THE MIDDLE ORDOVICIAN OF THE OSLO REGION, NORWAY

5. The Trilobite Family Styginidae.

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CONTENTS

A b s t r a c t. Norwegian and Swedish trilobites of the family Styginidae are described. From the material it is proposed to retain the genus *Bronteopsis* in the family and not include it in the family Scutellidae. Two new species,

Stygina minor and *Bronteopsis holtedahli* are described. Two baltic forms, described as *Ogygiocaris dilatata panderi* and *O.d. plautoni* (SCHMIDT, 1904, pp. 59—63), are included in the family also. They are the first Styginidae recognized from the Baltic.

Those species whose characters are intermediate between *Stygina* and *Bronteopsis*, such as *B. ardmillanensis*, *B. gregaria* and *Stygina? nitens* are here referred to the genus *Raymondaspis*.

Introduction and acknowledgements.

This paper appears as a result of an investigation of the Middle Ordovician of the Oslo Region, Norway, initiated by Professor Dr. L. Størmer (cf. STØRMER 1953). Originally the present paper was intended to be restricted to the Middle Ordovician styginids, but for sake of completeness as regards the family Styginidae, Lower and Upper Ordovician forms are also described. It became soon clear that it would be a great help to compare the Norwegian material with the often better preserved Swedish material. Thanks to the generosity of different geological institutions in Sweden, material of the family Styginidae from Sweden was made available to me for comparison and description. It is a pleasure therefore for me to express my gratitude and heartiest thanks to Professor Dr. E. Stensiö, Paleozoological Department, Riksmuseet, Stockholm (R.S.), Dr. F. Brotzen, Geological Survey of Sweden (S.G.U.) and Professor Dr. P. Thorslund, Paleontological Institute, University of Uppsala (P.U.).

Further I wish to express my best thanks to my two teachers, Professor Dr. A. Heintz and Professor Dr. L. Størmer for facilitating my work at the Paleontological Museum, and Paleontological Institute, Oslo. I am indebted to my friend, Curator G. Henningsmoen for help during the preparation of this paper. — Miss B. Mauritz has taken all the photographs — Mr. P. Padget kindly revised the manuscript.

Family Styginidae VOGDES 1893.

Remarks. — SALTER (1864) originally placed the genus *Stygina* in the family Asaphidae. VOGDES (1893) proposed the family Styginidae for trilobites of the *Stygina latifrons* type. RAYMOND (1920) included within this family three genera: *Stygina*, *Bronteopsis* and

Raymondaspis (,,*Holometopus*''). WARBURG (1925), not being aware of VOGDES' determination, also proposed the family Styginidae. She excluded the genus *Bronteopsis* and regarded this genus as more closely allied to *Bronteus* than to *Stygina*. THORSLUND (1940) retains the genus *Bronteopsis* in the family Styginidae.

WHITTINGTON (1950) was in agreement with WARBURG's opinion. According to him the family Styginidae includes trilobites of the type of *Stygina latifrons* and *Bronteopsis ardmillanensis, B. gregaria, Stygina? nitens, Protostygina* and probably the genus *Leptopilus*.

Diagnosis. — WHITTINGTON (1950, p. 547) gave the following diagnosis of the family:

«Trilobita with cephalon and pygidium moderately convex, subequal in size and semicircular in outline, the free cheeks prolonged beyond the rest of the cephalon as broad genal spines. The glabella poorly defined, narrow at base and expanding rapidly forwards. Eyes situated at inner posterior corners of cheeks. Sutures opisthoparian, anterior branches diverging out to the anterior margin, along which they are united by a rostral suture. Doublure broad, rostrum isolated by connective sutures. Hypostome shield-shaped, middle body convex, undivided, lateral and posterior borders flattened. Thorax of nine segments. Pleurae flat, fulcrum at half width, outside which the pleurae are bent gently down. Pygidium with axis defined laterally but not posteriorly, weakly segmented, side lobes without ribs and furrows, doublure broad.»

In my opinion the diagnosis seems to be too specific and only to apply to the genotype of the genus *Stygina*, viz. *Stygina latifrons*.

When including the above-mentioned species in the family Styginidae, additions necessarily have to be given to the above-cited diagnosis. Several of these species have well defined glabella. The eyes are sometimes placed at a good distance from the glabella (cf. *R. limbatus* ANGELIN). Eye-ridges are more or less clearly defined. Glabellar furrows when developed are of *Bronteopsis concentrica* type. The side lobes of the pygidium have ribs and furrows. The axis of the pygidium is in most styginids prolonged into a postaxial ridge.

I am not in agreement with WHITTINGTON'S and WARBURG'S opinions that *Bronteopsis* should be excluded from the family Styginidae. The diagnosis with the proposed additions applies to the genus *Bronteopsis*. This genus has eight thoracic segments. In this connection one must keep in mind that *Eobronteus*, the earliest of

the Scutellidae, has ten segments. It is a question if it is not more convenient to unite these two families in one and the same family.

The following classification is proposed for the family Styginidae:

Genus *Stygina* SALTER, 1853.

Stygina latifrons (PORTLOCK, 1843).
Stygina minor sp.n.
Stygina angustifrons WARBURG, 1925.
Stygina murchisoni REED, 1914.
Stygina plautoni (SCHMIDT, 1904).

Subgenus *Protostygina* PRANTL & PŘIBYL, 1949.

Stygina (*Protostygina*) *bohemica* (BARRANDE, 1872).

Genus *Raymondaspis* PŘIBYL, 1949.

Raymondaspis limbatus (ANGELIN, 1854)
Raymondaspis nitens (WIMAN, 1906).
Raymondaspis ardmillanensis (REED, 1904).
Raymondaspis gregarius (RAYMOND, 1920).
Raymondaspis angelini (BILLINGS, 1856).
Raymondaspis planus (RAYMOND, 1937).

Genus *Bronteopsis* NICHOLSON & ETHERIDGE, 1879.

Bronteopsis concentrica (LINNARSSON, 1869).
Bronteopsis holtedahli sp.n.
Bronteopsis panderi (SCHMIDT, 1904).
Bronteopsis? törnquisti (MOBERG & SEGERBERG, 1906).

Genus *Leptopilus* RAYMOND, 1924.

Leptopilus declivis RAYMOND, 1924.

Genus Stygina SALTER, 1853.

Type species. — *Asaphus latifrons* PORTLOCK, 1843, des. RAYMOND 1920, p. 282.

Diagnosis. — The following additions may be given to WHITTINGTON'S diagnosis (1950, p. 547). Glabellar furrows when visible are of *Bronteopsis* type. Eye-ridges more or less clearly defined. Anterior pits are situated in the axial furrows at the junction between the furrow and the inner margin of the doublure.

Stygina latifrons (PORTLOCK, 1843).

Pl. I. figs 1—8 Pl. II. figs. 1—8 Pl. III. fig. 7 Pl. IV. fig. 10.

1904[1] *Stygina latifrons* REED, p. 50, pl. VIII, fig. 10.
1906 *Stygina latifrons* OLIN, pl. III, fig. 10.
1907 *Stygina latifrons* WIMAN, p. 137, pl. VIII, fig. 1.
1914 *Stygina latifrons* REED, p. 26, pl. IV, fig. 7.
1925 *Stygina latifrons* WARBURG, p. 96.
1950 *Stygina latifrons* WHITTINGTON, p. 547—49, pl. 72, figs. 1—6, 9.

