A REVISION OF THE TRILOBITE DALMANITINA MUCRONATA (BRONGNIART) AND RELATED SPECIES

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Summary.

The systematics of the Upper Ordovician trilobite species *Dalmanitina mucronata* (Brongniart) and *D. eucentra* (Olin non Angelin) are examined, and a new species is erected for the forms usually included in the latter. Revised descriptions are given and the distribution of each species is outlined. The distinction between the two species is discussed, and the great variation to which both are subject is analysed: they are considered to belong to a single very variable suite, probably closely related to *D. socialis* (Barrande). A new variety of *D. mucronata* is recognised from the basal Silurian of the North of England.

Introduction.

The highest Ordovician strata of Great Britain and Scandinavia — respectively the upper Ashgillian and the Brachiopod Beds — are characterised by a trilobite fauna of which the outstanding components are the Phacopid *Dalmanitina mucronata* (Brongniart) and closely related forms. In Sweden this fauna was described during the first half of the last century in the classical works of Wahlenberg, Dalman and Angelin, whose descriptions were based mainly on the well-preserved specimens from Västergötland. Later, Salter recognised the same fauna from Central Wales, and towards the end of the century its extension to the North of England was discovered by members of the Cambridge school, and described, most notably, in the works of Marr. The stratigraphy and fauna of the Swedish Brachiopod Beds was revised by Professor Troedsson during the decade following 1918. By this time, however, Marr had ceased his researches, and during the succeeding years, although the study of the lower Ashgillian was continued by Professor King and others, the upper Ashgillian rocks and faunas of England and Wales did not undergo the revision necessary for an exact comparison with those of Sweden.

The present paper is concerned mainly with the systematics of *Dalmanitina mucro*nata and associated forms, this being a necessary preliminary to a revision of the upper Ashgillian. It is based on research undertaken in the Sedgwick Museum, Cambridge, under the supervision of Dr. O. M. B. Bulman, and during the tenure of a grant from the Department of Scientific and Industrial Research. To Dr. Bulman I would express my deep appreciation of his continued advice and encouragement, and to Professor W. B. R. King my gratitude for the ready assistance he has always given me, especially in first introducing me to the rocks in the field. Dr. C. J. Stubblefield has given me much valuable advice and has made available to me the collections of the Geological Survey, as has Mr. A. G. Brighton those of the Sedgwick Museum, while Professor King, Dr. W. J. Pugh and Dr. G. L. Elles have loaned me specimens from their private collections. Among Swedish geologists, Professor G. T. Troedsson has permitted me to re-examine his collections from the Brachiopod Beds and has most readily given me any information I have required. I had the privilege of being shown the Lower Palaeozoic rocks of Dalarne and Västergötland by Professor P. Thorslund and Dr. B. Waern, who have also been ever willing to offer any possible assistance. For the loan of material and access to collections, I must further thank the authorities of the British Museum (Natural History), the Palaeontological Institutions of Lund and Uppsala Universities, the Riksmuseum of Stockholm and the Swedish Geological Survey, and the Geological Museum of Oslo. I have received additional grants towards the cost of field work from the Department of Geology, Cambridge, the authorities of St. Catharine's College, and the trustees of the Worts Fund. The photographs illustrating this paper are the work of Mr. A. Barlow.

Terminology.

The terminology used in the descriptions of the trilobites follows in the main that of Miss Warburg (1925), with however one or two differences. The term »glabella» is used so as to include also the occipital ring, while the glabellar furrows and lobes are numbered from back to front, excluding the occipital furrow and ring. The furrows of the lateral lobes of the pygidium are referred to as the »sutural (or interpleural) furrows», and the »oblique (or pleural) furrows», these being a combination of the terms used by Miss Warburg and R. & E. Richter (1926). Where »length» and »width», and their derived adjectives and verbs have been used alone, they are intended to indicate respectively a longitudinal and a transverse measurement. In cases where this would be unsuitable, as with the dimensions of an appendifer or of a pygidial pleura, the terminology of R. & E. Richter (1940, pp. 16,17) has been adopted, and the contractions (sag.), (exs.) or (tr.) have been added to make the sense unambiguous. These contractions, however, are alone sufficient to make the meaning precise, and it is possible to use with each of them either »length» or »width», dependent on which is most suitable to the context; for instance, the »length (tr.) and width (exs.)» of a pygidial pleura are used in preference to »width (tr.) and length (exs.)» (contrast Whittington, 1950, p. 533).

In quoting the registered numbers of Museum specimens, the following abbreviations have been used: -

- SM: Sedgwick Museum, Cambridge.
- GSM: Geological Survey Museum, London.
- RM: Riksmuseum, Stockholm.

- SGU: Swedish Geological Survey, Stockholm.
- PIU: Palaeontological Institution, Uppsala.
- LO: Palaeontological Institution, Lund.

History of the species concerned.

- 1821 Wahlenberg described a trilobite from Sweden (p. 28, pl. II, fig. 3) as *Entomostracites caudatus*, considering it to be the same as *Trilobus caudatus* of Brünnich. His description was: *»Entomostracites caudatus*: oculis ad latera frontis turbinatae postice incisae, capite similunari: angulis posticis spinosis, cauda spinam mobilem exserente plicis duplicatis ornata.»
- 1822 Brongniart (p. 24, pl. III, fig. 9) repeated Wahlenberg's figure, but pointed out the differences between it and the typical *Trilobus caudatus* Brünnich; he suggested for it the specific name *mucronatus*, and included it in his genus *Asaphus*.
- 1826 Dalman described and figured new material (pp. 236, 268, pl. II, figs. 3a, b), describing it as:

»A. capite semilunari, angulis posticis in spinam extensis; glabella lata, utrinque 4-incisa; oculis granulosis loborum tertio pari proximis; pygidio costis bifidis, mucroneque spiniformi.

Loc. In Vestrogothiae schisto argillaceo supremo, praesertim in Mösseberg et Ålleberg; — in Ostrogothia ad Borenshult et ad Husbyfjöl; in Scania ad Röstånga.

Inveniuntur capita rarius, pygidia sat frequenter, nullum vero specimen integrum huc usque visum, quare segmentorum numerus latet. — Costae pygidii tenues, marginem attingentes, bifidae, vel potius ad ipsam basin per paria connatae. Oculi distinctissime reticulati.»

- 1851 Angelin published a new description and a new figure of *Phacops mucronata* Brongn. (p. 10, pl. VIII, fig. 1), and restricted the species to specimens from Västergötland and Östergötland, as occurring »In stratis argillaceis regionis E), *Vestrogothiae* in montibus Ålleberg et Mösseberg albique; etiam Ostrogothiae ad Borenshult et ad Husbyfjöl sec. Dalman.» Angelin separated the forms from Röstånga in Scania, formerly referred to *Phacops mucronatus*, as a new species *Phacops eucentra* (p. 11, pl. IX, fig. 1), which was described as: »Ph. cornigera, caudata, laevis; fronte protuberante 3 — loba; abdomine marginato, costis 9 dichotomis. *Loc. nat.* In stratis schistosis regionis E), *Scaniae* ad Röstånga.»
- 1864 Salter figured a cephalon and pygidium from Bala (Wales) as *Phacops (Odonto-chile) mucronatus* Brong.? (p. 48, pl. IV, figs. 11, 12). He compared them with *P. mucronatus* of which he figured a specimen from Ålleberg Mountain, but pointed out some differences, concluding »I am justified, therefore, in placing a ? against the same: indeed, had it not been already referred in the Decades

to *P. mucronatus*, I would have preferred keeping it distinct under the name *P. appendiculatus*. For the present I leave it in doubt.»

- 1866 Linnarsson founded a species *Phacops pulchellus* on a pygidium from Kinnekulle (p. 16, pl. II, fig. 1).
- 1906 Olin figured a cephalon and pygidium from Röstånga which he interpreted as *Phacops eucentra* Ang. (p. 41, pl. I, figs. 1—3).
- 1918 Troedsson revised the fauna of the Brachiopod Beds of Scania, and published figures of representatives from this area of both *»Dalmanites eucentrus* Ang., Olin emend.» and *»Dalmanites mucronatus* Brongn.», together with a discussion of the differences between the two forms.

Discussion of the species.

Wahlenberg's original specimens have not been found, and his figure, being schematic, is unsatisfactory for purposes of identification. The glabellar furrows are there shown almost parallel, becoming gradually more oblique anteriorly, while the lobes are very similar to each other and all of approximately the same length (exs.). The occipital furrow is not continued across the axis and there are no facial sutures. The pygidium shows 13 axial rings, of which the second to the fifth bear appendifers. The axis of the pygidium, tapering more rapidly behind the last ring than anteriorly, reaches to the posterior margin and is produced into an almost parallel-sided terminal spine five-sevenths as long as the pygidium alone. There are apparently 10 pleurae, the first seven of which correspond with the axial rings; the anterior band of each pleura widens (exs.) towards the margin, where it is about as wide as the posterior band. The sutural and oblique furrows both reach to the margin, the latter furrows being emphasised more greatly.

The main differences between this figure and extant specimens from Västergötland are the following. The glabellar lobes of the figure are much more regular than in nature. The number of pleurae of the pygidium does not in fact exceed nine, and the furrows of the pleurae do not reach the margin in the manner shown in the figure, the anterior band always being circumscribed before the margin is reached.

