-atlantique. *Palaeontographica A, 173 (5–6)*, 141–159.

Blieck, A. 1982a: Les Héterostracés (Vertébrés Agnathes) du l'horizon *Vogti* (Groupe de Red Bay, Dévonien inférieur du Spitsberg). *Cahiers Paléont.* Paris.

Blieck, A. 1982b: Les grandes lignes de la biogéographie des Hétérostracés Silurien supérieur – Dévonien inférieur dans le domaine nord-atlantique. *Palaeogeor. Palaeoclimatol Palaeoecol.* Amsterdam.

Blieck, A. & Heintz, N. 1979: The heterostracan faunas in the Red Bay Group (Lower Devonian) of Spitsbergen and their biostratigraphical significance: a review including new data. *Bull. Soc. géol. Fr. 7e sér. 21(2)*, 169–181.

Brotzen, F. 1933: Die Silurischen und Devonischen Fischverkommen in Westpodolien, I. *Palaeobiologica 5*, 423–466.

Brotzen, F. 1936: Beiträge zur Vertebratenfauna des Westpodolischen Silurs und Devons. I: *Protaspis arnelli* n. sp. und *Brachiopteraspis* n. gen. *latissima* Zych. *K. Sv.Vetenskaps-akad. Arkiv Zool. 28 A(22)*, 1–52.

Denison, R. H. 1956: A review of the habitat of the earliest vertebrates. *Fieldiana, Geol. 11(8)*, 359–457.

Denison, R. H. 1960: Fishes of the Devonian Holland Quarry Shale of Ohio. *Fieldiana, Geol. 11(10)*, 555–613.

Denison, R. H. 1963: New Silurian Heterostraci from Southeastern Yukon. *Fieldiana, Geol. 14(7)*, 105–141.

Denison, R. H. 1964: The Cyathaspididae, a family of Silurian and Devonian jawless vertebrates. *Fieldiana, Geol. 13(5)*, 311–473.

Denison, R. H. 1971: On the tail of the Heterostraci (Agnatha). *Forma et functio, 4*, 87–99.

Denison, R. H. 1973: Growth and wear of the shield in Pteraspididae (Agnatha). *Palaeontographica A, 143(1–6)*, 1–10.

Dineley, D. L. 1965: An occurrence of *Corvaspis* (Ostracodermi) in Canada. *Can. J. Earth Sci. 2*, 93–97.

Dineley, D. L. 1976: New species of *Ctenaspis* (Ostracodermi) from the Devonian of Arctic Canada. *In* Churcher, C. S., Essays on Palaeontology in honour of L. S. Russell. *Roy. Ontario Mus.* 26–44.

Dineley, D. L. & Loeffler, E. J. 1975: Ostracoderm faunas of the Delorme and associated Siluro-Devonian formations, North West Territories, Canada. *Palaeontology, Spec. Pap. 18*, 1–214.

Elliott, D. K. 1979: *New Pteraspididae from Arctic Canada.* Ph.d. Thesis Univ. Bristol, 165 pp., 81 figs., 23 pls. (unpublished).

Føyn, S. & Heintz, A. 1943: The Downtonian and Devonian vertebrates of Spitsbergen, VIII. The English–Norwegian–Swedish expedition 1939, geological results. *Skr. Svalb. Ishav. 85*, 1–51.

Friend, P. F. 1961: The Devonian stratigraphy of North and Central Vestspitsbergen. *Proc. Yorkshire Geol. Soc. 33(1)*, 77–118.

Goujet, D. & Blieck, A. 1977: La fauna de Vertébrés de l'Horizon 'Vogti' (Groupe de Red Bay, Spitsberg). Comparaison avec les autres faunes ichthyologiques du Dévonian inférieur européen. *C.R. Acad. Sci. Paris, 284 D(16)*, 1513–1515.

Heintz, A. 1933: Neuer Fund von *Archegonaspis* in einem obersilurischen Geschiebe. *Zeitschr. Geschiebeforsch. 9(3)*, 123–131.

Heintz, A. 1962: Les organes olfactifs des Heterostraci. *In* Problemes actuels de Paléontologie (Evolution des Vertébrés). *Coll. intern. Centre nation. Rech. scient. 104*, 13–29.

Holmgren, N. 1942: General morphology of the lateral line system of the head in fish. *Handl. K. Sv. Vetenskapsakad. 3, 20(1)*, 1–46.

Jaekel, O. 1927: Der Kopf der Wirbeltiere. *Ergebn. Anat. Entwickl. 27*, 815–974.

Kiær, J. 1930: *Ctenaspis*, a new genus of cyathaspidian fishes. A preliminary report. *Skr. Svalb. Ishav. 33*, 1–7.

Kiær, J. 1932: The Downtonian and Devonian vertebrates of Spitsbergen, IV. Suborder Cyathaspida. *Skr. Svalb. Ishav. 52*, 1–26.

Kiær, J. & Heintz, A. 1935: The Downtonian and Devonian vertebrates of Spitsbergen, V. Suborder Cyathaspida I: tribe Poraspidei, family Poraspidae. *Skr. Svalb. Ishav. 40*, 1–138.

Lankester, E. R. 1873: On *Holaspis sericeus* and the relationships of the fish-genera *Pteraspis, Cyathaspis* and *Scaphaspis*. *Geol. Mag. London 108, 10(6)*, 241–245.

Leriche, M. 1906: Les Poissons siluriens et dévoniens du Nord de la France. *In* Contribution a l'étude de Poissons fossiles du Nord de la France et des régions voisines. *Mém. Soc. géol. Nord 5*, 13–39.