Lectotype. — (Selected by WHITTINGTON, 1950, p. 547) — G.S.M. 1891. An internal mould, the original of PORTLOCK's pl. VII, fig. 6 (and SALTER, 1886, pl. 18, fig. 7, fig. 10 in part), from the Killey Bridge of Pomeroy, Co. Tyrone, N. Ireland.

Remarks. — WHITTINGTON (1950, pp. 547—549, p. 72, figs. 1—6, 9) gave an exhaustive description of the type species. Here only a few remarks on Scandinavian forms referred to this species will be added.

WARBURG (1925, p. 96) stated that the Swedish form is identical or very closely allied to the type species.

As it appears from the plates the forms here referred to as *Stygina latifrons* show great variations, which in the future may justify the erection of new species and subspecies.

Before doing this, however, further material and a better knowledge of the range of variations is necessary. A form (pl. II, figs 3) from the Tretaspis Shale, Vestergötland, has only a narrow preglabellar field and apparently shorter genal spines than the type. Many of the differences, however, may be due to different modes of preservation (shale or limestone).

Occurrence. — Upper Ordovician in Ireland (see WHITTINGTON 1950, p. 547), in Sweden (Tretaspis Shale, see WIMAN 1906 and 1907, p. 151) and in the Isotelus Beds (4*dβ*) at Lindøya in the Oslo Region, Norway.

Stygina minor sp.n.

Pl. III. Figs. 1—6.

Holotype. — P.M.O. no. 67010 (pl. III fig. 1). A nearly complete cranidium from the Upper Chasmops Limestone (4*bδ*), Bjerkøya, Oslofjord (Skjeseth coll.).

[1] For earlier synonyms see list in this paper.

Diagnosis. — The cephalon and pygidium of nearly the same size, semicircular in outline. The genal spines are broad. The glabella is well defined by dorsal furrows diverging a little forwards. The nine pairs of thoracic segments have flat pleurae with steep lateral parts.

The pygidial axis is relatively short and prolonged to the posterior border by a post-axial ridge.

Remarks. — Except for its smaller size the new species is very like *Stygina latifrons* and WHITTINGTON's exhaustive description of the type species nearly applies to the new species. The glabella is narrower and better defined, and the glabellar furrows more distinct in *Stygina minor.*

Further, the pygidial axis is shorter and narrower, and the pygidium relatively longer than the type species.

Affinities. — The new species seem to be closely allied to the type species and might be regarded as ancestral to it.

Occurrences. — *Stygina minor* sp. n. is one of the most common trilobites in the Upper Chasmops Limestone and contemporaneous deposits in the Oslo Region, p. 26 (For locs. see Størmer 1953).

Stygina angustifrons WARBURG, 1925.

1925. *Stygina angustifrons* WARBURG, pp. 96—97,pl. II, figs. 1, 2.

Remarks. — According to WARBURG (1925, p. 97) this species is charaterized by its elongate and distinctly defined glabella and comparatively long preglabellar field. The only species resembling *S. angustifrons* is, as far as I know, the species described as *Ogygia dilatata plautoni* by SCHMIDT (1904, p. 62—63).

Occurrence. — Upper Leptaena Limestone, Osmundsberg, Boda, Dalecarlia, Sweden.

Stygina plautoni (SCHMIDT, 1904).

1904. *Ogygia dilatata plautoni,* SCHMIDT, pp. 62—63, pl. VIII, fig. 11.

Remarks. — Judging from SCHMIDT's description and illustration of this form, it seems to be referable to the genus *Stygina.*

Occurrence. — C_{1b} - C_2. Tallinn (Reval), Esthonia.

Subgenus Protostygina PRANTL & PŘIBYL, 1949.

Type species. — *Illaenus bohemicus* BARRANDE, 1872, from Šárka Beds — $d\gamma_1$ (Llanvirnian), Central Bohemia.

Diagnosis. — (After PRANTL & PŘIBYL, 1949, p. 10.) — Subgenus of the genus *Stygina* SALTER, 1853, distinguished from the type by its narrow glabella only slightly broadened in front, with eyes situated in the middle, in the upper part of the lower half of the cheeks. The cheeks continue into powerful flatly concave genal spines, which reach to about the seventh or eight thoracic segment. The anterior branch of the facial suture turns in a characteristic curve to the anterior margin of the cephalon. The axis of the pygidium is long, distally not closed. It is delineated by shallow, concavely bent dorsal furrows, which do not unit distally.

Remarks. — According to PRANTL & PŘIBYL (1949, p. 10) the subgenus *Protostygina* represents in its general aspect the morphological transition between the families Styginidae VOGDES, 1893, and Illaenidae HAWLE & CORDA, 1847.

Genus Bronteopsis NICHOLSON & ETHERIDGE, 1879.

Type species. — *Ogygia? concentrica* LINNARSSON 1869 (pp. 75—76, pl. II, figs. 37—40), from Beyrichia Limestone, Ålleberg, Västergötland, Sweden.

Remarks. — REED (1904, p. 95) found that the form described as *Ogygia? concentrica* by LINNARSSON was very like *Bronteopsis scotica* REED. THORSLUND (1940, p. 139) agreed with this and stated: "In fact, the distinctive features between them appear to be small". The slight differences which might be seen from the material available, between the forms formerly described as *Br. scotica* REED and *Br. concentrica* (LNRS.) may be explained by their different modes of preservation. As it appears from the photographs the former is badly preserved. I therefore find it reasonable to regard the British form as a synonym for the Swedish *Bronteopsis consentrica* (LINNARSSON). The fact that the two forms in question occur in corresponding stratigraphic layers also seems to justify this view.

The specimen described as *Holometopus törnquisti* by MOBERG & SEGERBERG (1906, pp. 99—100) is here interpreted as the oldest known member of the genus *Bronteopsis*. A new species, *Bronteopsis*

holtedahli sp.n., of the same genus occurs in the lowermost part of the Ogygiocaris Shale (4*aα*) in the Mjøsa district. This species is most probably conspecific with the form described as *Ogygiocaris concentrica* (LNRS.) by FUNQUIST (1910. p. 23) from corresponding layers in Scania, Sweden. Judging from the description and illustrations of the form described as *Ogygiocaris dilatata panderi* SCHMIDT (1904, pp. 59—62), it belongs to the genus *Bronteopsis*, and is, if not conspecific with *Br. holtedahli* sp.n., at least closely allied to it.

WHITTINGTON (1950, p. 544) was not aware of any species other than the type that might be referred to the genus *Bronteopsis*, and he transfers the genus to the family Scutellidae. I consider that it is more correct to follow the old opinion and keep the genus within the family Styginidae.

Diagnosis. — The cephalon is transversely subsemicircular in outline. The free cheeks taper gradually into relatively broad genal spines. The glabella varies in shape, it is nearly parallel-sided in the earlier forms, but expanded in front in later forms. Four pairs of glabellar furrows are more or less clearly defined. The two first glabellar furrows converge towards the axial furrow, where they seem to meet. The third and fourth pairs are circular in outline. There is no preglabellar field.

The thorax shows eight segments. The pleurae are furrowed and have well defined anterior and posterior bands. The pygidium is subsemicircular in outline, and convex. The axis is raised above the side lobes and crossed by axial furrows. The axis reaches the distinct inner margin of the broad doublure. From here it is continued by a post-axial ridge to the posterior border. The pleurae are relatively broad and distinctly separated from each other by rib furrows. The test is ornamented with fine, curved lines.