Wahlenberg's figure was copied with some slight differences by Brongniart, but the next figure, that of Dalman, is original and a considerable improvement. The cephalon is much more true to nature, although there is still no facial suture. The shapes and disposition of the glabellar lobes are accurate except for minor details; for instance in tracing the posterior margin of the occipital ring, Dalman has followed the course of the doublure to the ring, which does bend forwards over the axis, although the actual posterior margin swings backwards. In the pygidium there are 11 axial rings followed by an un-annulated part, which is continued posteriorly into a terminal spine four-sevenths as long as the pygidium itself. The spine tapers less rapidly than the anterior portion of the axis. There is a well marked border outside the distal ends of the sutural and oblique furrows despite the remark in the description »Costae pygidii marginem attingentes» The anterior band of each pleura widens (exs.) outwards to a maximum at its distal end of about twice the width of the posterior band. In actual specimens the anterior band tapers rapidly beyond its maximum width, owing to a sharp bending backwards of the sutural furrow, which just before disappearing approaches the oblique furrow behind. Dalman's figure does not thus show the extreme, faintly incised, distal ends of the furrows. The sutural furrows are shaded as being more marked than the oblique.

There are in the Stockholm Riksmuseum a pygidium and three cephala (RM: Ar 9830-3) from the Dalman Collection, which were possibly used by that author in his descriptions and figures of this species. These are the earliest extant specimens to have been used in connection with *D. mucronata*, and are thus of importance in framing a definition of the species.

The next figure of *D. mucronata*, that of Angelin, is poor and inaccurate, and a discussion of it is not necessary.

The glabella and pygidium from Bala, figured by Salter as *Phacops mucronatus* are preserved in the Geological Survey Museum, registered numbers GSM: 19181, 19182. They are illustrated on pl. II, figs. 5, 6. The glabella is incomplete and extremely distorted, and is not considered determinate. The pygidium, a ventral mould, is rather better preserved and has suffered less shearing. The axis is wide and tapers rapidly, there are nine axial rings. Seven pleurae are visible, and it is most probable that the matrix covering the posterior part of the lateral lobe conceals an eighth. The anterior band of each pleura is almost as wide (exs.) as the posterior, that of the second pleura reaching to a maximum width greater than the posterior band. The anterior bands end well within the lateral margin, and their terminations are quite deeply incised. Salter's figure is inaccurate in that the posterior, instead of the anterior, pleural bands are shown as being distally circumscribed by the furrows. Apart from the rather deep incisions of the distal ends of the anterior bands, this pygidium fits well within the range of variation of D. mucronata. The lateral border is rather more undulate than is common in the latter, but this feature is not considered of sufficient importance to warrant separation from that species.

Salter suggested somewhat tentatively the specific name *appendiculatus* for these Bala specimens (1864, p. 47). Marr, however, stated that Salter »separated the North of England form from the type *mucronatus* as var. *appendiculatus*» (1907, p. 66). I have been unable to find any reference to such a separation in Salter's writings, and it is unlikely that Salter even knew of the existence of these forms from the North of England. In any case the name *appendiculatus* was originally put forward for the Bala fossils, and as these are now considered to be *mucronata*, it must be a synonym of the earlier name.

Salter's two figured specimens are described as coming from »Caradoc Slates of Pen-y-Rhiw, west of Bala, over the volcanic ash-bed.» There is a place on the 6-inch Ordnance Survey map of Bala (Merioneth 22 N. W.), marked as Pen-rhiw, about half a mile north-west of Bala town, which is apparently the Pen-y-Rhiw of Salter.

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The nearest outcrops to this are at Craig y Fron and in a Quarry by the roadside, both about 300 yards north-west of Pen-rhiw; the same beds are apparently exposed at both these places. At Craig y Fron, there is a volcanic ash band which forms the crag marked on the map, and the beds above this are well exposed a few yards to the south-east. These are then presumably the beds referred to by Salter and from which his fossils are supposed to have come. As was pointed out to me by Dr. Stubblefield, this ash is mapped by Miss Elles (1922, p. 139) as the Frondderw Ash, and the beds above it as the Allt-Ddu Mudstones. The latter occur very low in the sequence here below both the Rhiwlas Beds and the Gelli-grin Beds, and are of low Caradocian age: they were considered by Bancroft as being Lower Soudleyan, and are certainly far below the first occurrence of D. mucronata elsewhere. The beds above the ash at Craig y Fron are dark blue mudstones quite different in lithology from the matrix of Salter's specimens, and their fauna consists only of Orthidae and Brongniartella bisulcata (Salter) with no trace of D. mucronata. It seems then unlikely that Salter's specimens of the latter did in fact come from this locality, and as their matrix is more like that of the Foel-y-Ddinas beds which contain occasional D. *mucronata*, it is probable that they are from this higher horizon, even though these beds do not occur anywhere near Pen-rhiw. The reference to Pen-rhiw must be due to a mistake during collection, as the original Geological Survey Catalogue B. P. 212 includes *Phacops mucronatus* in the typically Caradocian faunal list of that locality.

Considering now *Phacops pulchellus* Linnarsson, there is a pygidium from Kinnekulle in the collection of the SGU in Stockholm, which Professor Thorslund believes to be the original of this species: it is illustrated here on pl. I, fig. 3. It is a small form, 3.5 mm. long, and the same size as Linnarsson's figure reduced to natural size, and it agrees well with the latter except that there are only eight pleurae whereas the figure shows nine. In view, however, of the close similarity in other features it is very probable that this specimen is the original of Linnarsson's species. The most noteworthy features of both are the convexity and elongated shape of the pygidium, the narrow axis and the wide (exs.) anterior pleural bands. It is considered here that, in view of the great variability of *D. mucronata*, it is better to regard *Phacops pulchellus* Linnarsson not as a distinct species, but as a synonym of *D. mucronata*.¹

Angelin's figure of his *Phacops eucentra*, the species erected to cover the Scanian forms previously included in *Phacops mucronatus*, differs greatly from his figure of the latter, and also from the earlier figure of Dalman. The following description is based upon the 1851 figure which differs slightly but insignificantly from that of the edition edited by Lindström in 1878. The glabella overhangs the frontal margin of the cephalon and is very swollen anteriorly, there is no anterior border. The eyes are very small, and are placed far forward and near the margin. The first glabellar furrows are distinctly connected at their inner ends with the occipital furrow.

The pygidium is longer than the cephalon, and is produced posteriorly into a

¹ It may be noted that *Phacops pulchellus* Foerste (1887, p. 99) is a homonym of *Phacops pulchellus* Linnarsson, 1866.

spine a little less than half the length of the pygidium itself. The axis is anteriorly almost as wide as each pleural lobe: it tapers rapidly and does not extend into the spine. There are apparently fourteen axial rings, each of approximately the same width (sag.), and behind these a terminal piece. There are twelve pleural segments, the first eleven of which correspond with the axial rings. Each pleura forms a smooth curve, but bends back more rapidly approaching the margin. The anterior pleurae leave the axial furrows almost at right angles to the axial line but the posterior ones are inclined backwards along their whole length (tr.). The sutural furrows are well marked, but appear not to reach the margin. The oblique furrows are fainter, dying out more rapidly towards the margin, but apparently approaching distally the sutural furrow next in front. The anterior bands are approximately as wide (exs.) as the posterior.

For purposes of identification Angelin's figure of *Phacops eucentra* is unsatisfactory. Some of the singular features of the figure of the cephalon are the very forward position of the eyes, their small size and great distance from the glabella, and the smallness of the free cheeks. These features are not found to the same degree in any specimen examined from Röstånga. As regards the pygidium, the first point of interest is the difference between the number of pleurae in the diagnosis (nine) and that figured (twelve), and in this respect it is advisable to trust the diagnosis and assume that Angelin was describing a pygidium with nine pleurae. The correspondence of the axial rings each to each with the pleurae has not been observed in any Röstånga specimens, in which also the axis is always continued into the terminal spine.

The cephalon and pygidium from Röstånga described by Olin as *Phacops eucentra* Angelin are refigured here (pl. III, figs. 5,7). Olin's figures are very good, and faithful to the originals. The cephalon resembles Angelin's figure only in respect of the frontal lobe of the glabella which in both overhangs the anterior border. This appearance is, however, probably due to the state of preservation of Olin's specimen. In other features, such as the position of the eyes, the cephala are quite different. The pygidium has seven pleurae, in contrast with the nine of Angelin's. This feature is here considered as characteristic of the species represented in Olin's figures, and it is thus clear that this species cannot be identical with *Phacops eucentra* Angelin; for it the name *Dalmanitina olini* is proposed.

There remains to be considered the question of the validity and recognition of *Phacops eucentra* Angelin. The cephalon of Angelin's figure is unlike any from the Brachiopod Beds of Scania, although it could be regarded as a caricature of specimens of D. mucronata and D. olini from Scania, in some of which the anterior border is often crushed, making the glabella appear to overhang. The cephalon also bears a great resemblance to a specimen, which may be an aberrant D. mucronata, from Kinnekulle (RM: Ar 9861).

The pygidium of *Phacops eucentra* came from Scania, and (following the diagnosis and not the figure) possessed nine pleurae. It thus belongs to D. mucronata (see below, p. 13). As is pointed out later, the Scanian forms of D. mucronata show

certain common characteristics possibly dependent on facies, for instance in all cases a long tail spine, and usually a narrow axis. These are not here considered sufficient to justify separation from the typical D. mucronata of Västergötland. If, however, on the basis of further collections, it should be found advisable to distinguish the Scanian forms of D. mucronata, then Angelin's name D. eucentra could be revived. For the time being the species as defined by the pygidium is regarded as a synonym of D. mucronata.