Loeffler, E. J. & Jones, B. 1976: An ostracoderm fauna from the Leopold Formation (Silurian to Devonian) of Somerset Island, North West Territories, Canada. *Palaeontology 19(1)*, 1–15.

Moy-Thomas, J. A. 1939: *Palaeozoic fishes*, Methuen & Co., London, 149 pp. 32 figs. (1st ed.).

Moy-Thomas, J. A. & Miles, R. S. 1971: *Palaeozoic Fishes*, Chapman & Hall, London, 259 pp. (2nd ed.).

Obruchev, D. V. 1964: Subclass Heterostraci (Pteraspides). *In* Orlov, J. A. *Fundamentals of Paleontology, I, A*(11). Agnatha and Pisces: 45–82 [in Russian].

Säve-Söderbergh, G. 1941: Notes of the dermal bones of the head in *Osteolepsis macrolepidotus* Ag. and the interpretation of the lateral line system in certain primitive vertebrates. *Zool. Bidrag. Uppsala. 20*, 523–541.

Stensiö, E. A. 1958: Les Cyclostomes fossiles du Ostracodermes. In Grasse, P. P. *Traité de Zoologie 13(1)*, 173–425, Masson ed. Paris.

Stensiö, E. A. 1964: Les Cyclostomes fossiles du Ostracodermes. *In* Piveteau, J. *Traité de Paléontologie, 4(1)*, 96–382, Masson ed. Paris.

Stensiö, E. A. 1968: The Cyclostomes with special reference to the diphyletic origin of the Petromyzontida and Myxinoidea. *In* Ørvig, T. *Current Problems of Lower Vertebrate Phylogeny, Nobel Symp. 4*, 13–71.

Stoll, N. *et al.* 1964: Code International de Nomenclature Zoologique adopté par le XV^{e} Congres International de Zoologie (Londres, 1958). *Intern. Trust Zool. Nomencl. edit.* London, 176 pp. (2nd ed.).

Strand, E. 1934: Zoologische und paläontologische Ergebnisse von den Svalbard- und Eismeer-Untersuchungen Norwegens, II. *Folia Zool. Hydrobiol. 5(2)*, 326–330.

Tarlo, L. B. Halstead 1962: The classification and evolution of the heterostraci. *Acta Palaeont. Polon. 7(1–2)*, 249–290.

Wills, L. J. 1936: Rare and new Ostracoderm fishes from the Downtonian of Shropshire. *Trans. Roy. Soc. Edinburgh 58(18)*, 427–447.

Woodward, A. S. 1891: *Catalogue of the fossil fishes in the British Museum (Natural History). Part II: Elasmobranchii (Acanthodii), Holocephali, Ichthyodorulites, Ostracodermi Dipnoi, and Teleostomi (Crossopterygii and Chondrostean Actinopterygii)*. London, 567 pp., 16 pls.

Zych, W. 1931: Fauna Ryb Dewonu i Downtonu Podola. Pteraspidomorphi: Heterostraci. *Publ. Paleont. Sbornik I, aL 1–91* [in Polish].

The following are previous publications in *The Downtonian and Devonian Vertebrates of Spitsbergen* series, started on the initiative of Professor Johan Kiær in 1927.

I. Stensiø, E. A: son: Cephalaspidae. A. Text, B. Plates. *Skrifter om Svalbard og Nordishavet* Nr. 12, 391 pp. 112 pls. 1927.

II. Heintz, A.: Acanthaspida. *Skrifter om Svalbard og Ishavet* Nr. 22, 81 pp. 1929.

III. Heintz, A.: Acanthaspida. – Nachtrag. *Skrifter om Svalbard og Ishavet* Nr. 23, 20 pp. 1929.

IV. Kiær, J.: Suborder Cyathaspida. *Skrifter om Svalbard og Ishavet* Nr. 52, 26 pp. 1932.

V. Kiær, J. and Heintz, A.: Suborder Cyathaspida. *Skrifter om Svalbard og Ishavet* Nr. 40, 138 pp. 1935.

VI. Heintz, A.: Lunaspis-Arten aus dem Devon Spitzbergens. *Skrifter om Svalbard og Ishavet* Nr. 72, 25 pp. 1937.

VII. Nilsson, T.: Order Antiarchi. *Norges Svalbard- og Ishavs-undersøkelser Skrifter* Nr. 82, 54 pp. 1941.

VIII. Føyn, S. and Heintz, A.: The English–Norwegian Swedish Expedition 1939. Geological Results. *Norges Svalbard- og Ishavsundersøkelser Skrifter* Nr. 85, 51 pp. 1943.

IX. Wängsjö, G.: Morphologic and systematic studies of the Spitsbergen Cephalaspids. A. Text, B. Plates. *Norsk Polarinstitutt Skrifter* Nr. 97, 653 pp. 1952.

X. Heintz, N.: Two new species of the genus Pteraspis from the Wood Bay Series in Spitsbergen. *Norsk Polarinstitutt Skrifter* Nr. 117, 13 pp. 1960.

XI. Heintz, N.: Gigantaspis – a new genus of fam. Pteraspidae from Spitsbergen. *Norsk Polarinstitutt Årbok 1960*, 22–27. 1962.

XII. Heintz, A.: New investigation on the structure of Arctolepis from the Devonian of Spitsbergen. *Norsk Polarinstitutt Årbok* 1961, 23–40. 1962.