Bronteopsis concentrica (LINNARSSON, 1869).

Text fig. 1. Pl. V. Figs. 1—3,5.

1869 *Ogygia? concentrica* LINNARSSON, pp. 75—76, pl. II, figs. 37—40.
1879 *Bronteopsis scotia* NICHOLSON & ETHERIDGE, p. 176, pl. X, figs, 21—22 pl. XI, figs. 1—4.
1904 *Bronteopsis scotia* REED, p. 94, pl. XIII, figs. 5—13.
1914 *Bronteopsis scotia* REED, p. 26, pl. IV. fig. 6.
1940 *Bronteopsis concentrica* THORSLUND, pp. 139—40, pl. 6, fig. 11.
1950 *Bronteopsis scotia* WHITTINGTON, pp. 544—47, figs. 9—12, text-fig. 4.
non 1919 *Ogygiocaris concentrica* FUNQUIST.

Fig. 1. *Bronteopsis concentrica* (LINNARSSON, 1869) Pygidium from the Ampyx Limestone (4aβ), Kojatangen?, Asker, Norway. P.M.O. no. 4030. Kiær coll. (x2).

Lectotype. — (Here selected.) A nearly complete cranidium, the original of LINNARSSON, pl. II, fig. 37 from the Beyrichia Limestone, Ålleberg, Vestergötland, Sweden.

Other material. — A pygidium and parts of thoracic segments, originals of LINNARSSON, pl. II, figs. 39—40, and a free cheek (1.c. pl. II, fig. 38) from the same locality as the lectotype. A pygidium from the Ampyx Lmst. (4aβ), Asker, Norway (text-fig. 1).

Remarks. — For discussion about the conspecificity of this species and *Bronteopsis scotica* REED see above (p. 15).

WHITTINGTON's exhaustive description of *Bronteopsis scotica* REED, applies to the Swedish form also, and I therefore find no reason to repeat it here.

Occurrence. — Beyrichia Limestone, Ålleberg, Vestergötland, Sweden, Balclatchie beds, Girvan, Scotland (Whittington, 1950, p. 544), Ampyx Limestone (4aβ) Asker, Norway.

Bronteopsis holtedahli sp.n.

Pl. V. Figs. 4 and 7.

1919 *Ogygiocaris concentrica* FUNQUIST. p. 23. Pl. II, fig. 10.

The name is given in honour of professor O. Holtedahl who initiated detailed work on the Middle Ordovician in the Mjøsa district (1909).

Holotype. — P.M.O. no. 67011. An incomplete cranidium from the lowermost part of the Ogygiocaris Shale (4*aα*) at Furnes church, at Mjøsa, Norway (pl. V, fig. 4).

Other material. — A complete pygidium (pl. V, fig. 7) and a cranidium from the same horizon and locality.

Diagnosis. — The species is like the type species, but differs from it in having a narrower parallel-sided glabella and well defined glabellar furrows.

Description. — The cephalon is subsemicircular in outline. The glabella is narrowest near the first glabellar furrows, but broadens slightly anteriorly. The glabella has four pairs of glabellar furrows. These furrows were formerly interpreted as one large triangular furrow (WHITTINGTON, 1950, p. 544, fig. 4). The first and second converge towards the axial furrow. The third and fourth are circular in outline. The occipital furrow is deep and the occipital ring strong and convex. The axial furrows are deep and nearly parallel to each other. The eyes seem to be placed about halfway between the axial furrow and the margin of the cephalon. Strong eyeridges run from the eyes towards the third pair of glabellar furrows. There is no preglabellar field but only a narrow brim. The doublure of the glabella is relatively broad. The pygidium is subsemicircular in outline, the length being a little more than half the width. The axis has seven axial rings and a strong articulating halfring. The length of the axis is a little more than half the pygidial length. The axis continues as a postaxial ridge, which tapers towards the posterior margin of the pygidium. The doublure is broad and reaches to the posterior end of the axis. The inner doublure margin is marked by a shallow furrow parallel to the outer pygidial margin. The pleurae turn backwards and swell, outside this furrow. The facets are nearly vertical and continue as pre-pygidial ridges towards the axis.

Affinities. — *Bronteopsis holtedahli* sp.n. is related closely to the type species but differs from it in having a glabella which is narrower and more clearly defined by deep subparallel dorsal furrows. The pygidial axis is also shorter.

Occurrence. — The species occurs in the lowermost part of the Ogygiocaris shale (4*aα*) at Furnes at Mjøsa, Norway. The specimen described by FUNQUIST occurs in a corresponding layer in Scania, Sweden.

Bronteopsis panderi (SCHMIDT, 1904).

1904 *Ogygiocaris panderi* SCHMIDT, pp. 59—62, pl. VIII, figs. 10a, b.
1912 *Homoglossa panderi* RAYMOND, p. 117.

Remarks. — In 1912 Raymond pointed out that this form is not a real member of the genus *Ogygiocaris* (p. 117). He proposed a new genus, *Homoglossa*, for the form described by SCHMIDT. This new genus should be a transitional one between *Ogygiocaris* and *Bronteus*. In my opinion, and judging from the illustrations and description of the species, there is no doubt that it is referable to the genus *Bronteopsis*.

Description. — The glabella is convex with concave axial furrows. It reaches the anterior margin of the cephalon where this has its greatest width. From SCHMIDT's fig. 10, pl. VII it seems as if the glabella has four pairs of glabellar furrows. The two first are arranged like a triangle. The two others are nearly perpendicular to the glabellar furrows. From the third pair, eye-ridges run to the eyes. The position of the eyes is unknown as the free cheeks are damaged. From the direction of the eye-ridges it seems as if they are placed near the posterior border. The anterior pits are situated at the junction between the glabellar furrows and the inner margin of the doublure. The free cheeks are broken on the figured specimen. The occipital furrow is deep. The hypostome is like that of the other members of the genus *Bronteopsis*. The species has a broad rostrum, which in itself excludes the species from the family Asaphidae.

The thorax has 8 segments. The pygidium is incomplete. It has faint pleurae as mentioned by SCHMIDT.

Affinities. — *Bronteopsis panderi* is like *Br. holtedahli* sp.n. in most characters and seems to be closely allied to this species.

Occurrence. — Limestone, Kukruse C_1, Esthonia.

Bronteopsis? törnquisti (MOBERG & SEGERBERG, 1906).

1906 *Holometopus törnquisti* MOBERG & SEGERBERG, pp. 99—100, pl. VII, fig. 6.

Remarks. — The pygidium found in the Ceratopyge Limestone, Ottenby, Scania, Sweden, shows intermediate characters between the genera *Bronteopsis* and *Raymondaspis*. The shape of the pygidium

and the development of its pleurae suggest closer affinity with the members of the genus *Bronteopsis*. Further material of this species, the oldest known Scandinavian styginid, may shed more light upon the whole family Styginidae as this form seems to lie close to the ancestral stock of this family.

Genus Raymondaspis PŘIBYL, 1949.

For the name of the genus see WHITTINGTON (1950, p. 549).

Type species. — *Holometopus limbatus* ANGELIN, 1854, des. MILLER, 1889, p. 550. RAYMOND (1925, pp. 67—68) not being aware of MILLER's designation, also proposed the same species as type for the genus.