Summary.

The above discussions leads to the following conclusions.

D. mucronata (Brongniart) is a valid species of which, however, no type material is preserved.

Phacops pulchellus Linnarsson is a synonym of *D. mucronata*, as is *Phacops appendiculatus* Salter.

The forms described by Olin as *Phacops eucentra* Angelin are not identical with the original description of that species. For these forms the name *Dalmanitina olini* is proposed.

It is doubtful whether *Phacops eucentra* Angelin can be recognised. The cephalon is probably aberrant, while the pygidium is apparently identical with *D. mucronata* from Scania.

Genus Dalmanites BARRANDE, 1852.

Subgenus Dalmanitina REED, 1905.

Dalmanitina mucronata (Brongniart).

Synonymy.

- 1821 Entomostracites caudatus. WAHLENBERG, Nova Acta Soc. Sci. upsal., viii, p. 28, pl. II, fig. 3.
- 1822 Asaphus mucronatus BRONGNIART, Hist. nat. des Crustacés..., p. 24, pl. III, fig. 9.
- 1823 Trilobus mucronatus. VON SCHLOTHEIM, Nachträge zur Petrefactenkunde II, p. 37.
- 1826 Asaphus mucronatus. DALMAN, Om Palaeaderna..., pp. 236, 268, pl. II, figs. 3a, b.
- 1837 Asaphus mucronatus Brongn. HISINGER, Lethaea Svecica, p. 13, pl. II, figs. 1a, b.
- 1846 Phacops mucronatus [partim]. BURMEISTER, Organisation of Trilobites, p. 95.
- 1851 Phacops mucronata Brongn. ANGELIN, Pal. Svecica, p. 10, pl. VIII, fig. 1.
- 1851 Phacops eucentra ANGELIN, Pal. Svecica, p. 11, pl. IX, fig. 1 [Pygidium, ? Cephalon].
- 1853 Phacops mucronatus Brongn. [partim]. SALTER, Organic Remains, dec. VII, pl. I, p. 12.
- 1864 Phacops (Odontochile) mucronatus Brongn. ? SALTER, Mon. Brit. Trils., p. 46, pl. IV, figs. 11, 12, text-fig. 10.
- 1864 Phacops appendiculatus SALTER, ibid., p. 47.
- 1865[?]Phacops Emm. mucronata Brongn. KJERULF, Veiviser ved geologiske Excursioner i Christiania omegn, p. 20.
- 1866 Phacops pulchellus LINNARSSON, Om de Silur. bild. i meller. Vestergötland, p. 16, pl. II, fig. 1.
- 1869 Phacops pulchellus Linsn. LINNARSSON, Om Vestergöt. Camb. och Silur. Afl., p. 59, pl. I, fig. 3.

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- 1869 Phacops mucronatus Brongn. LINNARSSON, ibid., p. 59.
- 1896 Phacops appendiculatus (Salt.) [partim]. ELLES & WOOD, Quart. J. geol. Soc., lii, p. 276.
- 1897 [?] Dalmanites mucronatus Brongn. KIAER, Etage 5 des norweg. Silursystems, pp. 74, 76, 33.
- 1901 Dalmanites mucronatus Brongn. HOLM, Kinnekulle dess geol., p. 59, text-fig. 54.
- 1901 [?] Dalmanites mucronatus Brongn. KIAER, Etage 5 i Asker, pp. 25, 32, 79, 85, 91.
- 1907 Phacops mucronatus Brong. REED, Geol. Mag., dec. 5, iv, p. 537.
- 1909 Phacops (Dalmannites) mucronatus Brongn. [partim]. ELLES, Quart. J. geol. Soc., lxv, p. 183.
- 1913 Phacops mucronatus [partim]. MARR, ibid., lxix, p. 5.
- 1916 Phacops mucronatus Brongniart [partim]. MARR, ibid., lxxi, p. 200.
- 1918 Dalmanites mucronatus Brongn. TROEDSSON, Om Skånes brachiopodskiffer, p. 68, pl. I, figs. 26, 27, text-figs. 12, 13.
- 1920 Dalmanites mucronatus Brongn. TROEDSSON, Geol. Fören. Stockh. Förh., xlii, h. 5, p. 265 et seq.
- 1921 Dalmanites mucronatus Brongn. TROEDSSON, K. fysiogr. Sällsk. Handl., N. F., xxxii, no. 3.
- 1922[?] Phacops mucronatus Brongniart. Elles, Quart J. geol. Soc., lxxviii, pp. 144, 156.
- 1925 Dalmanites mucronatus. RICHTER, Zbl. Min. Geol. Paläont., abt. B, no. 4, p. 111.
- 1929[?] Phacops mucronatus Brongniart. PUGH, Quart J. geol. Soc., lxxxv, pp. 262, 263.
- 1934 Phacops cf. mucronatus. KING & WILCOCKSON, ibid., xc, p. 17.
- 1934[?] Dalmanites mucronata. STØRMER, Proc. Geol. Ass., xlv., p. 330.
- 1935 Dalmanites mucronatus (Brongn.). THORSLUND, Nova Acta Soc. Sci. upsal., ser. 4, ix, no. 9, pp. 11, 13.
- 1935 Dalmanites n. sp. THORSLUND, ibid., p. 11.
- 1935 Dalmanites mucronatus (Brongn.). SCHMIDT, Senckenbergiana, xvii, no. 3-4, p. 121, text-figs. 2-4.
- 1935 Dalmanites mucronatus. TROEDSSON, ibid., p. 177 et seq.
- 1936 Dalmanites mucronatus. TROEDSSON, Rep. XVI Int. geol. Congr., vol. I, p. 496, table I.
- 1948 Dalmanitina mucronata Brongn. WAERN, THORSLUND & HENNINGSMOEN, Bull. geol. Instn. Univ. Upsala, xxxii, pp. 408, 435.
- 1858 [non] Phacops mucronatus Brongn. HOFFMANN, Verh. russ.-K.Min. Ges. St. Petersb., Jahrg. 1857-8, p. 42, pl. IV, fig. 5.
- 1885 [non] Phacops mucronatus Brongn., var. MARR & ROBERTS, Quart. J. geol. Soc., xli, pp. 480, 482.

[from Sholeshook Beds, Haverfordwest;=Phacops robertsi Reed.]

- 1887 [non] Phacops pulchellus FOERSTE, Bull. sci. Labs. Denison Univ., ii, p. 99, pl. VIII, figs. 4, 20, 21.
- 1888 [non] Phacops (Dalmannites) mucronatus Brongn. MARR & NICHOLSON, Quart. J. geol. Soc., xliv, p. 721, pl. XVI, figs. 5, 6. [from Stockdale Shales, Browgill; = Dalmanites cf. weaveri (Salter) var. tenuimucronata Whittard.]
- 1895 [non] Phacops (Acaste) appendiculatus (Salt.). ELLES & WOOD, Geol. Mag., dec. 4, ii, pp. 247, 248.

[from Drygill Shales, Carrock Fell, Cumberland; = Phacopidina apiculata (Salter).]

1907 [non] Phacops mucronatus Brong. FEARNSIDES, ELLES & SMITH, Proc. R. Irish Acad., xxvi, B, no. 9, p. 104, pl. VIII, figs. 10-13.

[from Lower Tirnaskea Beds, Pomeroy, N. Ireland; = D. olini, sp. nov.]

1928 [non] Phacops (Dalmanites) aff. mucronatus (Brongniart). KING, Quart. J. geol. Soc., lxxxiv, p. 700.

[from Lower Valentian, Meifod.]

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Type Material.

Wahlenberg's specimens being lost, there is no type material for *D. mucronata*, and the specimens form the Dalman Collection (RM: Ar 9830—3, two of which are figured on pl. I, figs. 7, 8), although important, have no systematic standing. It is thought best at present not to freeze the species to the extent of choosing neotypes. The following description is based on many Västergötland specimens, including those from the Dalman Collection.

Description.

Cephalon. The anterior outline is roughly semicircular, and the genal angles are produced into stout genal spines.

The glabella extends far forwards, with an anterior border in front; the sides of the glabella are approximately straight, but often bulge outwards around the third glabellar lobes. The third glabellar furrow is oblique and without an appendifer; it sometimes shows an inner transverse part somewhat deeper than the outer more oblique part, although in many cases the whole furrow is straight. The frontal lobe of the glabella is equal to half the total length of the cephalon; it is sometimes ornamented with coarse tubercles and often bears a depression on the mid-line just behind the centre. The second furrow is convex forwards but roughly transverse; its inner half is deepened to form an appendifer, while the outer half is shallow and often barely distinguishable. The first furrow is slightly oblique, and has a deep inner part forming an appendifer somewhat longer (tr.) than that of the second furrow. The occipital furrow consists of a lateral part on each side, deep and transverse and bearing an appendifer, which corresponds to the glabellar furrows, and a median part, reaching across the axial line of the glabella, which is shallow, broad (sag.) and convex forwards. The glabellar furrows and the occipital furrow are approximately equidistant from each other. The occipital ring widens (sag.) towards the axial line, and often bears a central tubercle. The inner ends of the glabellar furrows fall on a straight line parallel to the axis of the glabella.

The palpebral lobes of full-grown adults extend backwards from the junction of the third furrow with the axial furrow to a point usually just behind the projection of the second furrow: in sub-adult forms the lobes often reach back behind the first furrows. The palpebral lobes are raised distally above the general level of the cheek, and the visual surface of the eye is inclined at an angle of 30° to the surface of the cheek. The anterior facial suture follows closely the contour of the anterior lobe of the glabella, usually remaining dorsally on the anterior border, but occasionally becoming marginal in front. The posterior facial suture is gently convex forwards, crossing the lateral margin at a small angle, and continuing backwards across the doublure to end approximately opposite the occipital furrow. The posterior marginal furrow leaves the axial furrow a little behind the end of the occipital furrow: it is transverse, shallow, more steep anteriorly than posteriorly, and does not reach the lateral margin. The posterior border of the fixed cheek widens (exs.) outwards as the posterior margin curves backwards to the genal spine. There is a slightly raised lateral border around the cheeks, becoming thinner and flat anteriorly in front of the glabella, and a shallow marginal furrow inside the lateral border.

The doublure to the lateral margin is as wide (tr.) as the raised border and very concave, with the result that its inner edge bends vertically up so as almost to touch the dorsal shell. The doublure to the occipital ring widens (sag.) inwards, its edge being parallel to the occipital furrow. There is no doublure opposite the posterior ends of the axial furrows. The anterior edge of the doublure to the posterior margin is parallel to the posterior marginal furrow, and runs outwards in a smooth curve to join the inner edge of the doublure around the lateral margin of the cheek. The genal spines are circular in cross-section.

The surface of the cheeks may be coarsely ornamented with a shallow irregular reticulation. The whole dorsal surface, including the ventral surface of the doublure, is finely granulate, except in large individuals in which only the margin and doublure are granulate. The ventral surface is smooth.

Pygidium. The general outline varies from triangularly rounded to almost semicircular, and the convexity of the pygidium is also variable. The axis is of variable width, and usually shows eleven axial rings which become shorter (sag.) posteriorly. Each of the first five or six cross-furrows consists of a lateral part on each side, which is deepened into an appendifer and slopes forwards towards the axis, and a median wider (sag.) groove crossing the axis. The posterior cross-furrows are similar in shape to those in front, but do not bear appendifers. The axis is continued into a posterior spine of variable length, usually inclined upwards from the plane of the pygidium. There are not less than eight pleurae, and not usually more than nine. The anterior pleurae leave the axial furrow at right angles to the mid-line, but the more posterior leave at progressively smaller angles until the last lies almost parallel to the axial furrow. The pleurae may form an even curve or be geniculate. The oblique furrows are often deeper and wider than the sutural; they approach the sutural furrows towards the pygidial margin, but both furrows die out within the lateral border. The latter is flat, the terminations of the sutural and oblique furrows not being normally very deeply incised. The anterior pleural bands reach a maximum width (exs.) equal to or greater than that of the posterior bands.

The doublure is flat, and parallel to the dorsal surface. It widens posteriorly, and does not usually extend inwards beyond the terminations of the furrows.

The dorsal surface of the pygidium, and the ventral surface of the doublure, are finely granulate.

Hypostome. Central body gently inflated. Anterior margin curved, and extended laterally into two prolongations inclined a little below the general level. Posterior margin rounded. A marked marginal groove around the posterior tongue, becoming more faint anteriorly: the raised border outside this groove becoming wider posteriorly. Within the marginal groove there is on each side a parallel elongated depressed area. The surface is coarsely tuberculate.

Distribution of Dalmanitina mucronata.

This species has a wide range in space and time.

In Scandinavia it occurs in the *Staurocephalus* zone and Brachiopod Beds of Scania, Västergötland, Dalarne, Jämtland, Östergötland and Norway, while it has also been recorded from Poland.

In Britain it is found in beds equivalent to those of Scandinavia in the Lake District (Ash Gill and neighbouring localities), North West Yorkshire (Cautley), and Wales (Conway, Bala and Haverfordwest).

At Ash Gill, D. mucronata is found, together with a number of other trilobites, in the lower *mucronatus* Beds» (Marr, 1916, p. 193: this horizon is equivalent to the Staurocephalus zone of Sweden). Occasional specimens are found in the upper *mucronatus* Beds» (=Lower Brachiopod Beds of Scania) with an abundance of D. olini. The Ashgill Shales of Ash Gill and Cautley have yielded few good forms, but these also appear to be D. mucronata.

At Conway, *D. mucronata* is found with *D. olini* in the upper part of the Deganwy Mudstone just below the Conway Castle Grit in Deganwy Quarry (Elles, 1909, p. 183), while in the Bala area some of the specimens from the Foel-y-Ddinas Mudstones and corresponding beds are apparently *D. mucronata*.

There are some specimens of *D. mucronata* from the St. Martin's Beds (Basal Valentian) of Haverfordwest, and a new variety has been found in the basal Silurian limestones of Cautley and Keisley.

Dalmanitina mucronata (Brongniart) var. brevispina, var. nov.

Pl. II, fig. 2.

Synonymy.

1913 Phacops mucronatus. MARR, Quart. J. geol. Soc., lxix, p. 11.

Material.

Holotype SM: A 36372a, b (pygidium). Paratypes SM: A 36374a, b, 36378, 36379, 36384, 36385 (pygidia); SM: A 36373, 36376, 36386 (cephala).

All are from the limestone at the base of the Silurian, Watley Gill, Cautley, Yorkshire. Other specimens have been found in an equivalent limestone at Keisley, Westmorland.

Description.

The holotype is the ventral mould of a pygidium, of which the dorsal counterpart is also present. It is 4 mm. long, and is incomplete, the left lateral lobe being missing.

The axis is wide, almost as wide as the lateral lobe, and is produced posteriorly into a very short thorn-like spine which is set at an angle of about 45° above the plane of the pygidium. Although the axis tapers quite rapidly it is still wide even at the base of the spine, and the latter represents less an actual continuation of the axis, than a dorsal pulling-out of part of the axis. There are ten axial rings becoming shorter (sag.) posteriorly, the last being only a third as long as the foremost. The first three cross-furrows have two deep lateral portions trending backwards and outwards, joined across the axis by a wide shallow groove slightly concave forwards. The more posterior cross-furrows have the same shape as those in front, but the lateral parts are not deep, while the two last cross-furrows do not extend across the axis.

There are eight pleurae, the posterior one being very small, but quite distinct on the dorsal mould. Each pleura is an even curve, the foremost leaving the axial furrow transversely, those behind leaving at more and more oblique angles. The oblique furrow of each pleura is wider (exs.) and deeper than the sutural. While the posterior band is of even width (exs.) along its whole length, the anterior band widens outwards to a maximum slightly greater than that of the posterior band. The sutural furrow of each pleura and the oblique furrow behind it approach each other beyond this maximum width, but they both die out before meeting. Beyond the ends of the furrows, there is a wide (tr.) smooth border to the pygidium. The lateral margin is slightly wavy, the faint outward bulges probably corresponding to the continuations of the posterior bands. The external mould shows the dorsal surface to have been finely granulate: there is no ornamentation on the ventral surface.

The three paratypes of the cephalon are all more or less fragmentary. A detailed description will not be given. They show very well marked appendifers, and the pattern of the glabellar furrows is identical with that of D. mucronata s. str. The palpebral lobes of one specimen (A 36376) are very long, reaching back to the first glabellar furrows, and the fixed cheeks within them are markedly reticulate.

Discussion.

The specimens of D. mucronata var. brevispina from Cautley are all small, the largest pygidium (A 36378) being 4 mm. long, although its original length before distortion was probably double that figure. The other pygidia average 4 mm. long undistorted, while the three cephala are between 5 mm. and 6 mm. long, and probably correspond to the 4 mm. pygidia. There is in addition one fragmentary glabella (A 36377) which may represent an undistorted cephalic length of 10 mm: this glabella is on the same slab as the largest pygidium (A 36378), and the two may possibly belong to the same individual. The most frequent size would seem to be a pygidium of about 4 mm. long, and a cephalon slightly longer. The holotype shows a

slightly wavy lateral margin, as is found in specimens of similar size of *D. olini*, but there are no other signs of immaturity. Associated with *D. mucronata* var. *brevispina* at Cautley is a fauna consisting of many brachiopods all apparently of normal size, and a variety of the trilobite *Leonaspis girvanensis* (Reed), the specimens of which are the same size as those of *L. girvanensis* figured by Reed from the Upper Drummuck Group of Girvan (1914, pl. V, figs. 8, 9; pl. VI, figs 1, 2, 3). There is apparently no evidence that the associated fauna is of less than normal size.

Three other pygidia of var. *brevispina* have been found in a basal Silurian limestone near Keisley. The largest of these is of the same size as the Cautley forms, but the others are considerably smaller, 1 mm. and 2 mm., although, apart from some minute brachiopods, the associated fauna is not of less than average size. There are also some very small specimens, probably of var. *brevispina*, in the dwarfed shelly fauna interbedded in the base of the Skelgill Beds at Ash Gill Quarry, Torver, near Coniston. It seems however that the typical specimens of var. *brevispina* from Cautley and Keisley are best regarded, neither as immature nor as stunted forms, but as belonging to a local race of *D. mucronata* of which the smaller average adult size was characteristic.

In addition to the small size, the other distinctive features of D. mucronata var. brevispina are the broadly transverse shape of the pygidium, the short thorn-like tail spine, the wide axis and the presence typically of eight pleurae. It must be emphasised that one or more of these characteristics may be found in many specimens of D. mucronata s. str.; it is rather the combination of the five characters which distinguishes var. brevispina.