Remarks. — WHITTINGTON (1950, p. 550) does not think that the name *Raymondaspis* should be used until new material is available to show the characters of the type species and to afford the basis for selection of a neotype. For the present I find it adequate to keep and use the old name. When including trilobites, such as *"Bronteopsis" ardmillanensis* REED. *"Br." gregaria* RAYMOND and *"Stygina" nitens* (WIMAN) in the genus *Raymondaspis* as proposed in this paper, the genus includes a somewhat heterogeneous group of trilobites. Further material might probably justify a further subvision of the genus. The genus *Raymondaspis* shows intermediate characters between the genera *Bronteopsis* and *Stygina*.

Diagnosis. — The cephalon is of *Bronteopsis* type. The glabella has nearly parallel dorsal furrows in the earliest members, but it is expanded in front in later ones. The preglabellar field is narrow or absent. The glabellar furrows, when visible, are of *Bronteopsis* type. The eyes seem to be placed near the middle of the fixed cheeks in earlier species, but closer to the posterior margin in later species. The free cheeks also are of *Bronteopsis* type, and taper gradually into relatively broad and short genal spines which possess a median keel. The pygidium, especially in the earliest species, is of *Stygina* type. It is nearly semicircular in outline and vaulted. The axis in most species is sharply pointed and is prolonged to the posterior margin by a post-axial ridge. The pleurae are not visible in the earliest

members, but are slightly defined in later ones. The test of the cranidium and the pygidium shows the same ornamentation as members of the genus *Bronteopsis*.

Raymondaspis limbatus (ANGELIN, 1854).

Pl. IV. Figs. 2, 4—9. Pl. V. Figs. 6 and 8.

1854 *Holometopus* ANGELIN, p. 58, pl. 33, figs. 7, 7a.
1906 *Holometopus limbatus* WIMAN, pp. 293—94,pl. 29, figs. 21—22.
1950 *Raymondaspis limbatus* WHITTINGTON, p. 549, pl. 72, figs. 11—14.
1952 *Raymondaspis limbatus* SKJESETH, pp. 171—72, pl. IV, figs, 16—17, 19—21.

Description. — The glabella has subparallel sides and is slightly constricted between the eyes. Four pairs of glabellar furrows of *Bronteopsis* type are visible. (The two first pairs were interpreted as one single pair by the present author, 1952, p. 171.) The axial furrows are deep. Anterior pits are situated at the junction between these furrows and the inner margin of the doublure.

The occipital ring is provided with a node and is separated from the rest of the glabella by a deep occipital furrow. The preglabellar field is narrow. The eyes are situated a little further forwards than in the other members of the genus. Eye-ridges are poorly defined and run from the eyes to a point just in front of the third glabellar furrow. The anterior branches of the facial suture run from the eyes almost to the anterior border. The inner margin of the doublure is marked by a groove on the free cheeks. The free cheeks themselves taper gradually into broad, stout genal spines which are provided with median keels. The test of the cranidium has fine, subparallel striae. They are concentric around the occipital node, concentric around the occipital furrows on the glabella, and concentric around the eyes on the cheeks. The pygidium is subsemicircular in outline with a well-defined axis and deep axial furrows. Only the first axial ring is clearly set off. The axis is continued to the posterior margin by a post-axial ridge. The duplicated border is concave. The doublure is broad and reaches inwards as far as the termination of the axis.

Remarks. — For discussion and occurrences of the species see SKJESETH (1952, p. 172). From Prussia, POMPECKI (1890), described and figured (Pl. V, figs. 8—9) two new species which are closely allied, if not conspecific, with the Scandinavian form.

Raymondaspis nitens (WIMAN, 1906).
Pl. IV. Figs. 1 and 3.

1906 *Holometopus nitens* WIMAN, p. 112, pl. VII, figs. 19—20.
1914 *Holometopus nitens* REED, p. 27.
1925 *Stygina nitens* WARBURG, p. 72, 95.
1940 *Stygina ? nitens* THORSLUND, pp. 137—39, pl. 6, figs. 1—10.
1950 *Stygina nitens* WHITTINGTON, p. 54.

Lectotype. — (Here selected.) The cranidium described and figured by Wiman (1906, p. 112, pl. VII, fig. 19). P.U. no. ar. 1280. Block from Ekeby, Uppsala, Sweden.

Other material. — A complete pygidium, (P.U. no. ar. 1279.) A specimen from Ampyx lmst. — Lower Chasmops Lmst. ($4a\beta$ — $4b\alpha$), Kojatangen, Asker, Norway, (P.M.O. no. 4095, Kiær coll.).

Description. — The cephalon is semicircular in outline and strongly convex. The dorsal furrows are rather deep. They are subparallel in the posterior half, but diverge rapidly in the anterior.

There is no preglabellar field. The glabellar furrows are not visible, but muscle scars are developed in one of the specimens figured by THORSLUND (1.c. pl. 6, fig. 1). The free cheeks are convex and taper laterally into broad and stout genal spines, which have median keels.

The eyes are situated close to the posterior margin and to the glabella. The anterior branches of the sutures run nearly straight to the margin. The doublure of the cephalon is broad. Its inner border occurs as a groove, which marks the change of slope from the inner, steep part and the outer flat part of the cheeks.

The hypostome is strongly convex. The anterior middle body is triangular in outline, with the apex of the triangle directed into the deep middle furrow (see THORSLUND, 1940, pl. 6, fig. 5). The similarities between this hypostoma and the hypostomes of cambrian zacanthoids are remarkable (p. 24).

A specimen from Ampyx Limestone — Lower Chasmops Lmst. ($4a\beta$ — $4b\alpha$), Kojatangen, Asker, Norway (P.M.O. no. 4095, Kiær coll.) has parts of the thorax preserved. The thorax is like that of *Stygina minor* sp.n., but differs from this in having narrower segments with the lateral parts more vertically placed and acutely pointed.

The pygidium is subsemicircular in outline and strongly convex. The axis tapers rapidly backwards and is continued by a faint post-

axial ridge, which does not reach the posterior border. Eight axial rings are traceable. Of these, only the first is clearly set off by an axial furrow. The side lobes are smooth, with faint pleurae. Young adult forms seem to have flatter pygidia with stronger pleurae.

Affinities. — WARBURG (1925, pp. 93—96) referred *R. nitens* to the genus *Stygina*. THORSLUND (1940,p. 139) came to the conclusion: "it appears evident that *Holometopus nitens* WIMAN represents a transition form between *Bronteopsis* s.str. and *Stygina*, and the reference of it to either of these genera merely seems to be a matter of subjective conception". RAYMOND (1925) was of the opinion that "such a form as *Holometopus nitens* WIMAN must certainly be transferred to *Bronteopsis*", and REED (1914, p. 27) pointed to the resemblances between R. *nitens* (WIMAN) and *R. ardmillanensis* (REED).

It is evident that *R. nitens* is closely allied to both *R. ardmillanensis* (REED) and *R. gregarius* (RAYMOND).

Occurrences. — Lower Chasmops Limestone, from several localities in Sweden (see THORSLUND, 1940, p. 139). Ampyx Limestone — Lower Chasmops Lmst. (4*aβ* — 4*ba*) Kojatangen, Asker, Norway.

Raymondaspis gregarius (RAYMOND, 1920).

1920 *Bronteopsis gregaria* RAYMOND, p . 283.
1925 *Bronteopsis gregaria* RAYMOND, p. 69, pl. 3, figs. 12—12.
1946 *Bronteopsis gregaria* COOPER & COOPER, p. 113, pl. 3, figs. 1,2.
1950 *„Bronteopsis" gregaria* WHITTINGTON, p. 547.
1940 *Bronteopsis ardmillanensis* THORSLUND, p. 139.
1950 *Bronteopsis ardmillanensis* WHITTINGTON, p. 547.