Among Swedish specimens of *D. mucronata*, those that approach most closely to var. *brevispina* are some pygidia from Ålleberg (e. g. RM: Ar 9850, pl. I, fig. 2), and two small pygidia (PIU: ar 820, 821, pl. I, fig. 4) collected by Professor Thorslund from the *Staurocephalus* zone of the Brachiopod Beds of Amtjärn, Dalarne (bed 6, Thorslund, 1935, p. 11). The two last are obviously smaller editions of those from Västergötland. Although similar to var. *brevispina* in general shape and in the possession of a short terminal spine, these forms differ in their flatness which is probably original, and in the fact that their axes taper posteriorly more rapidly than is typical of var. *brevispina*; they have also slightly wider and better developed lateral borders than have the Cautley forms. In view of these differences, and of the stratigraphical horizon of the Dalarne specimens, they are not considered here as belonging to var. *brevispina*.

D. mucronata var. brevispina is defined essentially in contrast with the British specimens of D. mucronata s. str., which occur at a lower stratigraphical horizon, and from which var. brevispina is readily distinguishable. It is probable that the common characteristics of this variety were of limited extent in both space and time, and that the variety was in fact no more than a local race of D. mucronata. Although individual specimens from Sweden may exhibit features similar to those of var. brevispina, it is unlikely that the variety itself will be found, as a community, outside the North of England.

Intra-specific variation of Dalmanitina mucronata.

Pygidia.

The number of pleurae is never less than eight, and although the eighth pleura may be very small it is nevertheless always developed. Occasionally, a ninth pleura is present especially in large specimens, but this is not typical of the species. The form figured by Troedsson (LO: 2929t; 1918, pl. I, fig. 27; here pl. III, fig. 1) has nine pleurae, and in this respect as in others, differs from the norm of the species. The number of axial rings is less determinate, but does not usually exceed eleven.

The axis may be broad, in which case its width at the anterior margin of the pygidium is almost equal to that of the pleural lobe on either side, as in the specimen figured on pl. I, fig. 2; or it may narrow, when the axis at the anterior margin is little more than half the width of each pleural lobe. The pygidium figured by Troedsson (LO: 2929t) is, in this case also, abnormal, as the axis is narrower and more nearly parallel-sided than in the majority of specimens. It is to be remarked that in most cases where the width of the axis projected on a horizontal plane is relatively small, the axis itself is more convex than in forms with a wider axis. It seems probable that the actual width of the axis, as measured along the surface of the shell, does not show great differences, and that the apparent variation is due mainly to differences in convexity of the axis. Most of the Västergötland forms with the widest axes are probably merely flatter forms of those from the same area with less wide axes (contrast figs. 1 and 2 of pl. I): among the latter may be included the original of Linnarsson's Phacops pulchellus (pl. I, fig. 3). It is considered here that Linnarsson's form falls within the range of variation of D. mucronata, and is accordingly synonymous with the earlier species. If further collecting from Västergötland should demonstrate that the width of the axis allowed of subdivision of the forms from this area, then Linnarsson's species *pulchellus* might well be revived as typical of those with a narrower axis. The majority of specimens of D. mucronata from Scania possess a narrow convex axis, and it is perhaps significant to note that these specimens are preserved in shale, whereas those from Västergötland are mostly in a calcareous matrix. Among specimens of D. mucronata from Britain it is in most cases extremely difficult, owing to distortion, to establish the original proportions of the axis to the lateral lobes, but specimens from the lower *»mucronatus* Beds» of Ash Gill, the most plentiful in this country, are apparently identical in this respect with those from Scania (pl. IV, fig. 3). Specimens of var. brevispina from the lowest Silurian of the North of England possess wide axes similar to those of many Västergötland D. mucronata.

In addition to the variation in the convexity of the axis, there is also a wide degree of variation in the convexity of the pygidium as a whole. It is conceivable that part of this variation is due to later pressure, but the presence of both the flatter and the more convex forms in the same matrices in Scania (shale) and Väster-götland (mainly limestone) indicates that a component at any rate was original 2

variation. The convexity of the pygidium seems to vary independently of other characters. As examples of the flatter types there are some pygidia from Ålleberg (e. g. pl. I, fig. 2), those from Amtjärn (pl. I, fig. 4) and several from Scania, while the other extreme of very convex forms is represented by some specimens from Scania (pl. III, fig. 2), Linnarsson's *Phacops pulchellus* and several other Ålleberg forms. The Dalman Collection pygidium (pl. I, fig. 8) has almost completely flat lateral lobes, although the axis rises quite high above them. Specimens of *D. olini* are flat and show less variation than *D. mucronata*.

Perhaps related to the convexity of the pygidium is the general shape or outline. The variation here is between the elongated type in which the posterior outline is approximately parabolic (pl. I, figs. 1, 3; pl. III, fig. 2), and the broader form with a more circular posterior outline (pl. I, figs. 2, 4; pl. III, fig. 1). Although the former variety may be associated with greater convexity and vice-versa, this is not a general rule, there being for example elongated flat specimens (LO: 30 JT from Scania), and once again the variation is not systematic. Specimens of var. *brevispina* are broad-looking forms with a rather pointed parabolic outline.

There is much variation among D. mucronata from Västergötland as to the length of the terminal spine of the pygidium. In many cases this is broken off, and it is only possible to guess its original extent, as in the Dalman Collection specimen (pl. I, fig. 8): in the latter, however, the width of the spine would suggest that it was at least a further 5 mm. long. Spines of such a length, relative to a pygidial length (excluding spine) of, in this case, approximately 25 mm., are classed as »long» in contradistinction to those »short» thorn-like spines of the order of 1 mm. long. Among Västergötland material, spines of both sorts are present, as for example, the very short spine of PIU: ar 4078, and the much longer one of ar 4079, both from Ålleberg. It is probable that in many cases in which the preservation does not show spines, as in RM: Ar 9850 (pl. I, fig. 2) and others from Alleberg, these were of the short variety. In contrast to this, all the specimens from Scania have long spines, which are quite as marked in small as in large specimens (pl. III, fig. 3). In this respect the Scanian forms are similar to D. olini, where the spine is very long and stout (pl. III, fig. 7; pl. IV, fig. 4). British forms of D. mucronata have spines of the same order of length as those from Scania. Specimens of var. brevispina differ, however, in possessing only a very short pointed thorn-like spine. Most of these specimens are small (less than 5 mm. long), but of approximately the same size as many from the lower »mucronatus Beds» of Ash Gill and from Scania, in both of which the spine is well developed and long.

In the majority of specimens of D. mucronata, the anterior band of each pleura attains a width (exs.) equal to or greater than that of the posterior band (pl. I, fig. 1; pl. IV, figs. 1, 3). Some forms, however, show an approach to D. olini in that the anterior band is not as wide as the posterior although the difference in widths is not as marked as in typical forms of the latter species. Accompanying the increase in width of the anterior band is a deepening and widening of the oblique furrow, and within D. mucronata may be found all stages from that in which the sutural and

oblique furrows are both equally shallow and the surface of the lateral lobes almost flat — as is also the case of D. olini, to that in which the oblique furrow is very wide and deep (pl. II, fig. 1). In the latter case the anterior and posterior bands of the pleurae become quite convex in cross section, and the relief of the lateral lobe is greatly increased. With regard to the depths of the furrows, Dalman's specimen is not very well preserved, but neither of the furrows is very deep, and the oblique is very little more marked than the sutural: the anterior and posterior bands are of about equal widths.

The sutural and oblique furrows usually die out distally before uniting, and before reaching the margin: in a few cases, however, the furrows do reach almost to the margin as in the specimen figured by Troedsson (1918, pl. I, fig. 27), but this condition is not typical of the species. In most cases there is an almost smooth lateral border outside the furrows, of a width usually slightly less than that of the doublure. This lateral border is well marked in var. *brevispina* and in related forms (pl. I, fig. 4; pl. II, fig. 2).

Cephala.

Compared with the large variability of the pygidia of *D. mucronata*, that of the cephala is apparently small.

The outline of the glabella shows varying degrees of parallel-sidedness, and the frontal lobe shows differences in shape. There are slight variations on the basic plan of the glabellar furrows: the second furrow may be more or less convex towards the front, and the anterior furrow varies from almost straight to quite angular. There are differences too in the surface lengths (tr.) of the appendifers, especially that of the second furrow which is often very short, but may be half as long as the complete furrow. There is also variation in the depth of the appendifer of this second furrow, and in the depth of the outer part of the furrow between the appendifer and the axial furrow; in some cases the furrow is so shallow in this part that it is barely visible, while in others it is quite distinct right up to the axial furrow. Such differences in the lengths and depths of appendifers are, however, quite inapplicable to material which has been slightly crushed or distorted, for it is not possible in such material even to demonstrate the existence of appendifers. Most British specimens of both D. olini and D. mucronata have undergone some distortion which has made the glabellar furrows appear all of an even depth. Only in var. brevispina from the rotten limestone of Cautley is the preservation of British forms sufficiently good to show appendifers well. Crushing of the glabella has also the effect of straightening out the curve of, most noticeably, the second furrow, and also of accentuating the shallow outer part of this furrow which is a line of weakness. As a result, in most British forms, the second furrow is of even depth along its whole length and shows little forward convexity (pl. II, fig. 3).