Remarks. — As stated by RAYMOND (1925, p. 70) "This species is much more nearly related to *Bronteopsis ardmillanensis* REED than to the type of the genus". The similarities between this species and the Swedish *Raymondaspis nitens* are striking, and differences are only slight.

Raymondaspis ardmillanensis (REED, 1904).

Remarks. — Earlier writers regard this species as a transitional form between the genera *Stygina* and *Bronteopsis*, and come to the conclusion that it seems to be a matter of personal opinion whether

it shall be referred to the one or the other of the genera. For reasons given above (Diagnosis —) I transfer the species to the genus *Raymondaspis*. For affinities see the remarks on *R. nitens* and *R. gregarius*.

Phylogeny and relationships.

RICHTER (1932, p. 952) included the families Illaenidae and Scutellidae in the superfamily Bathyuriscidea. WHITTINGTON (1950, p. 547) considered, on account of the resemblances between these families and the Styginidae, that the latter should also be included within the same superfamily. HENNINGSMOEN (1951, p. 183) sharing this view, gave the synonyms of the superfamily but found that the name Zacanthoidacea RICHTER, 1932 has preference.

This assignment is strengthened by comparison of its members with some of the Cambrian zacanthoids.

The development and arrangement of the glabellar furrows are nearly the same. The first pair of furrows is directed backwards from the axial furrows, while the others are nearly perpendicular to it. For comparison see *Bronteopsis panderi* (SCHMIDT 1904, pl. VIII, fig. 10) and e.g. the zacanthoidacean figured by RASETTI (1948, pls. 47 and 48).

The misinterpretations which formerly have been made concerning the two last glabellar furrows in the genus *Bronteopsis*, were pointed out in an earlier chapter in this paper (p. 16). Here attention is paid to the genus *Hemirhodon* (RAYMOND, 1937). This genus resembles the styginids in many characters. The hypostome (see RAYMOND 1937, pl. 2, fig. 10) is very like that of *Raymondaspis nitens* described above and the pygidium may easily be mistaken for a *Bronteopsis* pygidium, (see RASETTI, pl. 52, fig. 8). The genus *Hemirhodon* thus seems to lie close to the ancestral stock of the family Styginidae.

The oldest known Scandinavian styginids occur in the lower Ordovician. They show intermediate characters between the genera *Stygina, Raymondaspis* and *Bronteopsis*. *Raymondaspis limbatus* (ANGELIN) for example, has a cephalon of *Bronteopsis* type, while the pygidium is more like that of *Stygina*. Parallelism in evolution within the three genera may be seen in the development of the glabella. The earliest members have relatively narrow, parallel-sided and well defined glabellae. In later members, however, the glabellae are ex-

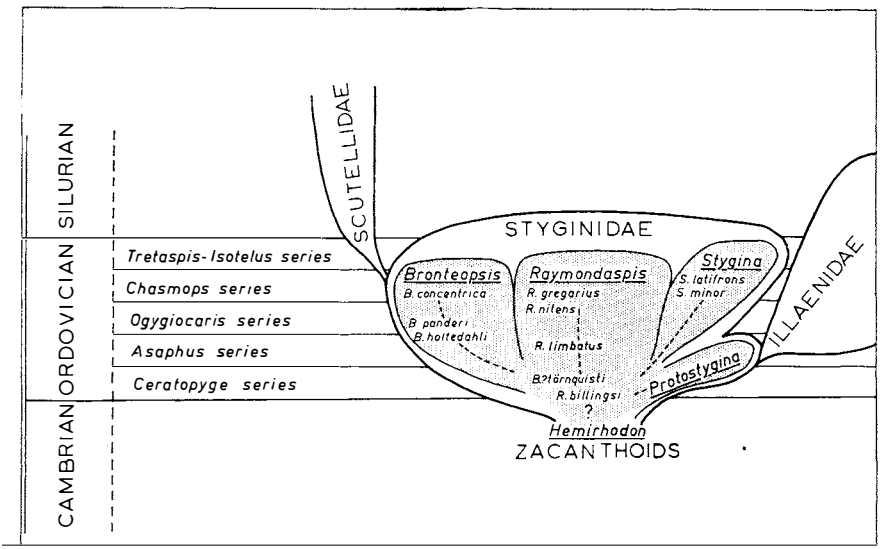

Fig. 2. Phylogeny and relationships of the styginids and their stratigraphical range shown schematically.

panded anteriorly. In text-fig. 2 the writer's opinion as to relationships among the styginids is shown schematically.

As pointed out by previous authors there seems to be no doubt about the close relationship between the families Scutellidae and Styginidae. In my opinion, however, the differences between the earliest scutellids and members of the genus *Bronteopsis* are too great, and the unity among the styginids too clear to include the genus *Bronteopsis* in the family Scutellidae. (Discussion see above, p. 11.) The subgenus *Protostygina* may be interpreted as transitional between the families Styginidae and Illaenidae. In addition to the similarities between these families, alluded to by WHITTINGTON (1950, p. 547), it is worth mentioning that some of the illaenid pygidia have developed a distinct postaxial ridge, which is characteristic for most members of the family Styginidae.

Some stratigraphical remarks.

The importance of members of the family Styginidae as zone fossils is restricted with our present knowledge of the family. Never-

theless, some of the members may be useful at least for local stratigraphical correlations.

Raymondaspis limbatus (ANGELIN) occurs in the Lower Ordovician Planilimbata Limestone in Norway and Sweden. It is reported from the upper part of the Lower Didymograptus Zone, at Heramb, Ringsaker, Norway (SKJESETH, 1953, p. 172), and from the Planilimbata Lmst. in Öland (MOBERG, 1891, p. 12), Västergötland (THORSLUND, 1938, p. 156), Närke (WESTERGÅRD, 1940, p. 44), N. Baltic (WIMAN, 1906, p. 98). The species is also reported from the overlying Megalaspis Lmst. in Sweden. POMPECKI (1880, p. 86) described two new species *R. laevis* and *R. gracilis* (closely allied, if not conspecific with *R. limbatus*) from drift boulders in Prussia.

Raymondaspis nitens (WIMAN) occurs in Middle Ordovician beds in Sweden and Norway. According to THORSLUND (1940, p. 139) it is found in the Lower Chasmops Lmst. at the following places in Sweden: Jämtland (central Lockne area, Hallen, overthrust beds at Lit), at Fjecka in Dalecarlia, File Haidar in Gotland and in boulders from the North Baltic district and from Tvären. A single specimen is found in the Ampyx Lmst. (4*aβ*) or Lower Chasmops Shale (4*bα*) at Kojatangen, Asker, Norway. The closely allied British and American forms *R. ardmillanensis* (REED) and *R. gregarius* (RAYMOND) are of corresponding age (p. 23).

Stygina minor sp.n. is one of the most common trilobites in the Upper Chasmops Lmst. (4*b*) and corresponding layers in the Oslo Region. (Upper Chasmops Lmst., Oslo — Asker District, Encrinite Lmst., Langesund — Gjerpen District, Upper Chasmops Lmst., Ringerike, Sphaeronide Lmst. and Gagnum Shale, Hadeland District (see STØRMER 1953).