Summary.

To sum up, there is within the species *Dalmanitina mucronata* a wide range of variation. This variation is in some cases due to posthumous causes, for example some of the variation in the width of the axis is due to later pressure on the pygidium; in other cases, the nature and extent of the variation are original and perhaps dependent on the facies of the containing rocks. It has been found that, apart from the earlier separation of »D. eucentra» (=D. olini) by Olin, and the erection here of a new variety, brevispina, the variation has no stratigraphical consistence. It is considered that separation of parts of the variation as distinct species or varieties having no stratigraphical significance would merely serve to burden the literature with additional names to no useful purpose. It is possible that further detailed collections from the Brachiopod Beds of Västergötland might reveal the existence of consistent stratigraphical variation not shown by the British material. As both D. mucronata and its synonym D. pulchellus were described from Västergötland, it is most appropriate that any future delimitation of these species should be carried out on the basis of further collections from that area than are now available.

Dalmanitina olini, sp. nov.

Synonymy.

- 1896 Phacops appendiculatus (Salt.) [partim]. ELLES & WOOD, Quart. J. geol. Soc., lii, p. 276.
- 1906 Phacops eucentra Ang. OLIN, Om de Chasmopskalken, p. 41, pl. I, figs. 1-2, [? fig. 3].
- 1907 Phacops mucronatus Brong. FEARNSIDES, ELLES & SMITH, Proc. R. Irish Acad., xxvi, B, no. 9, p. 104, pl. VIII, figs. 10-13.
- 1909 Phacops (Dalmannites) mucronatus Brongn. [partim]. ELLES, Quart. J. geol. Soc., lxv, p. 183.
- 1913 Phacops mucronatus [partim]. MARR, ibid, lxix, p. 5.
- 1916 Phacops mucronatus Brongniart [partim]. MARR, ibid, lxxi, p. 200.
- 1916 Phacops apiculatus Salter. MARR, ibid, p. 200.
- 1918 Dalmanites eucentrus Ang., Olin emend. TROEDSSON, Om Skånes brachiopodskiffer, p. 57, pl. I, figs. 19—24, text-figs. 10—11.
- 1920 Dalmanites eucentrus Ang. TROEDSSON, Geol. Fören. Stockh. Förh. xlii, h. 5, p. 265 et seq.
- 1921 Dalmanites eucentrus. TROEDSSON, K. fysiogr. Sällsk. Handl., N. F., xxxii, no. 3.
- 1925 Dalmanites eucentrus. RICHTER, Zbl. Min. Geol. Paläont., abt. B, no. 4, p. 111.
- 1929 Phacops mucronatus Brongniart [partim]. PUGH, Quart. J. geol. Soc., lxxxv, pp. 262, 263.
- 1935 Dalmanites eucentrus (Ang.). SCHMIDT, Senckenbergiana, xvii, no. 3-4, p. 121, text-fig. 1.
- 1935 Dalmanites eucentrus. TROEDSSON, ibid, p. 177 et seq.
- 1936 Dalmanites eucentrus. TROEDSSON, Rep. XVI Int. geol. Congr., vol. I, p. 496, table I.
- 1851 [non] Phacops eucentra Angelin, Pal. Svecica, p. 11, pl. IX, fig. 1.
- 1856 [non] Phac. eucentra Ang. BARRANDE, Parallèle entre... Bohême et Scandinavie, p. 50.

Type Material.

Syntypes LO: 1895 t (cephalon) — pl. III, fig. 5.

LO: 1896 t (pygidium) — pl. III, fig. 7.

All are from Röstånga Kyrkobäck, Scania. These are the specimens which, together with a fragmentary hypostome (LO: 1897 t) possibly belonging to the species, were figured originally by Olin.

Description.

Cephalon. The cephalon is similar to that of D. mucronata, except that the anterior lobe of the glabella is not coarsely tuberculate, the palpebral lobes of subadult forms do not reach back beyond the middle of the second glabellar lobe, while the occipital ring of the adult does not bear a central tubercle.

Pygidium. The general outline is roughly triangular but with rounded lateral margins, and the surface of the pygidium is relatively flat. The axis, which is anteriorly about two thirds as wide as each lateral lobe, is produced posteriorly into a long stout spine inclined upwards at a small angle to the plane of the pygidium. There are usually nine axial cross-furrows, each having two deep lateral portions connected across the axis by a shallow groove. The cross-furrows become more closely spaced and fainter posteriorly. The pleurae number six or seven, the most anterior of which is at right angles to the axis of the pygidium, the last, however, lying almost parallel to the axis. The first four pleurae correspond with the axial rings, but the posterior ones lag progressively further behind. The sutural and oblique furrows are equally developed, being shallow and narrow and dying out inside the lateral margin. The anterior band of each pleura is narrower (exs.) at its maximum than the posterior, but becomes thinner again towards the margin, and the sutural and oblique furrows of each pleura come close together before they disappear. The distal terminations of the sutural and oblique furrows are incised, and the part of the anterior band between them is depressed at its distal end below the posterior band, causing the lateral border to be somewhat undulate. The sutural and oblique furrows are usually geniculate at a point about two-thirds of the distance from the axial furrow to the margin.

The doublure extends inwards almost to the geniculation of the pleurae. It is parallel to the surface of the pygidium, and widens (tr.) posteriorly.

The whole dorsal surface and the ventral surface of the doublure are granulate.

Hypostome. As D. mucronata.

Distribution of Dalmanitina olini.

D. olini is found typically in Scania, Sweden, in the lower part of the Brachiopod Beds, where it characterises a zone between the *Staurocephalus* zone below and that of D. mucronata above: it has not been found in other parts of Scandinavia.

In Britain, this species has been found in beds corresponding to the Scanian zone of D. *olini* in the North of England, at Conway in North Wales, and in Pomeroy, N. Ireland.

J. T. Temple

In the Ash Gill tract of country, near Coniston, *D. olini* forms the bulk of the fauna of the upper part of the *»mucronatus* Beds» of Marr (=D. *olini* zone of the Brachiopod Beds of Scania), although a few specimens from this horizon are *D. mucronata*. At Cautley, *D. olini* occurs at the same horizon in the *»mucronatus* band of the *Staurocephalus* Group» (Marr, 1913, p. 1), and in the corresponding beds in Swindale Beck, Knock, in the Cross Fell Inlier.

In the Conway area, the Deganwy mudstones near Bryn-hendre (1 mile S. W. of Conway) have yielded some fine specimens of *D. olini*, including many small growth stages. On the other side of the Conway river, in Deganwy Quarry and at a higher

Head	Dalmanites eucentrus (= D. olini)	Dalmanites mucronatus
Frontal limb	very thin, commonly not visible:	broader and well developed.
Lateral furrows of glabella	shallow:	deep.
Frontal lobe	without tubercles:	covered with coarse tubercles.
Posterior branch of the facial suture	slightly sigmoid:	strongly sigmoid (young speci- mens: the largest specimens more like <i>D. eucentrus</i>).
Eyes	reaching from the anterior to the middle (large specimens) or to between the middle and poste- rior pairs of furrows (ephebic specimens):	Ephebic specimens: large, reach- ing from the anterior to the posterior pair of lateral furrows. Larger specimens $= D.$ eucentrus.
Tail		
Numbers of visible axial rings	(8—)9,	11—13.
Number of visible pairs of pleurae	6(—7),	8—9.
Furrows of lateral portions:	Oblique and interpleural furrows equally developed:	Oblique furrows commonly more marked than the interpleural ones.
Pleurae:	The anterior part about half as broad as the posterior one which widens outwards.	The 2 halves equally developed. Neanic specimens sometimes $=$ <i>D. eucentrus.</i>

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horizon just below the Conway Castle Grit, *D. olini* is found with *D. mucronata*. Some poor specimens, probably of *D. olini*, are found in the Foel-y-Ddinas Beds of Bala.

The specimens from the Lower Tirnaskea Beds of Pomeroy described by Fearnsides, Elles and Smith (1907) as *Phacops mucronatus* are *D. olini*.

Distinction of the species D. mucronata and D. olini.

Professor Troedsson summarised the differences between *»Dalmanites eucentrus»* and *»Dalmanites mucronatus»*, according to his interpretation of the two species, by the table reproduced opposite (1918, p. 96).

Cephala.

1. Width (sag.) of the anterior border.

In specimens of D. mucronata from Västergötland there is a well-marked horizontal anterior border to the cephalon, stretching around the frontal lobe, whereas in specimens of D. olini from Scania the border appears to be less well developed. Olin's syntype cephalon for example, a quite well-preserved example of D. olini, appears to have no anterior border (pl. III, fig. 5). It is probable, however, that in this specimen the border, which belongs in both species to the free cheeks, has been thrust backwards beneath the glabella, and that the facial suture now forms the visible anterior margin of the cephalon. None of the Scanian forms either of D. olini or of D. mucronata show well-developed anterior borders, and this is probably due mainly to the crushing which they have suffered, but which the Västergötland forms have escaped. Although it is possible that the border of D. mucronata was originally somewhat wider than that of D. olini, a great deal of the apparent difference is due to post-depositional crushing of the Scanian fossils.

2. Depths of glabellar furrows.

Troedsson's second character of distinction between *D. mucronata* and *D. olini* was that in the former the glabellar furrows are deep, while in the latter they are shallow.

This is another instance in which the appearance of Olin's syntype is illusory. It appears superficially that the furrows are all shallow and of the same depth as the anterior furrow. In this specimen the shell substance has been removed over most of the shield, and the ventral mould is preserved. If the second and first glabellar furrows and the lateral parts of the occipital furrow are examined under alcohol, the test is visible along each side of these furrows, plunging steeply down beneath matrix. This matrix is thus resting on the dorsal surface of the test within the glabellar furrows, and obscures the real depths of the latter by giving the im-

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pression of being the bottom of the ventral moulds of the furrows. In the majority of uncrushed specimens of both species, it has been found that when the matrix has been removed from the glabellar furrows, these are all, with the exception of the anterior furrow, produced ventrally along part of their length (tr.) into hollow appendifers formed by a fold of the test with very little local thickening. In badly crushed shale specimens, however, the appendifers are not visible, and the glabellar furrows are made to appear all of the same depth.

In some specimens of D. olini such as LO: 2924 t, figured by Troedsson (1918, p. 59, text-fig. 10:10), the glabellar furrows do, however, appear to be in fact shallow, and the second furrow, which normally shows a short appendifer, is apparently as shallow as the anterior furrow. This specimen is a very large gerontic headshield, and the shallowness of the furrow is almost certainly due to senility. In individuals of comparable size, there is no difference in the depths of any of the glabellar furrows, between forms belonging to D. olini and D. mucronata.

3. Tubercles on frontal lobe.

The third distinction of Troedsson between D. olini and D. mucronata was that the frontal lobe of the former was "without tubercles" whereas that of the latter was "covered with coarse tubercles". In most specimens from Västergötland and from Scania, which on other grounds are referable to D. mucronata (e. g. RM: Ar 9839), the anterior lobe of the glabella is provided with coarse and irregular tubercles, which however have not been observed on specimens of D. olini from Scania. Tubercles have not been found on any British specimens, but as regards Swedish forms they constitute a valid difference between the species.

4, 5. Lengths of palpebral lobes and curvature of posterior facial suture.

Troedsson's fourth and fifth points of distinction are closely related to each other. The fifth is that in immature specimens of D. mucronata the palpebral lobes reach back to a point opposite the posterior pair of glabellar furrows, while in the same stages of D. olini the palpebral lobes reach only to between the second and the posterior furrows. Adult stages of both species are alike in that the eye lobes reach as far back as in the immature forms of D. olini — not very far behind the second glabellar furrows. This character would seem, from an examination of the material available, to be the most reliable distinction between the cephala of the two species: the difference is best seen in cephala about 5 to 10 mm. in length, for in larger forms the lengths of the lobes rapidly become equal.

The fourth criterion is a corollary of the above, since the greater length of the eye-lobes in sub-adult *D. mucronata* makes the course of the posterior facial suture »strongly sigmoid» whereas in *D. olini*, the lobes being shorter, the forward curvature of the suture is less and its course is straighter. There appears to be considerable variation in the course of the posterior facial suture, and for any position of the

posterior end of the eye-lobe the curvature of the suture varies considerably, so that the point furthest forward reached by the suture is not determined solely by the backward extension of the palpebral lobe.

The criteria of backward extension of the palpebral lobes and curvature of the facial suture are extremely difficult to apply to cleaved or distorted material, and can be determined accurately only from uncrushed cephala with the free cheeks preserved. In cephala in which the free cheeks are missing the fixed cheeks are held in place only by the width (exs.) of cheek between the posterior end of the eye and the posterior margin of the cheek. In a large number of cephala without free cheeks, it is found that the fixed cheeks have been displaced form their original positions, the movement having been accompanied by the development of cracks or folds in the area of weakness behind the eyes. In such cases, the appearances of the extension forwards of the posterior facial suture relative to the glabellar furrows are quite illusory.

6. Other characters.

Although the impression is gained from some specimens, that in D. mucronata the anterior glabellar furrow is more angular than in D. olini, that also the second glabellar furrow is rather more backwardly directed and more convex towards the front, while the second lobes are rather smaller relative to the third lobes (contrast pl. I, figs. 5, 6 with pl. III, figs. 5, 6), it is considered that all these apparent differences are due to differences of preservation. In an area such as Ash Gill or Scania where both species occur in similar matrices and under similar conditions, none of these features based on the relative proportions of the glabellar lobes, or on the orientation of the glabellar furrows, proves to be consistently different in one from the other species.

Many specimens of D. mucronata of more or less adult status (up to 15 mm. cephalon length) still possess the median tubercle on the occipital ring, which is present in the ontogeny of D. olini, while this tubercle has not been observed in any undisputed specimens of comparable size of D. olini. This, although a minor point of distinction, is nevertheless quite a useful guide in practice.

It has been found that the cephala of D. *olini* and D. *mucronata* are of less assistance than the pygidia in distinguishing between the two species. There is more variation in the pygidia, and the variable characters of the latter are less dependent on preservation.

Pygidia.

With regard to the pygidia Troedsson's distinction between the two species are well-founded, these were: —

- 1. Number of visible axial rings: 8-9 in *olini*; 11-13 in *mucronata*.
- 2. Number of visible pairs of pleurae: 6-7 in olini; 8-9 in mucronata.

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- 3. Furrows of lateral portions: sutural and oblique furrows equally deep in *olini*; oblique furrows more marked in *mucronata*.
- 4. Pleurae: anterior band thinner (exs.) than posterior in *olini*; anterior band equal to, or wider than posterior in *mucronata*.

It is considered here that there is a distinct assemblage of forms of which that figured by Olin as D. *eucentra* is typical, and which differ from the common D. *mucronata* of Västergötland mainly in the features of the pygidium listed above. These features are each of equal importance in very well preserved material, but in dealing with the cleaved British specimens, it has been found that the most important diagnostic character is the number of pygidial pleurae.

Dalmanitina olini (= D. eucentra Olin) is interpreted here in a narrow sense to include those specimens which show only a very small amount of variation from the type used by Olin. There are always six well-developed pleurae, while the seventh may be either rudimentary or fully formed. An eighth pleura is never present. The number of axial rings is less determinate, although nine are usually developed. The other two main characters, the ratios of the widths of the anterior and posterior pleural bands, and the relative depths and widths of the sutural and oblique furrows are quite distinct in medium sized forms (10 mm. and under). In large specimens of D. olini, however, the anterior band becomes relatively wider, and is either as wide as, or rarely wider than, the posterior band (pl. IV, fig. 5).

Relation between D. mucronata and D. olini.

Professor Troedsson discussed the question of the mutual relations of these two species in his work on the Brachiopod Beds of Scania. He remarked that D. mucronata is found both below and above the beds containing D. olini. The underlying Staurocephalus zone contains a fairly rich trilobite fauna in addition to D. mucronata, but in the zone of *D. olini* this fauna is almost entirely missing, for apart from the zone fossil the only trilobites are Ampyx acus Troedsson and Acidaspis centrina (Dalman). In the higher D. mucronata zone the fauna is slightly more prolific, but the main difference is the replacement of D. olini by D. mucronata. Troedsson suggested that the sudden impoverishment of the earlier Staurocephalus zone fauna in the D. olini zone was due to a change of environment at the base of the Brachiopod Beds, which most of the fauna was unable to survive. D. mucronata, however, adapted itself to the new and unfavourable conditions by becoming modified to D. olini. Later, when conditions improved again, the true D. mucronata was once more developed. D. mucronata and D. olini were, in fact, »two very closely allied species (or varieties)». Troedsson related this change in environment during the D. olini zone to the transgression at the base of the Brachiopod Beds (1918, p. 97; 1924, p. 222).

This interpretation was criticised by Richter (1925, p. 112) who denied that there was any close relation between the two species. He pointed out the great differences

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between the pygidia figured by Troedsson (1918, pl. I, figs. 19b and 27), and suggested that the species were quite distinct: the reappearance of D. mucronata above D. olini was due to its migration back to Scania whence it had been driven during D. olini times. Richter's argument was based largely on the differences between the two pygidia figured by Troedsson. It is rather unfortunate that the figured pygidium of D. mucronata is not typical of the species.

A similar argument was used by Herta Schmidt (1935, p. 122) while commenting on her discovery at Nyham in Scania of D. mucronata and D. olini on the same bedding-plane. She concluded that, if the two existed under the same conditions. D. olini could not be merely a facies-controlled variety of D. mucronata, nor could the two fossils be mutually exclusively zone fossils. In his reply, Troedsson (1935) defended the value of D. mucronata and D. olini as zonal indices, and pointed out that the presence of two zone fossils together in the same bed as at Nyham, may mean no more than that such a bed is on the junction between the two zones.

When collections of these two species from various localities are examined it is found that D. mucronata is subject to great variation, and that some of this variation is directed towards the condition found in D. olini, and forms a link between the two species. D. mucronata and D. olini form the end terms of a wide range of variation in several characters, and there are many intermediate forms which it is extremely difficult to assign with certainty to either species. For practical purposes, this difficulty has been met by interpreting D. olini in a narrow sense, while allowing much more scope to D. mucronata, so that the forms in between are included somewhat arbitrarily in the latter.