This species is a forerunner of *Stygina latifrons* (PORTLOCK) which is reported from the Upper Ordovician in England, Ireland, Norway and Sweden. The lectotype (WHITTINGTON, 1950, p. 547) is from the Killey Bridge beds of Pomeroy, Co. Tyrone, N. Ireland. The species is found in Tretaspis Shale in Sweden (WIMAN 1900 and 1907 p. 151), and in the Isotelus Beds (4*dβ*) Lindøya, Oslo area, Oslo Region, Norway, and at Hadeland, Oslo Region, Norway.

The earliest member of the genus, *Bronteopsis törnquisti*, occurs in the Ceratopyge Limestone, Ottenby, Scania, Sweden (pp. 11—12). *B. holtedahli* sp.n. is found in the transition beds between the Ortho-

ceras Limestone (*3c*) and the Ogygiocaris Shale (*4aα*) at the church of Furnes, Mjøsa district, Norway (STØRMER 1953, p. 102). From Sweden the form is reported from corresponding layers in Scania (FUNQUIST 1919, p. 23). The baltic species *Bronteopsis panderi* (SCHMIDT 1904) occurs in the Kukruse C_2, Estonia.

The type species *Bronteopsis concentrica* (LINNARSSON 1869) has a wider geographical distribution as it occurs in the Beyrichia Limestone, Ålleberg, Vestergötland, Sweden; Balclatchie beds, Girvan, Scotland (WHITTINGTON 1950, p. 544) and in the Ampyx Limestone (*4aβ*), Asker, Oslo Region, Norway.

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PLATES I—V

PLATE 1

Stygina latifrons (PORTLOCK, 1843).

Fig. 1. R. S. no. Ar. 14972. Tretaspis Shale, Kungslena, Vestergötland, Sweden. (x 1.5)

Fig. 2. P.U. no. 1343. Block 16, Norskedika, Sweden. Orig. WIMAN 1906. Pl. VIII, fig. 1. (x 3).

Fig. 3. *Stygina* cf. *latifrons*. P.M.O. no. 33807. 4b—c. Lunner, Norway, Holtedahl coll. (x 3.3).

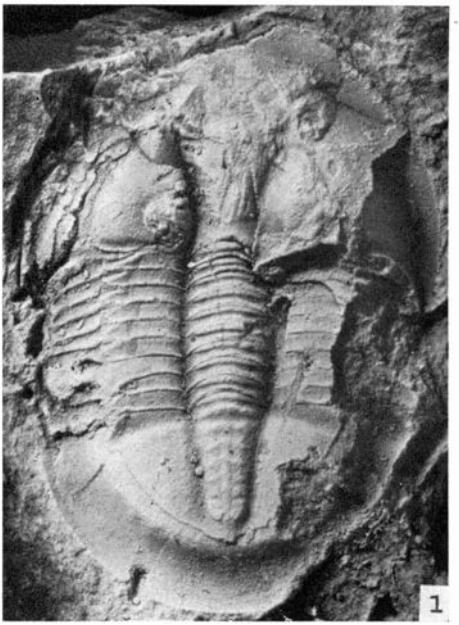
Fig. 4. P.U. no. 2223. Block 55. Öjle myr, Gotland, Sweden. Orig. WIMAN 1901. Pl. V, fig. 16. (x 2.5).

Fig. 5. P.U. no. 2228. Block 84. Öjle myr, Gotland, Sweden. Orig. WIMAN 1901. Pl. VII, fig. 17. (x 3.5).

Fig. 6. P.U. no. 1393. Block 33. Målby, Söderön, Sweden. Specimen showing muscle scars, anterior pits and faint eye-ridges. (x 2.5).

Fig. 7. P.M.O. no. 20485. Isotelus beds. 4d. Lindøya, Oslofjord, Norway. Kiær coll. (x 2).

Fig. 8. P.U. no. 1394. Block 33. Målby, Söderön, Sweden. (x 2.5).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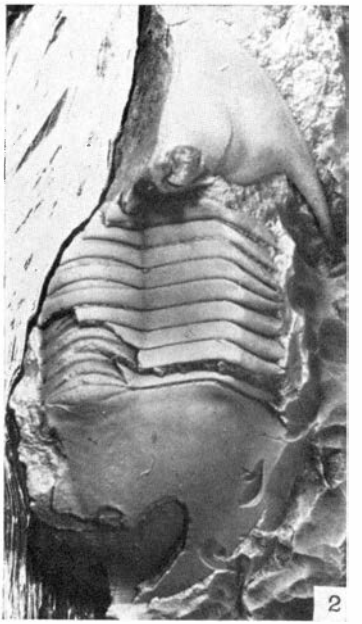
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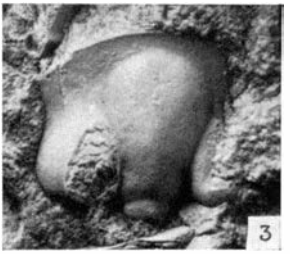
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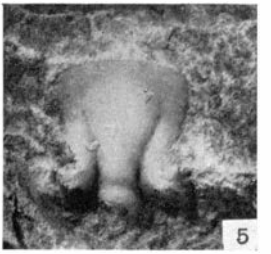
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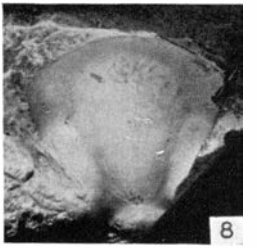
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PLATE 2

Stygina latifrons (PORTLOCK, 1843).

Fig. 1. P.M.O. mo. 20485. Isotelus beds. 4d. Lindøya, Oslofjord, Norway. Kiær coll. (x 2).

Fig. 2. P.U. no. 2226. Block 24. Öjle myr, Gotland, Sweden. (x 2).

Fig. 3. R.S. no. ar. 14970. Tretaspis Shale. Vestergötland, Sweden. (x 2).

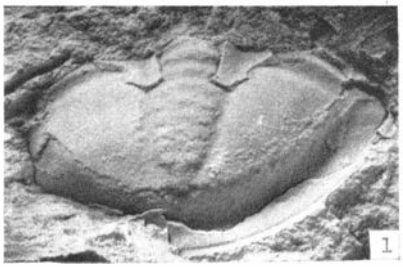
Fig. 4. S.G.U. Tretaspis Shale. Kungslena, Vestergötland, Sweden. (x 1.5). (LINNARSSON, 1869, pl. 2, fig. 41—42.)

Fig. 5. S.G.U. Loc. and horizon the same as fig. 4. (x 1.7).

Fig. 6. *Stygina* cf. *latifrons* (PORTL.) 4b—c. Lunner, Norway. Holtedahl coll. (x. 3).

Fig. 7. P.U. no. 2241. Block 62. Öjle myr, Gotland, Sweden. (x 2). (WIMAN, 1901, pl. V, fig. 19.).
Specimen showing the test ornamentation, the muscle scars and the post-axial ridge.