It seems that a very plastic stock of Dalmanitinids was present over the Anglo-Scandinavian area from the period of the Scandinavian Staurocephalus zone until well into Lower Llandovery times. The earliest forms in the Staurocephalus zone of Sweden and the equivalent strata of Britain, although variable, possessed the characters common to all D. mucronata. During the period corresponding to the Lower Brachiopod Beds, the D. olini zone, the other end of the range of variation was predominant, and almost all the Dalmanitinae from this zone in Northern England, North Wales and Scania are D. olini itself. Later the amount of variation increased and reached local maxima as at Nyham, and at Deganwy in North Wales, at a time probably corresponding to the transition between the zones of *D. olini* and D. mucronata: at both these places the two species are found with a wide range of intermediate forms. Later still, at the time of the D. mucronata zone and the lowest Silurian, the D. mucronata type became predominant everywhere, although still with much variation and with occasional individuals approaching D. olini. Locally, in the basal Silurian of Cautley, particular conditions gave rise to a small local race, var. brevispina, while at the same time there were still forms elsewhere, as for instance in South Wales, identical with some of those from the Staurocephalus zone.

The causes of the predominance of some part of the range of variation at any

particular time and place were probably ecological, and in this respect, as in the close relation admitted between the two species, the above hypothesis is essentially similar to Troedsson's.

Relation of D. olini and D. mucronata to earlier and later Phacopidae.

D. mucronata first appears in the Staurocephalus zone of Scandinavia and in the equivalent beds of Britain. It and D. olini are both quite primitive Dalmanitinae, with a small number (six to eight) of pleurae in the pygidium and an unspecialised disposition of the glabellar furrows. The dominant members of the Phacopidae in the Lower Ashgillian rocks of Britain had been the forms usually referred to Pterygometopus brongniarti (Salter) and Dalmanitina robertsi (Reed). The former has a very specialised glabella with much reduced second glabellar lobes and very enlarged third lobes, and is certainly far removed from close affinity to D. mucronata. D. robertsi (Reed, 1904, p. 106, pl. V) is similar to D. mucronata in the general shape of the glabella, differing by the first glabellar furrows being deeper and more pronounced, while the second furrows do not have appendifers: the former probably a more specialised character, the second more primitive. There is a very short genal spine, the posterior margin of the cheek is curved forwards and the pygidium is posteriorly rounded with no terminal spine. In view of these differences it is unlikely that D. robertsi is ancestral to D. mucronata and its associates. Similarly, the lower Ashgillian rocks of Sweden contain such specialised forms as »Phacops» recurva Linnarsson, »Phacops» ecclesiastica Olin and »Phacops» sandbyensis Olin. It does not seem probable then that any of the existing Phacopids either in Britain or in Sweden could have given rise to D. mucronata, and it appears that the species reached these two countries by migration.

If comparisons are made with other foreign species the closest affinities are with D. socialis (Barrande, 1852, p. 552, pl. 26) from Bohemia, the type-species of Dalmanitina Reed (1905, p. 224). This has a cephalon which shows negligible and probably not consistent differences from D. mucronata. The pygidium also is very close to the latter, although the axis tapers somewhat less rapidly and is produced into a spine rather stronger than is usual in D. mucronata. Certainly the two species are very close. D. socialis, however, occurs in Bohemia earlier than the equivalent of the Staurocephalus zone, and is thus possibly ancestral to D. mucronata. As the latter has been recorded from Poland in beds which are probably of the same age as the Brachiopod Beds of Sweden, it is possible to envisage a migration of the D. mucronata stock from Bohemia, where it probably originated as an off-shoot from D. socialis, through Poland to Sweden and Northern England.

D. hastingsi (Reed, 1915, p. 82, pl. XII, figs. 12-22) from the Northern Shan States of Burma, where it occurs in beds coeval with the Brachiopod Beds, is also almost indistinguishable from D. mucronata, while from North America, D. danae (Meek & Worthen, 1868, p. 363, pl. 6, figs. 1a-t) is very similar. This species comes

from the Edgewood Limestone of the Alexandrian in Illinois, a formation which is approximately Richmond in age and thus broadly equivalent to the Ashgillian. Returning to Europe, there is very little difficulty in pointing to descendants of *D. mucronata*. The tendency to increase the number of pleurae seems to have conti-

D. mucronata. The tendency to increase the number of pleurae seems to have continued, so that nine or ten became the standard number by Upper Valentian times, giving rise to such a form as the *Dalmanites vulgaris* (Salter) var. Whittard from Shropshire (1938, p. 133, pl. V, figs. 15, 16), and thence probably to the bulk of the Dalmanitids of the Wenlock and Ludlow.

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PLATE I

Figs. 1-8. Dalmanitina mucronata (Brongniart).

- Fig. 1. Pygidium (PIU: ar 4076), x 2. Brachiopod Beds, Ålleberg, Västergötland.
- Fig. 2. Ventral mould of pygidium (RM: Ar 9850), x2. Brachiopod Beds, Ålleberg, Västergötland.
- Fig. 3. Pygidium (SGU), x 4. Brachiopod Beds, Kinnekulle, Västergötland. Probably the original of *Phacops pulchellus* Linnarsson (1869, pl. I, fig. 3).
- Fig. 4. Pygidium (PIU: ar 820), x 4. Staurocephalus zone, Amtjärn, Dalarne.
- Fig. 5. Ventral mould of cephalon (PIU: ar 4077), x 2. Brachiopod Beds, Ålleberg, Västergötland.
- Fig. 6. Ventral mould of cephalon (RM: Ar 9837), x 2. Brachiopod Beds, Ålleberg, Västergötland.
- Fig. 7. Ventral mould of cephalon (RM: Ar 9831), x 1.5. Brachiopod Beds, Bestorp, Mösseberg, Västergötland. (Dalman Collection).
- Fig. 8. Ventral mould of cephalon (RM: Ar 9833), x 1.5. Brachiopod Beds, Ålleberg, Västergötland. (Dalman Collection).

PLATE II

- Fig. 1. Dalmanitina mucronata (Brongniart). Ventral mould of pygidium (RM: Ar 9841), x 2. Brachiopod Beds, Ålleberg, Västergötland.
- Fig. 2. Dalmanitina mucronata var. brevispina, var. nov. Ventral mould of pygidium (SM: A 36372a), x 6. Holotype. Basal Silurian limestone, Watley Gill, Cautley, N. W. Yorkshire.
- Fig. 3. Dalmanitina mucronata. Ventral mould of glabella (SM: A 32016), x 3. St. Martin's Beds, Haverfordwest.
- Fig. 4. Dalmanitina mucronata. Ventral mould of pygidium (SM: A 32017a), x 3. Same horizon and locality.
- Fig. 5. Dalmanitina (?) sp. Ventral mould of glabella (GSM: 19181), x 1.5. Exact horizon and locality uncertain; Bala area. The original of Salter, 1864, pl. IV, fig. 11.
- Fig. 6. Dalmanitina mucronata. Ventral mould of pygidium (GSM: 19182), x 1.5. Exact horizon and locality uncertain; Bala area. The original of Salter, 1864, pl. IV, fig. 12.

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PLATE III

Figs. 1-4. Dalmanitina mucronata (Brongniart).

Brachiopod Beds, Röstånga, Scania.

- Fig. 1. Ventral mould of pygidium (LO: 2929t), x 2. The original of Troedsson, 1918, pl. I, fig. 27.
- Fig. 2. Ventral mould of pygidium (LO: 91 JT), x 4.
- Fig. 3. Dorsal mould of pygidium (LO: 88 JT), x 4.
- Fig. 4. Ventral mould of cephalon (LO: 87 JT), x 4. This specimen was lit from the north-east.

Figs. 5-8. Dalmanitina olini, sp. nov.

- Fig. 5. Ventral mould of cephalon (LO: 1895t), x 1. Brachiopod Beds, Röstånga, Scania. Syntype. The original of Olin, 1906, pl. I, fig. 1.
- Fig. 6. Ventral mould of cephalon (SM: 36235a), x 2. Deganwy Mudstones, Bryn-hendre, Conway, N. Wales.
- Fig. 7. Ventral mould of pygidium (LO: 1896t), x 1. Brachiopod Beds, Röstånga, Scania. Syntype. The original of Olin, 1906, pl. I, fig. 2.
- Fig. 8. Ventral mould of pygidium (SM: A 36279), x 2. Deganwy Mudstones, Bryn-hendre, Conway, N. Wales.

PLATE IV

- Fig. 1. Dalmanitina mucronata (Brongniart). Ventral mould of pygidium (SM: A 36465), x 2. Deganwy Mudstones, Old Quarry, Deganwy, Conway, N. Wales.
- Fig. 2. *Dalmanitina olini*, sp. nov. Ventral mould of pygidium (SM: A 36455), x 2. Same horizon and locality.
- Fig. 3. Dalmanitina mucronata. Ventral mould of pygidium (SM: A 36001a), x 4. Lower »mucronatus Beds», Ash Gill Beck, Torver, Lancashire.
- Fig. 4. Dalmanitina olini. Ventral mould of pygidium (SM: 36115a), x 4. Upper »mucronatus Beds», Ash Gill Beck, Torver, Lancashire.
- Fig. 5. *Dalmanitina olini*. Ventral mould of pygidium (SM: A 36084b), x 1. Same horizon and locality.
- Fig. 6. *Dalmanitina olini*. Ventral mould of cephalon (SM: A 36132), x 3. Same horizon and locality.
- Fig. 7. Dalmanitina mucronata. Ventral mould of pygidium (SM: A 36299), x 2. Ashgill Shales, same locality.

Tryckt den 12 febr. 1952.

Pl. I











x 1.5





х





Pl. H















x 1·5

Pl. III











X 4





x 2

Pl. IV















X 4