Fig. 8. P.U. no. 2242. Block. 27. Öjle myr, Gotland, Sweden. (x 2).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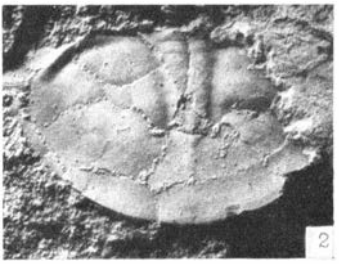
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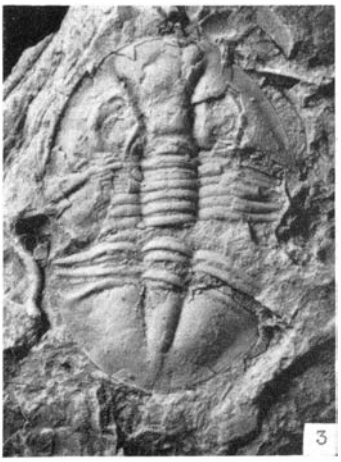
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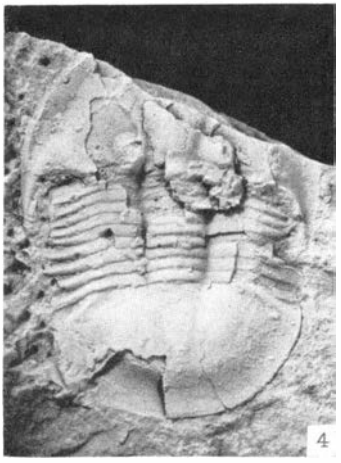
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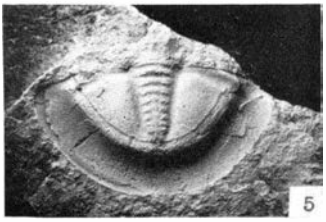
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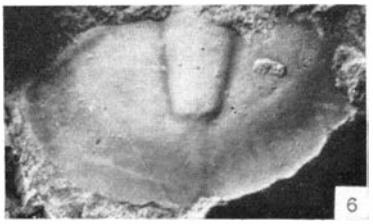
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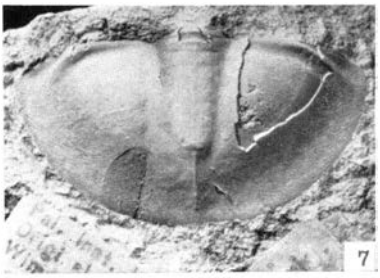
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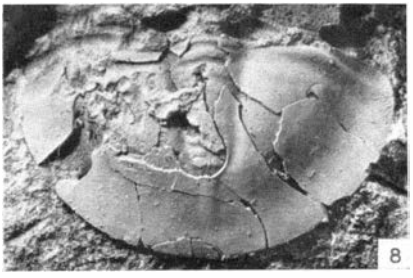
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PLATE 3

Stygina minor sp.n.

Fig. 1. P.M.O. no. 67010. Holotype. Upper Chasmops Limestone (4b). Bjerkøya, Oslofjord, Norway. Skjeseth coll. (x 5).

Fig. 2. P.M.O. no. 20436. Upper Chasmops Lmst. (x 4). Ostøya, Oslofjord, Norway. Th. Vogt coll.

Fig. 3. P.M.O. no. 66455. Upper Chasmops Lmst. Terneholmen, Oslofjord, Norway. (x 5). N. Spjeldnæs coll.

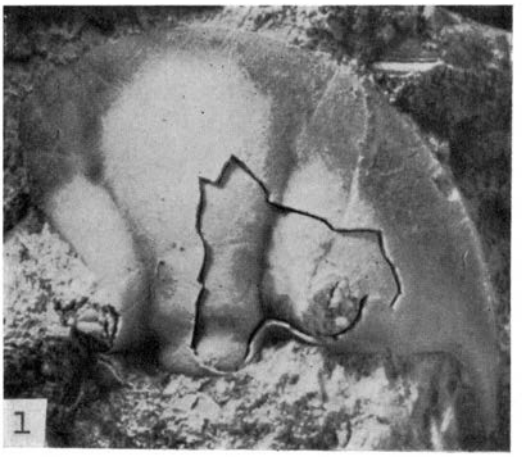
Fig. 4. P.M.O. no. 64456. Sphæroid Lmst. Nerby, Lunner, Hadeland, Norway. (x 3). Størmer — Henningsmoen coll.

Fig. 5. P.M.O. no. 64457. Encrinite Lmst. Skjælbukta, Frierfjord, Norway. (x 2). Størmer — Major coll.

Fig. 6. P.M.O. no. 8120. Upper Chasmops Lmst. Frognøy, Ringerike, Norway. (x 5). Kiær coll.

Stygina latifrons (PORTLOCK, 1843).

Fig. 7. P.U. no. ar. 2225. Block 47. Öjle myr, Gotland, Sweden. (x 3). Orig. WIMAN 1901. Pl. II, fig. 18.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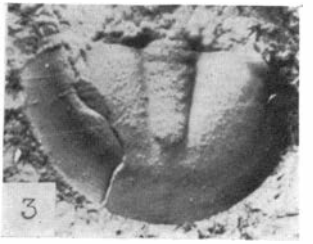
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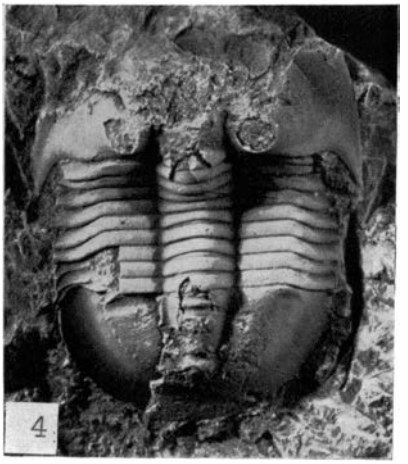
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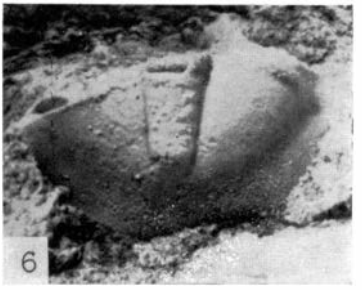
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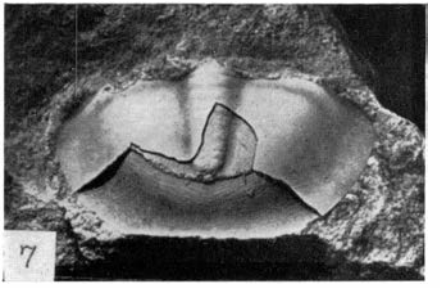
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PLATE 4

Raymondaspis nitens (WIMAN, 1906).

Fig. 1. P.U. no. ar. 1280. Lectotype. Block. 11. Ekeby, Uppsala, Sweden. (WIMAN, 1907, pl. VII, fig. 19.) (x 3.9).

Fig. 3. P.U. no. ar. 1279. (WIMAN, 1907, pl. VII, fig. 20.) Same locality as fig. 1. (x 3).

Raymondaspis limbatus (ANGELIN, 1854).

Fig. 2. R.S. no. ar. 27480. Horn, Öland, Sweden. (x 3).

Fig. 4. P.U. no. ar. 4164. Borghage, Öland, Sweden. (x 3). Wiman coll.

Fig. 5. P.M.O. 66302. Lower Didymograptus Shale (3be). Heramb, Ringsaker, Norway. (SKJESETH, 1953, pl. IV, fig. 20.). (x 3).

Fig. 6. R.S. no. ar. 21910. Öland, Sweden. (x 3).

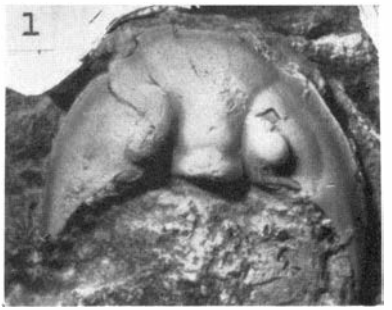
Fig. 7. P.U. no. ar. 24165. Borghage, Öland, Sweden. (x 4).

Fig. 8. R.S. no. ar. 21482. Horn, Öland, Sweden. (x 3).

Fig. 9. R.S. no. ar. 21910. Öland, Sweden. (x 4).

Stygina latifrons (PORTLOCK, 1843).

Fig. 10. (Young specimen?) P.U. no. 2224. Block 30. Öjle myr, Gotland, Sweden. (WIMAN, 1901, pl. V, fig. 17.) (x 3).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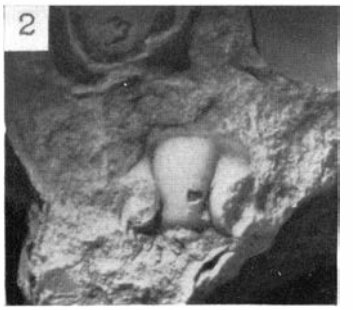
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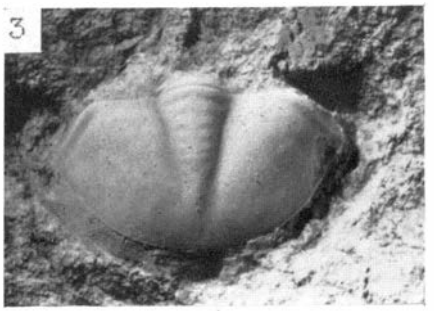
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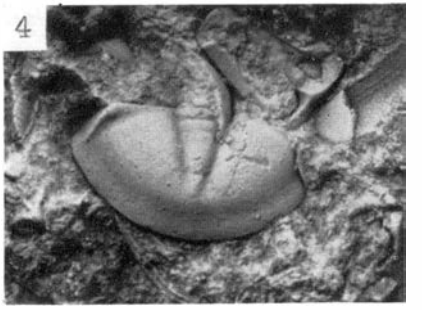
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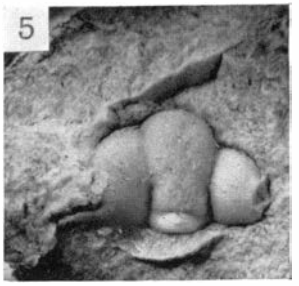
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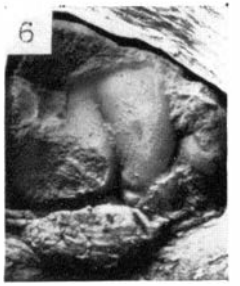
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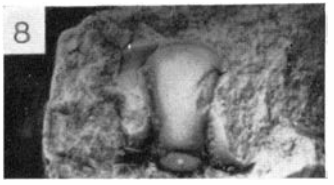
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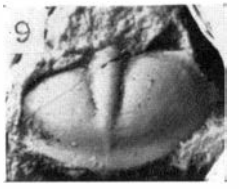
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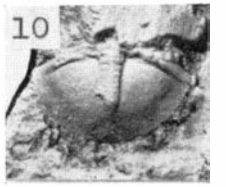
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PLATE 5

Bronteopsis concentrica (LINNARSSON, 1869). Beyrichia Limestone. Ålleberg, Vestergötland, Sweden. S.G.U.

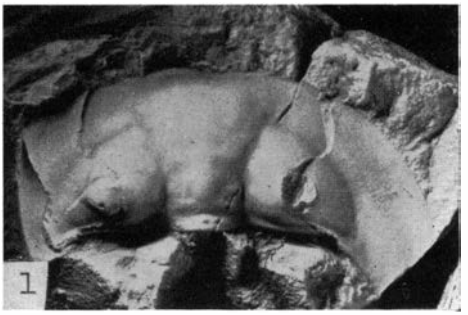
Fig. 1. Holotype. (x 1.7) (LINNARSSON, 1869, pl. II, fig. 37.)
Fig. 2. (l.c., pl. II, fig. 37.) (x 2.5).
Fig. 3. (l.c., pl. II, figs. 39, 40.) (x 2).
Fig. 5. (l.c., pl. II, figs. 39, 40.) (x 2).

Bronteopsis holtedahli sp.n. Top of Orthoceras Limestone. (3c—4aα). Furnes church, Norway.

Fig. 4. P.M.O. no. 67011. Holotype (x 5). Skjeseth coll.
Fig. 7. P.M.O. no. 64458. (x 6). Skjeseth coll.

Raymondaspis limbatus (ANGELIN, 1854). Lower Didymograptus Shale (3b) Heramb, Ringsaker, Norway. (SKJESETH, 1953, pl. IV, figs. 19 and 21.).

Fig. 6. P.M.O. no. 66302. (x 4).
Fig. 8. P.M.O. no. 66301. (x 3.4).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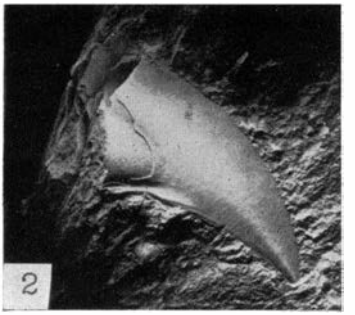
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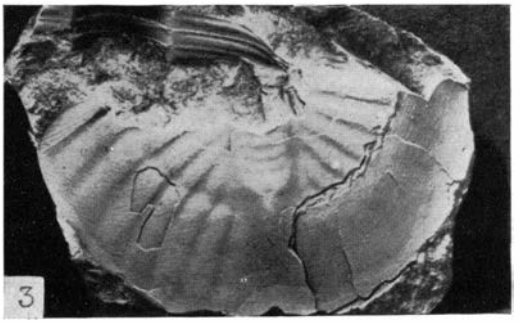
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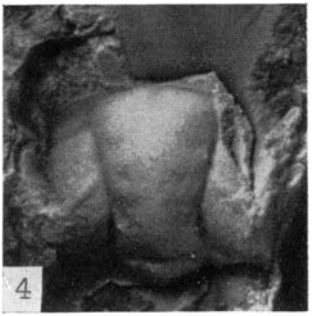
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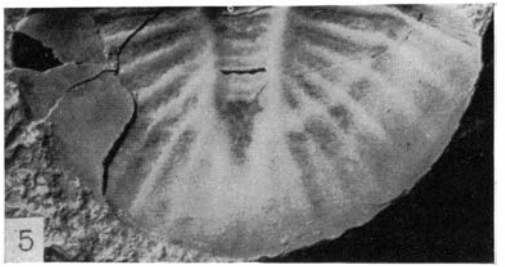
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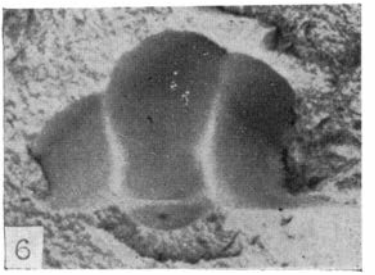
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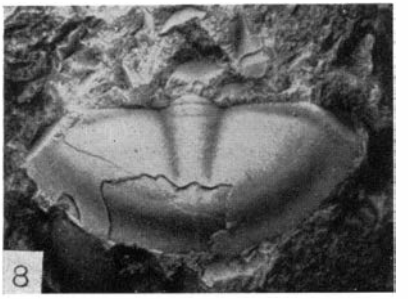
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